## DISTURBANCE HISTORY AND ITS INFLUENCE ON DROUGHT TOLERANCE OF INTERIOR DOUGLAS-FIR (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) IN THE CARIBOO-CHILCOTIN REGION OF BRITISH COLUMBIA, CANADA

by

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Abstract:

Disturbance-the death of trees due to external forces such as wildfire or windstormsdrives forest stand dynamics and shapes ecosystems. Natural disturbances arising from the interaction of climate, topography, and established tree species have often occurred with some regularity, resulting in apparently perpetual renewal of particular forest structures. Minor changes in climate can have profound impacts on these disturbance regimes, breaking historically observed cycles and introducing novel stand conditions. Long-term historical baselines are critical to understanding such changes. Observational records are often inadequate, especially in western North America, where 400 year-old stands are common but reliable data are generally unavailable prior to the 20<sup>th</sup> century. I use tree ring analysis to investigate the history of Douglas-fir beetle and western spruce budworm infestations, and the influence of partial disturbances on the drought tolerance of surviving trees, developing baseline understanding of disturbance interactions in interior British Columbia. No evidence is found of any outbreaks of western spruce budworm or Douglasfir beetle that exceed the magnitude of outbreaks in the early 21<sup>st</sup> century, suggesting that recent outbreaks represent historically high levels of insect activity. Both natural and anthropogenic partial disturbances are demonstrated to positively affect the drought tolerance of surviving trees in old-growth remnants and younger managed stands, respectively. Access by roots to areas with uninterrupted precipitation throughfall appears to be the driving force behind observed drought resistance, and will likely become more important under climate scenarios where droughts are prolonged and intensified by warmer temperatures. A major growth release ca. 1800 brought previously suppressed trees from a number of age classes into preeminence within their respective stands across the study

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area, forming the basis of the structure we now consider to be representative of old forests in the region. I propose that mountain pine beetle is the leading cause of this regionally synchronous growth release, based on the number of sites affected and the survival of sapling-sized Douglas-fir. Silvicultural prescriptions designed to provide open growing space to residual trees may help reverse overstocking resulting from wildfire exclusion and enhance resilience of stands within the timber harvesting area to increased temperatures. Table of Contents

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### 1. Introduction

#### 1.1. Preface

"After due reproofs of the late impolitic waste and universal sloth amongst us, we should now turn our indignation into prayers, and address ourselves to our better-natured countrymen, that such woods, as do yet remain entire, might be carefully preserved, and such as are destroyed, sedulously repaired: It is what all persons who are owners of land might contribute to, and with infinite delight, as well as profit, who are touched with that laudable ambition of imitating their illustrious ancestors, and of worthily serving their generation."

-- J. Evelyn in the preface to the 1678 print edition of Silva

Forest disturbances shape ecological communities by killing or damaging established trees, making growing space and other resources available to survivors or new individuals (Oliver & Larson, 1996). In many regions, interactions between climate, topography, and established tree species have resulted in repeated patterns of natural disturbance and renewal that are taken as normative and used as a benchmark for managed forests (Cooper, 1913; Pickett & White, 1985). This perspective is represented by Aldo Leopold's reflections on land health and conservation, which he defined as "the capacity of land for self-renewal" and "our effort to understand and preserve this capacity" respectively (Leopold, 1949). Under this paradigm, natural disturbances are seen as a part of the environment with which species regularly interact, and an understanding of this ecological dynamic between forests and disturbances is considered to be the keystone of both active conservation in production forestry and stewardship of parks and preserves (Smith *et al.*, 1997).

A question facing ecologists and foresters around the world is whether the range of disturbances observed today are a continuation of the patterns that shaped the structure and composition of ecosystems in the recent past, or if they are a novel response to human influence and the beginning of an unknown trajectory (Romme & Despain, 1989; Turner, 2010). Historical knowledge of disturbance type, extent, rate and severity, as well as the predisposing factors and outcomes of numerous events, is prerequisite to approaching this question on a regional basis: that baseline is the theme of this dissertation.

A broad range of natural disturbances affect the succession of forest communities over time, but insect outbreaks are often among the most common and influential (Dale *et al.*, 2001; Bentz *et al.*, 2010). Trees may be predisposed to insect attack by local environmental conditions, climate change, stand composition and density, host genetics, other biotic and abiotic disturbance events (Manion, 1981), and these factors may interact positively and negatively at different spatial scales (Raffa *et al.* 2008). Mechanisms of predisposition include influences on the lifecycle of the pest, the defensive capacity of the host, and the triggering of systemic defensive responses in the tree (Franceschi *et al.*, 2005; Eyles *et al.*, 2010), while accumulation of susceptible trees on the landscape can promote insect population buildup that leads to density-dependent attack behaviors more threatening to healthy trees (Burke & Carroll, 2017).

Interaction between individual disturbances and their respective predisposing factors has been a subject of recent study. Increased insect activity has been linked to observed changes in local and global climate (Allen *et al.*, 2010), though some have suggested that competition between trees has thus far exerted a stronger influence on tree growth and mortality than climate change (Zhang *et al.*, 2015). Co-occurrence of several predisposing factors can have a synergistic influence on forest insect populations (Powers *et al.*, 1999), while some forms of inter-tree competition have been shown to exacerbate climatic stresses more than other forms of competition (Mölder & Leuschner, 2014).

Some of these trajectories from predisposing conditions to actual widespread mortality can be interrupted by silvicultural treatments that disturb the stand in a way that removes or dulls the effect of a predisposing factor (Smith *et al.*, 1997). This has been done by thinning to increase the growth rate and efficiency of individual trees, thereby increasing their defensive capacity (Mitchell *et al.*, 1983) and by removing overtopped trees that are likely to attract pests to the stand in their decline (Williamson & Price, 1971). Other studies of disturbance interactions reveal no preventative measures, but do suggest assessment practices to accurately predict disturbance hazard and impact under specific conditions (Hood *et al.*, 2007; Day & Pérez, 2013).

Natural disturbances that kill only a fraction of the trees in a stand have been described as thinning agents that confer definite benefits to surviving trees and the overall stand, such as Weaver's "Fire—Nature's Thinning Agent in Ponderosa Pine Stands" (1947). Weaver's (1947) argument emphasized a point that had been hinted at before, and has been rigorously tested since: that regular fire in the dry forests of western North America is necessary not only for stand development and the perpetuation of ecosystem services that residents have come to rely on, but also as a preventative measure against catastrophic fire (Hardy & Arno, 1996; Agee & Skinner 2010). Without using the language of modern disturbance ecology, Weaver distilled its key point: disturbances interact with one another over the course of decades and centuries, and those interactions shape forest ecosystems.

This principle is not limited to wildfire. Each disturbance consumes its own 'fuel' and reduces the immediate availability of that fuel in the stand and on the landscape (Raffa

*et al.*, 2008). If the disturbance is excluded and its fuel preserved, the next event may consume the accumulation in surprising ways. The effects of various disturbances on predisposing conditions and 'fuel loads' for other disturbance agents over time are still being actively investigated, but the net effects are already understood to be constraining management options in some regions, especially western Canada (Dhar *et al.*, 2013).

The Province of British Columbia (BC), Canada has a 25 million hectare timber harvesting landbase, and the majority of that area has been affected by insect pests in the 21<sup>st</sup> century. Mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*D. rufipennis*), and western balsam bark beetle (*Dryocetes confusus*) have infested approximately 18 million, 1 million and 2.7 million hectares of their respective host trees and caused substantial reductions in projected allowable annual cuts in the coming decades (BC MoF, 2012). The severity of these outbreaks has been attributed to warm temperatures associated with climate change (Bentz *et al.*, 2010) and overstocking of mature host stands that has resulted from long-term fire suppression (Whitehead *et al.*, 2001; Shore *et al.*, 2006).

Douglas-fir forests offer one of the remaining sources of accessible and merchantable live trees in central BC, having weathered a decade of insect outbreaks with relatively low mortality. These forests are often overstocked, making density-related stagnation and competition stress a serious concern (Day, 1998a). Mature Douglas-fir stands also provide critical mule deer winter habitat, and conserving that habitat is the primary objective of management over several hundred thousand hectares of public land (Armleder *et al.*, 1994; Day, 1998b; Figure 1.1). Designated mule deer wintering ranges are established to provide critical thermal and forage habitat, and in the study area are

legally protected under the Cariboo-Chilcotin Land Use Plan (CCLUP;

https://www.for.gov.bc.ca/tasb/slrp/plan129.html accessed 2017). Douglas-fir leading stands cover 4.58 million hectares of the British Columbian landscape; this dissertation considers 1 million hectares near the northern portion of that range, and 373 000 hectares within that area are designated mule deer winter range.

The interior Douglas-fir ecosystem type under study (Steen & Coupé, 1997) is bounded by a moisture limitation at the lower elevation dry bunchgrass zone and a temperature limitation at the higher elevation sub-boreal pine-spruce zone. Stands near the drier margin will be at higher risk in a warmer climate (Griesbauer & Green, 2010) and many are expected to convert to bunchgrass over the course of the 21<sup>st</sup> century, while the cooler margin is expected to advance to higher elevations and latitudes beginning as early as 2025 (Hamann & Wang, 2006). These changes may jeopardize the mule deer winter range strategy within its current boundaries, forcing an adaptive approach as the effects of climate change are realized. Drought stress can kill trees directly and is a key predisposing factor for Douglas-fir beetle, but a drought does not impact all stands or trees equally as the stand structure and occupancy of the growing space strongly affect the microenvironment that individual trees interact with.



Figure 1.1: Study area and distribution of Douglas-fir leading stands in British Columbia. Douglas-fir leading stands in designated mule deer winter range (MDWR) highlighted in black within the study area. MDWRs outside of the study area are not shown.

Douglas-fir is commercially important throughout its range as raw material for log homes, timber frame homes, glulam beams, utility poles, plywood, and other visual grade and structural products. Standing volume is approximately 91 million cubic meters on 1 million hectares of Douglas-fir leading stands in the study area (BC VRI Rank 1 Polygon layer, accessed 2015). This inventory of raw material is in principle worth \$6.3 billion (CAD) at a rate of  $70/m^3$  (BC Interior Log Market Report, 2016) and substantially more once manufactured. Salvage logging of lodgepole pine (*Pinus contorta*) stands killed by mountain pine beetle has been the focus of most harvesting efforts in the study area over the past decade, but attention is returning to Douglas-fir as the merchantability of dead pine degrades over time (Lewis *et al.*, 2006.). Harvesting of Douglas-fir within mule deer winter ranges is permitted under area-specific guidelines, and is often required to prevent stagnation and maintain the desired stand conditions in the absence of natural wildfire (Dawson *et al.*, 2007).

The major insect disturbance agents of Douglas-fir in the study area are Douglas-fir beetle (*Dendroctonus pseudotsugae*; DFB) and western spruce budworm (*Choristoneura freemani* = *C. occidentalis*; WSB), both native to British Columbia (Maclauchlan & Buxton, 2016). Douglas-fir beetle has historically been found at the northern limits of its host in scattered stands near Fort St. James in British Columbia and Jasper National Park in Alberta (Paulson, 1995). Drought stress, windthrow, and wildfire are known predisposing factors that have been involved in positive feedback loops with one another (Johnson & Belluschi, 1969). Western spruce budworm was recorded in a small infestation near Riske Creek in 1975 (Harris *et al.*, 1985) but otherwise no observational records of infestation in the study area exist prior to the outbreak that began in 2000. Adjacent areas near Bella Coola to the west and Quesnel Lake to the east were defoliated by western spruce budworm in 1970 and 1987/88 respectively (Harris *et al.*, 1985; Forest Insect and Disease Survey data accessed June 2016).

Tree-ring reconstructions of wildfire in the 18<sup>th</sup> and 19<sup>th</sup> centuries identified a mixed-severity regime with an average return interval of 20–26 years depending on location, with forests adjacent to grasslands burning more frequently (Daniels & Watson, 2003; Harvey, 2017). That regime was interrupted ca. 1920 by fire suppression efforts and the proliferation of cattle grazing (which consumes fine grass fuels) on forested range, though both lightning and human-initiated fires burned extensively in 1931. The Ministry of Forests, Lands and Natural Resources Operations classifies the Douglas-fir type in this region as an "ecosystem with frequent stand-maintaining fires" (record accessed January 2017: https://catalogue.data.gov.bc.ca/dataset/biogeoclimatic-attribute-catalogue) and stands adjacent to low-elevation grassland areas are known to have burned more frequently than higher elevation areas (Harvey, 2017). Exclusion of wildfire in the latter 20<sup>th</sup> century facilitated a substantial increase in stand density, proliferation of an understory horizon of Douglas-fir, and incursion of trees into grassland areas (Strang & Parminter, 1980; Daniels & Watson, 2003; Wong & Iverson, 2004).

Provincial survey records from the 21<sup>st</sup> century (2000-2015) indicate that wildfire and insect disturbances affecting Douglas-fir have been of similar magnitude in the study area, though their spatial patterns have been distinct. Wildfire has affected 51 000 hectares containing 4.3 million m<sup>3</sup> of Douglas-fir inventory volume from 2000–2015 (https://www.for.gov.bc.ca/hts/vridata/accessed June 2016; Figure 1.2). Douglas-fir beetle surveys (https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/ accessed

June 2016) have recorded an estimated 3.2 million trees killed from 2000–2015, amounting to approximately 6.2 million m<sup>3</sup> loss assuming a merchantable volume of 1.88 m<sup>3</sup> per tree (personal communication, Ken Day, University of British Columbia, 2015; Figure 1.3). At a rate of \$70/m<sup>3</sup> these wildfires and beetle outbreaks have affected \$301 million and \$431 million worth of raw material respectively. Western spruce budworm has defoliated approximately 650 000 hectares of Douglas-fir leading forests since 2000 (https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/ accessed June 2016; Figure 1.4).

Mountain pine beetle has recently had a devastating effect on the lodgepole pine that commonly grew in mixture with Douglas-fir in the study area (Figure 1.5). In three years of fieldwork for this dissertation only a handful of surviving pine greater than 20cm diameter were found, though standing and fallen snags killed in the 2000–2010 outbreak were abundant in many stands (Figure 1.6). This outbreak is discussed thoroughly elsewhere (Shore et al., 2006; de la Giroday et al., 2012; Hrinkevich, 2012), but bears mentioning here as many Douglas-fir stands in the study area included a component of lodgepole pine. Previous mountain pine beetle outbreaks have influenced the growth of Douglas-fir in the study area, with more than half of Douglas-fir sampled in mixed stands recording growth release following the previous outbreak in the 1970s (Hawkes *et al.*, 2004). Reconstructed mountain pine beetle outbreaks in the 1890s/early 1900s, 1930s/1940s, and 1970s are likely to have affected the growth of Douglas-fir throughout the study area (Alfaro et al., 2004; Hawkes et al., 2004). The relatively short lifespan of lodgepole pine precludes positive identification of outbreaks in the study area prior to 1890, but it is probable that undescribed infestations have influenced the growth of trees in mixed stands.



Figure 1.2: Distribution of human and lightning initiated fires from 2000 to 2013, highlighting affected stands of interior Douglas-fir (<u>https://catalogue.data.gov.bc.ca/dataset/fire-perimeters-historical</u> accessed 2016)



Figure 1.3: Distribution of Douglas-fir beetle from 2000 to 2013 according to provincial fixed-wing aerial overview surveys and more detailed regional helicopter surveys. Polygons recorded as "trace" severity class (<1% mortality) excluded from the map to reduce visual clutter. Helicopter survey data accessed 2015: http://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys/methods/standards-for-detailed-surveys fixed-wing survey data accessed 2014: https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/



Figure 1.4: Western spruce budworm defoliation identified in provincial aerial overview surveys from 2000 to 2013. Survey data accessed 2014: https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/



Figure 1.5: Distribution of mountain pine beetle in the study area from 2000 to 2013. Areas displayed in red are not Douglas-fir leading stands. Shades of red indicate the maximum severity recorded at a location in any single year, not the cumulative impact. Severe records indicate >30% mortality, moderate 11–29%, and light 1–10%. Data accessed 2014: https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/


Figure 1.6: Tree PYP02 (ca. 1641) in 2013 surrounded by fallen lodgepole pine and dense pine regeneration, with younger Douglas-fir at the edge of the frame to left and right, and in the background in front of dense sapling pine.

Mean annual temperatures recorded at weather stations in the study have risen significantly in the 1950–2001 period, with temperatures at Quesnel Airport increasing at a rate of  $0.34^{\circ}$ C per decade and those at Tatlayoko Lake increasing at  $0.22^{\circ}$ C per decade, implying a  $1.1-1.7^{\circ}$ C increase (Dawson *et al.*, 2008). Temperatures are projected to continue rising in the  $21^{\text{st}}$  century, while no significant change in precipitation has been observed and relatively minor changes are projected (Dawson *et al.*, 2008). This increase in temperature is expected to lead to more severe and widespread outbreaks of many pest species, including those affecting Douglas-fir (Rudinsky & Vite, 1956; Woods *et al.*, 2010; Murdock *et al.*, 2013). Increased temperature without a substantial increase in precipitation is expected to lead to more frequent and severe drought stress, a predisposing factor for many disturbance agents including Douglas-fir beetle. Understanding the baseline relationships between natural disturbance agents and predisposing conditions under historical climatic conditions will provide context necessary to describe change over time and identify predisposing factors that may be monitored or managed.

#### **1.2. Study objectives and rationale:**

The objectives are 1) to delineate historical relationships between disturbance events and subsequent drought tolerance in surviving trees, 2) identify those disturbances that are attributable or partially attributable to Douglas-fir beetle, building a historical timeline of outbreak activity directly comparable to those developed for wildfire history, 3) to develop new methods of tree ring analysis that provide the greatest possible temporal resolution for Douglas-fir beetle reconstructions, and 4) to expand and refine western spruce budworm outbreak history reconstructions in the study area. The aim of this dissertation is to describe disturbance histories and disturbance/drought interactions as they have been historically, which may suggest ways of directly reducing the impact of projected climate change on the defined objectives of mule deer winter range conservation and timber production.

#### **1.3. Organization of dissertation**

This dissertation has an introduction, four data chapters, a concluding synthesis chapter, and two appendices providing computer code and statistical outputs referenced in the text. The first two data chapters are conceptually related, as each explores changes in drought tolerance apparent after disturbance: the first is based on known anthropogenic disturbances while the second considers natural disturbances inferred from the growth response of surviving trees over the past three centuries. The last two data chapters contribute to the development of timelines of insect outbreaks over the past three to four centuries. The third data chapter builds a chronology of Douglas-fir beetle outbreaks based on scars left by failed attacks, while the fourth critically explores the reconstruction of western spruce budworm outbreaks based on analysis of growth rates of tree species that are and are not hosts of this common forest pest.

# 1.3.1. A note on maps:

All maps of the study area are shown with the grassland benchmark area (https://catalogue.data.gov.bc.ca/dataset/grassland-benchmark-for-the-cariboo-region accessed January 2017) obscuring stands which are classified in the Vegetation Resources Inventory as Douglas-fir leading, but in actuality are sparsely treed and best defined by their herbaceous component, especially in a historical context. All GIS data are used under the BC Open Government License v2.0; all maps were composed entirely by the author.

# 2. Adjacency to a harvest corridor in partially harvested stands increases drought resistance of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) near the grassland interface in central British Columbia

#### 2.1. Abstract:

Drought tolerance of trees may be modified by competition, but most studies quantifying the relationship do not consider the effect of stem clustering. Interior Douglasfir forests near the grassland interface in central British Columbia are managed under a clumpy retention system to facilitate the conservation of mule deer winter habitat through timber harvesting. Climate change projections indicate continued increases in temperature, potentially stressing trees and jeopardizing winter range conservation. Trees incidentally placed in different states of competition by mechanical harvesting in the 1970s are sampled to provide a 40-year comparison of clustered and open growing trees. Tree-ring analysis is used to assess the reduction in growth rate during drought years and resumption in subsequent years. Following harvest, a clear separation of growth patterns is evident between trees that were fully released, partially released, and not directly released. Partially released trees show intermediate growth but no difference is found in the longterm climate/growth relationship compared to fully released trees. Trees growing within the matrix between skid trails have stronger correlations with several monthly climatic variables and greater growth reduction during drought events. These results suggest silvicultural practices recommended for the winter ranges are likely to provide concurrent benefits in drought tolerance.

Chapter 2 has been submitted for publication with the following authorship: Thompson N.T, Lewis K.J., Poirier L.M.

### **2.2. Introduction**

Climate change projections for central British Columbia indicate a rise in temperature over the coming century without a commensurate increase in precipitation, leading to more frequent and severe drought stress in forest stands (Dawson *et al.*, 2008). Mortality resulting directly from moisture deficit is expected to increase under such climate change (Allen *et al.*, 2010), while disturbances from insect pests and pathogens are expected to become more frequent (Currano *et al.*, 2008; Woods *et al.*, 2010). Stand thinning has been recommended as a means of reducing these risks (Mitchell *et al.*, 1983; Sohn *et al.*, 2013) while maintaining productivity in the short- to mid-term (Elkin *et al.*, 2015; Calev *et al.*, 2016). Thinning reduces canopy interception of rainfall and inter-tree competition for soil moisture, resulting in greater moisture availability to residual trees (Stogsdili *et al.*, 1992; Bréda *et al.*, 1995). Trees in thinned stands have maintained higher transpiration rates during droughts compared to controls (Lagergren *et al.*, 2008) and have shown less growth reduction in drought years (Laurent *et al.*, 2003).

The spatial distribution of trees following thinning may be uniform, random, or clustered depending on the objectives, stand conditions, and harvesting equipment used. Uniform spacing has been recommended for centuries as a means of maximizing yield, but a random pattern often emerges as compromises are made to retain the best growing stock (Evelyn, 1662). Clumpy distributions are common in naturally established forests (Hamilton, 1984; Harrod *et al.*, 1999) and this pattern is sometimes encouraged to support specific wildlife habitats (Long & Smith, 2000; Dawson *et al.*, 2007). Clumpy distributions also result from row thinning in plantations (Makinen *et al.*, 2005) and the practice of harvesting trees from corridors at more or less equal intervals, referred to as systematic

thinning by Makinen (2005) in Finland and partial harvesting by Fuller *et al.* (2004) in Maine.

Experiments comparing clustered tree distributions with uniform or random spatial patterns have found lower growth rates in clumped vs. regularly spaced red pine (*Pinus resinosa*; Stiell, 1982), slash and loblolly pine (*Pinus elliotii, Pinus taeda*; Baldwin *et al.*, 1989), and Norway spruce (*Picea abies*; Makinen, 2005) after treatment. While uniform or random spacing may be implied by the absence of modifiers such as row thinning or systematic thinning, authors discussing the forest health benefits of thinning often do not specify whether the post-treatment stand had a uniform, random, or clustered arrangement of trees (Williamson & Price, 1971; Mitchell *et al.*, 1983; Giuggiola *et al.*, 2013; Gebhardt *et al.*, 2014). Similar oversights are found in tree-ring evaluations of the climate/growth relationship in stands thinned to various residual densities (Kohler *et al.*, 2010; Sohn *et al.*, 2013). This gap in the literature is problematic as clumped distributions are common in regions where row or systematic thinning is employed and in areas where clumped distributions are encouraged to meet wildlife habitat objectives.

Conservation of mule deer (*Odocoileus hemionus* (Rafinesque)) winter range is legally mandated on select public lands in the interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forests of British Columbia (Dawson *et al.*, 2007). Mule deer in this region migrate to relatively low elevation areas and preferentially utilize mature stands of Douglas-fir with moderate crown closure, as interlocking crowns intercept snow and provide browse through crown abrasion (Armleder *et al.*, 1986). A system of harvesting with clumpy retention in these forest types has been under development since 1983 to conserve such winter range (Armleder, 1999; Day *et al.*, 2003). These designated

ranges cover 373 000 hectares and include some of the driest forested areas in the region, receiving a mean annual precipitation of 435mm per year from 1961–1990 (http://www.climatewna.com/ accessed 2016).

Studies from other regions suggest that thinning may mitigate the increased drought stress introduced by climate change (Elkin *et al.*, 2015; Calev *et al.*, 2016), but there is no information available on the net effect of clustered distributions on drought response in a dry environment. The percentage of gross rainfall lost to interception has been found to progressively decline with increased thinning intensity in established plantations in mesic and xeric systems (Teklehaimanot *et al.*, 1991; Molina & del Campo, 2012). Strip thinning of a Japanese cypress plantation (1 265mm annual precipitation) reduced total interception from 28.7% to 20.8% of gross precipitation (Sun *et al.*, 2015). These studies are based on relatively young plantations managed for wood production. The Douglas-fir forests under study here are typically older, were not originally established on a regular spacing, and are now managed to facilitate canopy interception of snow within clumps.

Long-term (>30 years) silvicultural trials are not available to assess the drought tolerance of clustered Douglas-fir in the study area, but mechanical harvesting in the latter half of the 20<sup>th</sup> century provides regular spatial patterns that are in some cases analogous to those recommended for mule deer conservation. Presence of these conditions in the same stand provides an opportunity to compare trees growing in different competitive situations, addressing the following research questions:

- 1. What was the average postharvest growth response among trees in three competition classes: open growing, skid trail edge, and matrix interior?
- 2. Which monthly temperature and precipitation variables have long-term correlations to radial growth and are there differences in climate correlations among these three competition classes?
- 3. How do drought resistance and resilience (Lloret *et al.*, 2011) vary among these three classes?
- 4. How do live crown ratio and sapwood basal area vary among the competition classes four decades after harvest?

The first question follows from the existing literature on clumpy spatial arrangements, which suggests a reduction in growth and yield at the tree and stand level, though only individual tree metrics are applicable in this study (Stiell, 1982). The second looks for differences in the long-term climate/growth relationship among classes, while the third considers the response to short-term drought events. The final question addresses indicators of crown vigor, also following from literature describing reduced canopies in clumped trees (Stiell, 1982).

# 2.3. Methods

### 2.3.1. Site Selection and Sample Collection

Candidate sites were first screened using the British Columbia Vegetation Resources Inventory dataset (VRI; https://www.for.gov.bc.ca/hts/vridata/, accessed June 2015) to identify stands between 80 and 130 years old with intermediate crown closure (30–70%). Historical wildfire perimeters were overlaid to ensure that potential sites were not affected by recent fires, either natural or human-caused (records extending to 1917 in the study area; https://catalogue.data.gov.bc.ca/dataset/fire-perimeters-historical). Inventory polygons meeting these criteria were exported from ArcMap<sup>®</sup> to Google Earth<sup>®</sup>, where aerial imagery (dated 2005) was examined to confirm the presence of regularly spaced skid trails (Figure 2.1). Candidate sites were assessed in the field to determine whether there were sufficient numbers of trees in all three competition classes (Figure 2.2): Open (fully released from crown competition during the harvest), Edge (on the edge of skid trails) and Interior (the unharvested matrix between skid trails).

Most remotely identified sites had two of the classes in abundance but lacked the third; three sites contained all classes and were deemed appropriate for sampling (Figure 2.3). Both the Colpitt and Sting Lake sites showed visually apparent growth releases in 1976 consistent with a 1975 harvest, while Vert Lake was released in 1980, suggesting a harvest in 1979. These dates are corroborated by harvest records in the VRI database for Colpitt and Sting Lake sites, but there are no records for the Vert Lake site, likely due to incomplete digitization of datasets. Patterns of cut stumps at all sites suggest that large sawtimber was targeted for removal and the smaller stems constituting the population now under study were only cut if necessary for removal of the primary product (as in

Maclauchlan and Brooks, 2009).

Vegetation resources inventory (VRI) data were clipped to the designated mule deer winter range boundaries (http://www.env.gov.bc.ca/wld/frpa/uwr/approved\_uwr.html accessed 2015) and total merchantable volumes were calculated by age class and crown closure class to describe the stands surrounding the study sites. VRI age estimates were consolidated to six 40-year age classes and one class including all trees greater than 240 years. Percent crown closure values were reduced to five equal classes. Volume estimates were the sum of the inventory volume that was calculated with a merchantability threshold of 12.5cm top diameter.



Figure 2.1: Aerial image of Vert Lake site showing the regular pattern of harvesting trails radiating from clearings where wood was collected and processed.



Figure 2.2: Conceptual schematic of interior, edge and open growing trees following harvest (trees not drawn to scale). Labeled trees show the relative position of the three competition classes within the stand.



Figure 2.3: Location of study sites. Douglas-fir dominated stands are those where Douglas-fir is classified as the leading species in the Vegetation Resources Inventory; the grassland benchmark describes historical grassland areas that may now be sparsely treed.

Subject trees were selected to represent three levels of post-harvest competition: between harvest trails, with no potential competitors removed ("Interior"), on the edge of harvest trails with potential competitors removed on only one side ("Edge") and within the harvested area with all potential competitors removed ("Open"; Figure 2.2). Only dominant and codominant trees were considered as subject trees; no overtopped trees were sampled and saplings (less than ½ the height of the subject trees) were not considered to be competitors. Subject trees were selected systematically along transect lines established on a 50m grid with a random azimuth as a starting point. Subject trees were selected as the closest trees meeting the above criteria every 20m, enforcing a minimum 20m distance between two trees of the same competition class. Twenty or more subject trees from each competition class were selected at each of the three sites, and two increment cores were removed from opposite sides of each tree at breast height (1.3m). A variable-radius forest inventory plot was centered on each subject tree, using an 8m<sup>2</sup>/ha glass prism to determine plot level basal area.



Figure 2.4: Typical examples (left to right) of Open, Edge and Interior class trees indicated by white triangles.

2.3.2. Laboratory Preparation

Increment cores were dried, glued to wooden mounts, and processed according to standard methods, progressing from 120 to 600 grit sanding belts (Stokes & Smiley, 1968). The sapwood boundary was delineated based on visual assessment of color change, which is readily apparent in Douglas-fir (Figure 2.5). Sapwood width, heartwood width, and distance from last measurable ring to estimated pith location were measured to the nearest millimeter using calipers and a ruler. Sapwood basal area was calculated by subtracting the area of the heartwood from the total basal area of the tree inside bark on each core, and a mean of the two measurements was produced for each tree.

Ring widths and earlywood/latewood boundary locations were measured in Windendro<sup>®</sup> 2012. Crossdating of series was accomplished by scanning in batches of 20 or more cores and visually comparing the graphed ring width measurements in Windendro<sup>®</sup>, beginning with the known date of the final ring and utilizing regionally established marker years 2010, 1988/89/90 and 1959 to confirm later dates. When ring width was less than 0.3mm, both ring width and latewood width values were checked using an Olympus<sup>®</sup> SZ61 stereo microscope and Velmex<sup>®</sup> measuring slide. Correct assignment of calendar years to ring width measurements was confirmed using the dendrochronological program COFECHA (Holmes, 1983). Ring widths were converted to basal area increments using the package dplR (version 1.6.4) in the open source statistical program R (version 3.2.2.).

# 2.3.3. Statistical Analysis

Growth response to thinning was quantified on the basis of 10-year increments to provide a dataset statistically analogous to remeasurements in a standard thinning study. Basal area (inside bark) was calculated for the years 1955, 1965, 1975, 1985, 1995, 2005, and 2015, while mean annual basal area increment (BAI) was calculated on the basis of 10-year means in the periods 1956–1965, 1966–1975, 1976–1985, 1986–1995, 1996–2005, and 2006–2015. Two time steps in the 1950s and 1960s were included to test the assumption that the population had similar growth rate prior to the modification of the competitive environment in the 1970s, and the 1975 basal area was used to check that trees were initially of a similar size. Oneway ANOVA with a Bonferroni post-hoc test ( $\alpha$ =0.05) was used to assess the significance of differences in 10-year basal area and basal area increment among competition classes at each site. Data were tested for normality in Stata 12.1<sup>®</sup> and transformed as noted to meet the assumption of normal distribution.

Drought events were defined as years in which the total precipitation from the beginning of the previous June to the end of the current June was in the 30<sup>th</sup> percentile (1936-2012, (http://www.ec.gc.ca/dccha-ahccd/ accessed 2017) and where study-wide mean ring width index was in the 10<sup>th</sup> percentile (1936-2012). This index was a biweight mean chronology generated using a 10-year smoothing spline on raw ring widths to minimize the influence of stand dynamics on annual variability, and inter-annual autocorrelation was reduced by adding the residuals from an autoregressive model to each series prior to averaging to create the mean index (Bunn et al., 2017). Three years meeting these criteria were identified after the harvest (1988, 1995, and 2010). Precipitation was above the 30<sup>th</sup> percentile in 1989, but the ring width index was the lowest in the series, so that year was averaged with 1988 for analysis (following Lloret et al., 2011). Drought resistance was quantified as the ratio of the basal area increment in the event year (mean of two years in 1988/1989) to the mean basal area increment in the 5 years preceding the event (Figure 2.5; Lloret et al., 2011). Drought resilience was quantified as the ratio of the 5-year mean basal area increment after the event to the 5-year mean basal area increment before. An additional metric particular to this study was the drought resistance relative to pre-harvest growth (hereafter "baseline resistance"): the ratio of the basal area increment in the event year(s) to the 5-year mean basal area increment in the period 1970-1974, prior to harvesting in all stands. Oneway ANOVA (Bonferroni post-hoc test,  $\alpha=0.05$ ) was used to assess the significance of differences in drought resistance and resilience, with variables transformed as noted to meet the assumption of normal distribution in the population under comparison.



Figure 2.5: Examples of cores from Open (COL59A) and Interior (COL58A) classes at Colpitt Lake site, harvested 1975 (black arrow). Drought years 1988/89 marked by black rectangles labeled "D" above each core, and magnified for each sample at lower right. Drought years 1995 and 2010 marked by black rectangles beneath each core. Resistance equals D/Y, resilience equals Z/Y, and baseline resistance equals D/X, where X Y and Z are average basal area increment over the 5-year periods indicated and D is the average basal area increment of 1988 and 1989. Hollow triangles indicate the color change at the heartwood/sapwood boundary. Pencil marks indicate decade years, from the left: 1940, 1950, 1960, 1970, 1980, 1990 (also in magnification), 2000, and 2010.

Total ring width, earlywood width, and latewood width indices were calculated using a 10-year smoothing spline to recover annual growth variation with minimal interference from the growth response to harvesting. Pearson correlation coefficients between these indices and the monthly climatic variables measured at the Williams Lake Airport (previous June to current September; <u>http://www.ec.gc.ca/dccha-ahccd/</u>) were calculated for the 1975–2012 period using the package treeclim (version 1.0.16) (Zang & Biondi, 2015) in the open source statistical program R (version 3.2.2; script in Appendix A). Each ring width component was detrended and analyzed separately as these components of growth have previously been found to respond to distinct climatic variables (Lebourgeois, 2000; Watson & Luckman, 2002).

Live crown ratios of sample trees were calculated on the basis of the lowest live branch (non-epicormic) and the lowest live whorl of three or more branches by the formula

(Total Height – Lowest Branch Height)/Total Height).

#### 2.4. Results

#### 2.4.1. Drought conditions in event years

Average precipitation from the beginning of the previous June to the end of the current June (pJJ) was 548mm at the Williams Lake Airport from 1937 to 2012. 1988 had the lowest pJJ on record, measuring 394mm. 1989, 1995, and 2010 measured 510mm, 485mm, and 462mm respectively. Pairwise correlation between pJJ and the mean ring width index among all trees at all sites from 1937 to 2012 was significant (n=76, r = 0.58, p < 0.0001).

# 2.4.2. Stand Conditions and Tree Characteristics

Differences in height to lowest live branch and lowest live whorl were never significantly different among the Open and Edge classes at any site, and ranged from 7.5–9.7 and 10.4–12.5m respectively among all sites (Table 2.1). Interior trees had significantly higher crown bases by both single-branch and three-branch whorl metrics at all sites. Mean height of residual trees in 2015 varied by as much as 1.9m among competition classes at individual sites, and differences were statistically significant at two of the three sites. The 1975 diameter inside bark calculated from the tree rings was not significantly different among the classes at the Colpitt and Sting Lake sites, but a significant difference between the Open and Edge trees was identified at Vert Lake.

Table 2.1: Mean 2015 stand characteristics measured in the field and 1975 diameter inside bark calculated from tree rings. BA/ha value includes the basal area of subject tree (accounting for  $8m^2$ /ha). LLB = lowest live branch (single), LLW = lowest live whorl of branches (3 or more), DBH = diameter at breast height (1.3m measured on the high side of the tree), BA/ha = basal area per hectare measured with  $8m^2$ /ha prism. DIB = diameter inside bark. Classes that do not share a letter with others at the same site are significantly different (Bonferroni post-hoc test,  $\alpha$ =0.05); significant differences are in bold.

		Heig (m	ght )	LLE (m)	8	LLV (m)	V	DBF (cm)	ł )	BA/h (m2	ia )	197 DI (cn	'5 B 1)	Ag (201	;e 15)
Colpitt	Open	23.6	ns	8.7	a	10.8	a	39.6	a	17.6	A	13.4	ns	118	ns
	Edge	23.6	ns	9.7	a	12.5	a	34.9	b	29.2	B	13.5	ns	121	ns
	Interior	23.1	ns	14.1	b	16.4	b	29.6	c	56.4	С	15.4	ns	121	ns
	Open	21.9	a	7.5	a	10.4	a	40.4	a	16	A	16.5	ns	130	a
Sting	Edge	21.3	ab	8.7	a	11.7	a	34.5	b	33.2	B	15.3	ns	124	b
	Interior	20.1	b	12.4	b	14.6	b	27.2	c	48.8	С	15.2	ns	152	ab
Vert	Open	22.0	a	8.5	a	10.5	a	37.0	a	17.2	A	17.5	a	123	ns
	Edge	20.2	b	9.4	a	11.3	a	31.5	b	28.7	B	14	b	118	ns
	Interior	20.1	ab	11.5	b	13.4	b	28.8	b	46.4	С	16.4	ab	122	ns

Annual BAI since 1950 is summarized among all sites by competition class; an increase in growth rate is evident ca. 1975 in both Edge and Open classes (Figure 2.6).



Figure 2.6: Mean annual basal area increment plotted by competition class among all sites since 1950. Vertical dashed line indicates the first recorded defoliation by western spruce budworm in 2001. Black bars above the X axis indicate the drought years under study (1988/89, 1995, and 2010). Two sites (Colpitt and Sting Lakes) were harvested in 1975, one (Vert Lake) harvested in 1979.

Live crown ratios were significantly higher in the Open and Edge classes compared to the Interior class in all cases. Values in the Open class were consistently higher than the Edge class and these differences were significant in 50% of the comparisons (Table 2.2). Sapwood basal area followed a clear high-low gradient from Open to Edge to Interior, with significant differences among all classes at all sites.

Table 2.2: Live crown ratios on the basis of lowest live branch (LCR(B)), lowest live whorl of three or more branches (LCR(W)), and sapwood basal area (m<sup>2</sup>) among three competition classes at three sites (Bonferroni post-hoc test,  $\alpha$ =0.05); significant differences are in bold.

						Sapwo	ood
		LCR(	B)	LCF	R(W)	BA (ci	$m^2$ )
Colpitt	Open	0.63	a	0.54	a	319	a
	Edge	0.59	a	0.48	a	247	b
	Interior	0.39	b	0.29	b	129	c
	Open	0.65	a	0.53	a	290	a
Sting	Edge	0.59	a	0.45	b	221	b
	Interior	0.38	b	0.27	c	105	c
Vert	Open	0.61	a	0.52	a	293	a
	Edge	0.54	b	0.44	b	226	b
	Interior	0.43	c	0.33	c	121	c

Of the 373 000 hectares identified for conservation as mule deer winter range in the Cariboo-Chilcotin region, 309 000 are listed as Douglas-fir leading stands in the BC VRI Rank 1 polygon layer (accessed 2015). Total inventory volume in this area is approximately 33 million m<sup>3</sup>, with the majority of both volume and area in mature stands (>80 years old) with intermediate crown closure (41–60%; Figure 2.7). Allowing for a difference of 20 years between age at coring height and true age (Wong & Lertzman, 2001), all three sites currently fall in the age class (121–160 years) that contains the highest volume on the landscape while occupying the second greatest area. At the time of harvest, the stands would have been in the age class (81–120 years) that presently contains the second highest volume while occupying the greatest area in the winter ranges.



Figure 2.7: Live volume (m<sup>3</sup> based on 12.5cm utilization) in areas designated for mule deer winter range conservation by crown closure (%) in 40-year age classes. Total area (hectares) in each age class is noted beneath X axis.

# 2.4.3. Postharvest Growth

Differences in mean basal area and mean annual BAI among classes in the two 10year time steps prior to the harvest were not statistically significant at Colpitt and Sting Lakes (Figure 2.8). Vert Lake showed a significant difference in BA and BAI prior to the harvest between the Open and Edge categories only, with the Open class being the larger and faster growing (Figure 2.8).

Mean annual basal area increment in the first postharvest period (1976–1985) was significantly higher in the Open class at all sites, with the Edge trees intermediate between the Open and Interior classes (Figure 2.8). Differences in BAI between the Edge and Interior classes were significant at Colpitt and Sting Lakes in the first period after harvest, but not Vert Lake. All classes were significantly different from one another in the second and third decades; by the final period differences in BAI among the Edge and Open classes were statistically insignificant at all sites.

Mean basal area was significantly different among all classes at the Sting Lake site by 1995 and Colpitt Lake by 2005 (Figure 2.8). Edge trees at Vert Lake did not achieve a significantly higher basal area than the Interior trees by the end of the study period, though the Open class had a significantly higher basal area since 1965, a decade prior to the harvest, and maintained that position throughout the postharvest period.



Figure 2.8: Basal area and mean annual basal area increment at each site (cm<sup>2</sup>). Raw data are displayed below; differences among the classes are significant for a given period if values do not share a letter (Bonferroni post-hoc test,  $\alpha$ =0.05).

# 2.4.4. Climate Correlations

Several significant correlations were found between detrended total ring/latewood/earlywood widths and monthly weather record (Table 2.3). Total precipitation in the November prior to the growing season had a positive correlation with both earlywood and latewood width among most of the classes and sites tested, though the correlation values were lower for the total ring width series. Previous-December precipitation was correlated with earlywood and latewood width in the Interior competition class at all sites, and also with the latewood width in the Open class at Sting Lake. Precipitation in the current April had a negative correlation with latewood width in most classes at all sites. June precipitation and temperature respectively had strong positive and negative correlations with latewood width in nearly all classes at all sites, while temperature in July was often negatively correlated with latewood width. Previous-summer temperature and precipitation variables were inconsistent between sites; the precipitation of the previous August was the most common variable with a statistically significant correlation in this analysis while the mean temperature of the previous July had a significant correlation with earlywood width in all classes at Sting Lake and the Edge class at Vert Lake. Correlation values between latewood width and June temperature and precipitation were consistently higher in the Interior class than the Open class, while the Edge was usually intermediate between the two.

Table 2.3: Pearson correlation coefficients between monthly mean temperature and total precipitation and total ring, earlywood, and latewood widths each detrended with a 10-year cubic smoothing spline. Only significant (p < 0.05) correlation values are shown. Lower and uppercase headings indicate months in previous and current year respectively.

				jun	jul	aug	sep	oct	nov	dec	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
Colmitt I also		or	Total			0.25		0.20	0.25	0.23						0.28		-0.25	
		teri	Early			0.34			0.50	0.38				-0.27		0.19		-0.43	0.24
	e	Ini	Late			0.21			0.41	0.35				-0.42		0.46		-0.42	
	Lai	е	Total			0.25										0.28		-0.28	
	itt ]	dg	Early	0.36					0.30									-0.51	
	olp	Щ	Late											-0.44		0.49		-0.46	
	Ŭ	n	Total													0.23			
Ē		.ed	Early																
u () u		0	Late													0.30			
		or	Total	0.14		0.32			0.29	0.22				-0.25		0.31			
tio		eri	Early			0.47			0.51	0.36								-0.50	
ita	o	Int	Late			0.30			0.41	0.31			0.20	-0.38		0.58		-0.37	
cip	ak	e	Total	0.15	0.18	0.35			0.25	0.23						0.29			
re	Б	dg	Early			0.47			0.45									-0.51	
ył	tin	Щ	Late						0.41					-0.41		0.53		-0.37	
th	S	n	Total	0.16	0.22	0.34				0.23						0.34			
0 U		be	Early	0.35		0.44			0.40									-0.48	
Σ		0	Late						0.39	0.42						0.49		-0.31	
tal		or	Total			0.29			0.29	0.25				-0.26		0.36			
T		teri	Early						0.57	0.37						0.27		-0.39	
Vert Lake	0	dge Int	Late						0.44	0.39				-0.37		0.59			
	ake		Total	0.19		0.31			0.26		0.20			-0.26		0.34	0.23		
	τŢ		Early	0.45		0.34			0.40							0.25		-0.39	
	Ver	Щ	Late						0.42		0.23			-0.41		0.54		-0.39	
	-	ц	Total	0.16		0.30			0.27	0.22				-0.25		0.31	0.19		
		pe]	Early	0.39					0.41									-0.43	
		0	Late						0.45					-0.38		0.46		-0.38	
		or	Total												-0.16	-0.26	-0.22		
		eri	Early				-0.29						0.20		-0.28	-0.32		0.34	-0.21
	e	Int	Late						-0.25							-0.32	-0.27		
	Lal	е	Total													-0.22			
	itt ]	dg	Early								0.31		0.27		-0.33			0.46	
	olp	Щ	Late													-0.27	-0.25		
	Ŭ	n	Total																
Ũ		bei	Early												-0.24				
。) a		0	Late																
n		or	Total		-0.20											-0.29			-0.19
rat		teri	Early		-0.26											-0.28		0.37	
pe	е	Ini	Late											0.23		-0.40			-0.23
em	ak	е	Total		-0.18											-0.24			-0.18
Ţ	50 L	gþ	Early		-0.29													0.46	
ţĦ	tin	щ	Late													-0.34	-0.30		
0U1	S	n	Total		-0.20											-0.21			-0.19
ž		be	Early		-0.34											-0.33		0.43	
30		0	Late													-0.32	-0.32		
era		or	Total													-0.31	-0.23		
AV		teri	Early													-0.33			
		Int	Late													-0.42	-0.34		
	ake	е	Total		-0.21											-0.29	-0.24		
	τΓ	gb	Early		-0.27	-0.31										-0.29	-0.27		-0.18
	Ver	Щ	Late													-0.39	-0.39		
		n	Total													-0.28	-0.22		
		be	Early													-0.34		0.34	
	0	Late													-0.36	-0.38			

# 2.4.5. Drought Resistance and Resilience

Drought resistance values were similar between the Open and Edge classes at all sites in all years. In all cases where statistically significant differences were found, the Interior class underperformed either the Open or the Edge class, and in three cases (all years at Colpitt Lake) drought resistance in the Interior class was significantly lower than both other classes.

Table 2.4: Drought resistance values (drought/5-year pre-drought mean) among three competition classes at three sites for the years 1988/89, 1995, and 2010 (Bonferroni posthoc test,  $\alpha$ =0.05).

		Drought R		
		1988/89	1995	2010
	Open	0.56 a	0.64 a	0.94 a
Colpitt	Edge	0.52 a	0.72 a	0.88 a
	Interior	0.34 b	0.52 b	0.71 b
-	Transformation	Log	Log	Log
	df	2, 57	2, 56	2, 57
	F	13.95	8.90	9.42
	Prob > F	<0.01	<0.01	<0.01
	Open	0.46 a	0.35 ns	0.39 ns
Sting	Edge	0.39 ab	0.34 ns	0.38 ns
	Interior	0.32 b	0.34 ns	0.33 ns
-	Transformation	Log	Sqrt	None
	df	2, 57	2, 57	2, 57
	F	3.55	0.21	1.98
	Prob > F	<0.01	0.81	0.15
	Open	0.60 a	0.50 ns	0.45 ab
Vert	Edge	0.53 ab	0.54 ns	0.47 a
	Interior	0.40 b	0.46 ns	0.40 b
-	Transformation	1/sqrt	Inverse	Sqrt
	df	2 <i>,</i> 59	2, 59	2, 59
	F	4.25	1.48	4.18
	Prob > F	0.01	0.24	0.02

Only two statistically significant differences were found among the drought resilience values, and the highest value did not belong to the Open class in either case (Table 2.5). In one case the Open class significantly underperformed both other classes, and in the other the Open class was not significantly different from the interior. Both significant comparisons occurred in the 1988/89 period, when all values exceeded 1.0 indicating a positive resilience (increasing growth trend) among all classes.

Table 2.5: Drought resilience values (5-year post-drought mean/5-year pre-drought mean) among three competition classes at three sites for the years 1988/89, 1995, and 2010 (Bonferroni post-hoc test,  $\alpha$ =0.05).

		Drought R	esilience			
		1988/89	1995	2010		
	Open	1.31 ns	1.00 ns	1.17 ns		
Colpitt	Edge	1.37 ns	1.04 ns	1.12 ns		
	Interior	1.21 ns	0.90 ns	1.09 ns		
-	Transformation	Log	1/sqrt	1/sqrt		
	df	2, 57	2, 56	2, 57		
	F	0.90	2.68	0.81		
	Prob > F	0.41	0.08	0.45		
	Open	1.16 a	0.70 ns	0.91 ns		
Sting	Edge	1.31 b	0.74 ns	0.98 ns		
	Interior	1.54 b	0.77 ns	1.01 ns		
-	Transformation	Log	1/sqrt	1/sqrt		
	df	2, 57	2, 57	2, 57		
	F	4.12	1.00	0.17		
	Prob > F	0.02	0.37	0.85		
	Open	1.22 a	0.83 ns	0.86 ns		
Vert	Edge	1.44 b	0.84 ns	1.00 ns		
	Interior	1.29 ab	0.73 ns	0.90 ns		
-	Transformation	Log	Inverse	Log		
	df	2, 59	2, 59	2, 59		
	F	3.68	2.14	2.81		
	Prob > F	0.03	0.13	0.07		

Significant differences in baseline resistance were identified between one or more competition classes at all sites in all the years considered (

Table 2.6). Values in the Interior class were significantly lower than the other two classes in all cases. Baseline resistance was significantly higher in the Open class than the Edge class in two cases; differences between these classes were insignificant in the remaining seven tests. Baseline resistance values exceeded 1.0 (indicating higher growth in the drought year(s) compared to the pre-harvest average) in eight of nine cases for both Open and Edge classes, while the Interior class exceeded 1.0 in one out of nine cases.

Table 2.6: Baseline drought resistance values (drought/1971–1975 mean) among three competition classes at three sites for the years 1988/89, 1995, and 2010 (Bonferroni posthoc test,  $\alpha$ =0.05).

	•		
	1988/89	1995	2010
Open	4.37 a	6.46 a	5.29 a
Colpitt Edge	2.64 a	4.26 a	3.41 a
Interior	0.63 b	1.10 b	0.94 b
Transformation	1/sqrt	Log	Log
df	2, 57	2, 56	2, 57
F	31.39	43.81	24.85
Prob > F	<0.01	<0.01	<0.01
Open	5.00 a	3.91a	1.74 a
Sting Edge	1.95 b	1.96 b	0.93 a
Interior	0.54 c	0.78 c	0.39 b
Transformation	Log	Log	Log
df	2, 57	2, 57	2, 57
F	26.23	20.85	13.44
Prob > F	<0.01	<0.01	< 0.01
Open	2.49 a	2.19a	0.96 a
<b>Vert</b> Edge	2.08 a	3.08 a	1.18 a
Interior	0.66 b	0.95 b	0.41 b
Transformation	Log	Log	Log
df	2, 59	2, 59	2, 59
F	17.34	15.96	14.00
Prob > F	<0.01	<0.01	< 0.01

# **Baseline Drought Resistance**

#### 2.5. Discussion

Trees growing in the open since the 1970s had higher growth, greater sapwood basal area, and larger crowns, but the Open class had no clear advantage over the Edge class in terms of drought resistance or resilience. Interior trees had poorer drought resistance, as well as the lowest growth, least sapwood basal area, and shortest crowns. Earlywood and latewood widths in the Interior classes showed a correlation with precipitation in the month of December that was less pronounced in the other classes, and correlation values with current-June precipitation were generally higher in the Interior class. These findings suggest a lower sensitivity to drought stress in both the Open and Edge classes following harvest, with few distinctions between the two. Negative correlations between both earlywood and latewood widths and temperatures in June/July suggest that the rise in summer temperatures indicated by climate change projections will have a negative influence on Douglas-fir growth.

Increased throughfall of precipitation in the trails offers an explanation for the lack of difference between the Edge and Open class in drought resistance. In conventional thinning trials, gaps created between canopies permit rainfall to reach the forest floor directly rather than striking and potentially adhering to the canopy, leading to increased moisture availability in the soil (Stogsdili *et al.*, 1992; Bréda *et al.*, 1995). The same phenomenon has been observed in harvesting trails established to facilitate a thinning treatment, and partially linked to the increased growth of trees adjacent to the trails compared to the interior of the thinned stand (Wallentin & Nilsson, 2011). When trees are harvested exclusively from skid trails in a strip thinning, those corridors experience increased throughfall and available moisture (Sun *et al.*, 2015). Trees retained within the

trails would have access to this resource in all directions and those on the edges have partial access, while those in the interior receive no such benefit from the harvest and some face competition from their better-supplied neighbors on the edge of trails.

Inter-tree competition offers the simplest explanation for the differences found in live crown ratio, sapwood basal area, and growth rate, though increased soil moisture in the trails likely contributes to growth as well. Mechanical abrasion between crowns commonly leaves gaps between tree canopies (Franco, 1986; Meng et al., 2006), an effect known as crown shyness that appears to limit the crown dimensions of both Edge and Interior trees (Figure 2.9). Crown recession, the process by which lower branches die (reflected in live crown ratios), is also attributed to inter-tree competition (Maguire & Hann, 1990). Open growing trees have little to no crown abrasion or shading from competitors, while Edge trees face that competition on one side and Interior trees are entirely surrounded. Greater crown size and conductive structure implies a greater demand for moisture, potentially leading to a greater relative loss in growth when that demand cannot be met. Dominant Douglas-fir with fully exposed crowns have been found to experience increased water stress, with negative consequences for oleoresin exudation pressures critical to initial defense against Douglas-fir beetle (Rudinsky, 1966). The moderate demand of the smaller-crowned, partly-shaded Edge trees may explain their occasionally superior drought resistance and resilience.

Increased radial growth rate following release from competition also implies increased capacity to set aside starch reserves that may carry trees through brief periods of stress, especially defoliation (Waring, 1987; Loescher *et al.*, 1990). The mechanisms of mobilizing starch reserves are poorly understood, but the general equation for converting

starch to glucose includes an input of water (Ray & Behera, 2011). In a study of sudden aspen decline in Colorado, substantial loss of hydraulic conductance was observed in affected trees, while little difference was found in carbohydrate reserves (Anderegg *et al.*, 2012). If the process of mobilizing starch reserves is moisture-limited at any step, then the starch reserves may not play a substantial role in drought resistance. If starch reserves are proportional to stem growth (Mitchell *et al.*, 1983), higher resistance might be expected in the Open class compared to the Edge class on account of their significantly higher growth rate. This trend is not apparent in the results of this study, providing no support for or evidence against the hypothetical relationship between starch reserves and drought tolerance.


Figure 2.9: Example of crown shyness where the crown of the edge tree (left) has been limited by an interior tree (right) of similar height.

The growth reduction apparent among all classes starting in 2002 (Figure 2.6) is likely related to the defoliation by western spruce budworm (*Choristoneura freemani* (Razowski) = *C. occidentalis* (Freeman)) that began in 2001 and continued intermittently at the sites through 2012. Western spruce budworm is a defoliating insect native to western North America that causes growth reduction by consuming buds and needles of Douglasfir, true firs and white spruce (Nealis, 2016). Budworm defoliation was mapped at site Colpitt for eight years, beginning in 2002, and sites Sting and Vert for nine years beginning in 2001. The negative effect of defoliation on growth is expected to continue for several years after defoliation has ended while the tree recovers its foliage (Alfaro *et al.*, 2002). Regeneration in the skid trails was not quantified in this study, but its presence offers another explanation for the growth reduction in the overstory. Regeneration has become substantial in many of the trails, potentially intercepting rain and snow and competing for soil moisture and likely causing growth reduction in combination with western spruce budworm defoliation (Figure 2.10; Sterba *et al.*, 1993; Dolph *et al.*, 1995).



Figure 2.10: Regeneration in a skid trail at Vert Lake

The mechanical harvests that form the basis of this study differ from mule deer conservation practices (Dawson et al., 2007) in several potentially important ways. First, mule deer guidelines suggest the creation of discrete clumps of 4–10 trees, while these harvests created more or less open corridors several hundred meters in length, with a largely unmanipulated matrix between them. "Clumpy retention" silviculture would leave far fewer trees in the interior of clumps than were found in these stands, more trees on the edge of clumps, and fewer in complete isolation (Dawson et al., 2007). Second, thinning from below is recommended during the first pass in a young stand of Douglas-fir in the winter ranges, and in subsequent harvests where a substantial pole-size (12–35cm diameter) component remains (Dawson et al., 2007). This would control the most severe inter-tree competition, while in the study stands there was no such treatment within the matrix. Finally, the single-tree selection harvesting recommended for mature stands includes a basal area target that varies by habitat class, ranging from  $16-29 \text{ m}^2/\text{ha}$ depending on the moisture regime of the stand (Dawson *et al.*, 2007). Inventory on a perhectare basis is a notoriously unreliable indicator of the competition experienced by trees growing in clumped arrangements due to the variability inherent in the structure (Hamilton, 1984), but imposing the recommended stand-level maximum basal area may further reduce competition stress in clumps maintained for mule deer conservation.

The methods of this study limit inference to individual codominant and dominant trees following the removal of older cohorts from an uneven aged stand. While young regeneration and saplings of intermediate age were present at all sites, there were no substantially larger or older trees remaining within 50m of any of the subject trees. The applicability of these conclusions to other age classes and structures remains to be tested.

Coordinates of individual subject trees were not recorded, preventing analysis of spatial autocorrelation. Distances between different trees within the same competition class ranged from 20m to approximately 50m, with the minimum distance enforced to avoid sampling trees directly interacting through root grafts, mycorrhizal networks, or competition. Spatial autocorrelation may be positive or negative depending on distance, such that growth patterns may be more similar between trees at short distances, more different at intermediate distances, and more similar again at greater distances (Dale & Fortin, 2014). These correlations may reflect differences in the underlying soil, the influence of topography on the water table, or the spatial legacy of the primary-growth forest that was partially harvested. Conclusions of this analysis would benefit from further investigation in stem-mapped plots to assess autocorrelation at a range of distances, perhaps building on work by LeMay et al. (2009), who measured spatial patterns of mortality in the same interior Douglas-fir ecosystem type. This would better inform the design of the inferential statistical test, as effective sample size may be less than the nominal value if spatial autocorrelation is positive (Dale & Fortin, 2014). As it could not be determined whether spatial autocorrelation would affect statistical tests positively, negatively, or at all, no adjustments were made. If positive autocorrelation was affecting the results, less variation would be seen in the sample compared to the overall population, while negative autocorrelation would lead to an overestimate of variability.

## 2.6. Conclusion

Reduction of inter-tree competition through complete release supports larger crowns and conductive structures, leading to higher basal area growth rates but providing no commensurate increase in drought tolerance relative to partially released trees. Increased precipitation throughfall in the harvest corridors, similar to that noted in thinning trials, offers the most parsimonious explanation for the similarity in drought resistance between fully and partially released trees, though a variety of interacting factors are certainly at play. These benefits are likely to be realized operationally in stands managed for mule deer conservation as recommended practices include more gaps than were created in the harvests of the 1970s. Long-term negative correlations between summer temperature and growth indicate a higher risk of drought stress under projected climate change, but these risks may be mitigated in the short to mid-term by the creation of canopy gaps and either complete or partial release from competition.

## 3. Drought resistance of old-growth interior Douglas-fir (*Pseudotsuga menziesii* var. glauca (Beissn.) Franco) in the context of disturbance history in the Cariboo-Chilcotin region of British Columbia

### 3.1. Abstract

Old-growth forest reserves in managed landscapes are threatened by changes to the moisture regime under which they developed, and that threat may be magnified by exclusion of density-regulating disturbances. In this study I investigate the influence of gaps created by natural disturbances on the drought tolerance of surviving interior Douglas-fir during seven droughts in the presettlement era (1717–1869) and seven in the modern period. I use tree ring analysis to describe the relationship between drought resistance (relative growth reduction) and age, and growth response to a disturbance. Multinomial logistic regression models explaining drought resilience (return to pre-drought growth rate) are compared in an information theoretic approach, assessing the relative influence of five site-level and five tree-level factors. Regional growth release rates varied from 5–25% per decade in the presettlement era, with the exception of 1800–1809 when 38% of trees recorded release. Drought resistance is higher in young trees and those with ongoing growth release. Adjacency to canopy gaps reduces competition, explaining growth release, and canopy gaps are known to facilitate increased precipitation throughfall, explaining drought resistance. Density-regulating disturbance of any kind is expected to enhance drought tolerance in structurally complex stands of interior Douglas-fir.

#### **3.2. Introduction**

Conservation of primary-growth and complex late-successional forests is a cornerstone of ecologically oriented landscape-scale forest management in production forests around the world (Seymour & Hunter, 1992; Frelich & Reich, 2003). These reserves are functionally, aesthetically, and culturally valued. They provide required habitat (Müller *et al.*, 2010), serve as a benchmark of ecosystem composition and function for managed forests (Fraver *et al.*, 2007), and they are a preferred setting for activities ranging from the educational to the spiritual, recreational, and sporting (Ananda & Herath, 2003).

Climate change threatens old-growth forest structures by altering the moisture regime under which the stands developed (Noss, 2001). In dry ecosystems of western North America, the direct effects of climate change on moisture availability are potentially compounded by decades of fire exclusion (Cocke *et al.*, 2005). Absence of densityregulating disturbance for a prolonged period has led to higher stand densities with increased transpiration demand and canopy interception of rainfall, intensifying the stress of reduced moisture availability (Pypker *et al.*, 2005). Increased drought stress in these forests has increased both direct mortality and predisposition of stands to disturbance by native insects and catastrophic fires (Franceschi *et al.*, 2005; Guarín & Taylor, 2005).

Thinning has been found to increase drought tolerance of managed stands in a number of ecosystems (Sohn *et al.*, 2013; Elkin *et al.*, 2015; Calev *et al.*, 2016), with increased precipitation throughfall and decreased competition for available moisture identified as underlying mechanisms (Stogsdili *et al.*, 1992; Mazza *et al.*, 2011; Nanko *et al.*, 2016). Most studies have focused on relatively young, even-aged stands, often plantations. The simplicity of these stands supports straightforward and repeatable experimental design, but

it is difficult to translate the conclusions to older and more structurally complex forests.

Precipitation throughfall in late-successional forests with complex vertical and horizontal structure has been found to be directly related to the quantity of plant material overhead (Nadkarni & Sumera, 2004). Disturbance can reduce the amount of overhead plant material in the short term, leading to increased throughfall (Zirlewagen & von Wilpert, 2001) which is known to have a substantial effect on the overall water balance of resultant stands (Bouten *et al.*, 1992). Exclusion or suppression of natural disturbances may have a substantial effect on the water balance of forest stands by reducing the frequency of patches and gaps in the canopy, with measurable effects on the ability of trees to tolerate short-term droughts.

Old-growth interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests without evidence of direct anthropogenic disturbance are scattered throughout the Cariboo-Chilcotin region in central British Columbia. Permanent old-growth management areas (OGMAs) limit harvesting on over 200,000 hectares of Douglas-fir forest in the region (Figure 3.2; https://catalogue.data.gov.bc.ca/dataset/old-growth-management-areas-legalcurrent accessed January 2017), while hundreds of other old-growth stands have been avoided by chance or choice. In addition to OGMAs, where harvesting is limited to specific situations related to forest health and wildlife habitat, Community Areas of Special Concern are protected as socially essential no-harvest areas (Ministry of Agriculture and Lands, 2011).

Unharvested stands tend to be both horizontally and vertically complex, with diverse canopy strata punctured by gaps and patches initiated by windthrow, root disease, bark beetles or wildfire. The range of common natural disturbances includes factors that act

from above, mostly killing larger trees, and from below, (Smith *et al.*, 1997) primarily killing smaller trees: Douglas-fir beetle (*Dendroctonus pseudotsugae*) preferentially attacks trees over 40cm diameter (Kano, 2006), while wildfire more readily kills smaller trees with thinner bark. Wildfire frequency has decreased since the 1920s due to firefighting efforts and consumption of fine fuels by cattle (Daniels & Watson, 2003; Harvey, 2017), and the general exclusion of this disturbance has led to increases in average stand density and proliferation of a dense understory (Wong & Iverson, 2004).

Most Douglas-fir leading stands in the region historically included a component of lodgepole pine (*Pinus contorta*) that was almost completely destroyed by the mountain pine beetle (*Dendroctonus ponderosae*) outbreak of the 2000s (Figure 1.5), leaving stands of pure or nearly-pure Douglas-fir (Figure 3.1). Previous mountain pine beetle outbreaks ca. 1890–1900, 1930–1940, and 1970–1985 caused extensive damage to the lodgepole pine component of mixed stands, in some cases causing substantial growth release in more than half of the Douglas-fir (Hawkes *et al.*, 2004). Lodgepole pine may have been largely removed from many stands for the near future, but the past has been defined by a two-species system, with each conifer species affected by a native bark beetle on a more or less regular basis. These insect disturbance regimes are distinct, with mountain pine beetle tending to affect extensive swaths of timber periodically while Douglas-fir beetle typically affects small groups or patches of trees, but rarely all mature trees within a stand (Erickson, 1992).



Figure 3.1: Tree PUD18, ca. 1721, surrounded by dead lodgepole pine and regeneration of pine and Douglas-fir, with mature Douglas-fir in the background.

Precipitation at the nearby Williams Lake Airport averaged 435mm per year from 1961–1990 (http://www.climatewna.com/) and has not significantly changed in recent years, while temperatures have increased and are projected to continue increasing over the next century (Dawson *et al.*, 2008). Outbreaks of Douglas-fir beetle have been severe in the 21<sup>st</sup> century, and western spruce budworm (*Choristoneura freemani* = *C. occidentalis*) is expected to increase its range, frequency and severity in a warmer climate (Murdock *et al.*, 2013; Marciniak, 2015). Droughts lasting one or two years are common, and are considered to be predisposing factors for both Douglas-fir beetle (Powers *et al.*, 1999) and mountain pine beetle (Shore *et al.*, 2004) in addition to wildfire (Daniels & Watson, 2003; Harvey, 2017) and potentially western spruce budworm (Flower *et al.*, 2016).

Susceptibility to Douglas-fir beetle is largely dependent on the tree's vigor and ability to produce and mobilize defensive compounds. Pressure of toxic oleoresin is a major determinant of success in rejecting the initial attack, while secondary resins produced after the attack can prevent brood development (Rudinsky, 1966). Oleoresin pressure and productive capacity are closely related to water balance, which is found to fluctuate substantially both within the day and throughout the season. Trees on a southern aspect and those with fully exposed crowns record higher daily variation, and pressure levels are typically lowest midday and in the afternoon when beetle flights most commonly occur. Even a brief period of moisture deficit within the tree is expected to substantially increase vulnerability to an attack, making competition for moisture and its overall availability particularly important to survival.

Stand thinning has been found to reduce mortality to Douglas-fir beetle in the long term (Williamson & Price, 1971), an effect probably attributable to improved water

economy and removal of weak and dying trees responsible for spillover attacks. Prevention of natural wildfire over the past century has led to the opposite effect, allowing stands to reach densities at which stand stagnation is a major concern due to competition from dense populations of seedlings and saplings (Day, 1997).

In this study I investigate the influence of openings created by natural disturbances on drought resistance and resilience in interior Douglas-fir using tree ring analysis (Lloret *et al.*, 2011). Radial growth is used to estimate trees' response to drought, but can be a proxy for other allocations of photosynthate, including the generation of carbohydrate reserves and the ability to create and mobilize chemical defenses against bark beetles (Waring, 1987; Franceschi *et al.*, 2005). The specific research questions are:

- Does adjacency to gaps created by natural partial disturbances, inferred by a sudden increase in basal area increment, correspond to higher drought resistance of surviving trees?
- 2. Does age at the time of disturbance affect the drought resistance of trees in unevenaged stands?
- 3. Is the return to pre-drought growth rate (drought resilience) more closely related to site-level factors (solar radiation, elevation, annual heat-moisture index, northing, easting) or tree-level factors (age, resistance to current drought, basal area, average latewood proportion, prior growth rate)?

#### 3.3. Methods

#### 3.3.1. Site Selection and Field Methods

Study sites were identified using aerial imagery in Google Earth<sup>®</sup> (dated 2005, accessed 2013 and 2014) to locate stands that had not been previously logged and were likely to contain old trees. Lack of visual evidence of skid trails was the primary criterion for selection of study sites; the size of the stand and presence of trees with large crowns was also considered. A number of candidate sites were identified throughout the range of Douglas-fir forests in the region. The largest stands were visited first and sampling took place immediately if the sites were found to be appropriate. Presence of cut stumps or lack of trees >250 years old was grounds for dismissing the site and moving to an alternate. A total of 46 sites were sampled (Figure 3.2).

Approximately 20 sample trees were selected along a transect perpendicular to the prevailing slope at each site, with two trees selected at points every 20m (paced distance). Sample trees were generally >40cm DBH and evidently older trees were preferentially sampled. Charred bark and absence of branches on the lower bole were generally reliable indicators of old age. Two 5.1mm increment cores were taken at breast height from opposite sides of each tree, perpendicular to the slope to avoid reaction wood. Trees obviously damaged by fire (i.e. an open catface), lightning, or wind breakage were avoided whenever possible, though minor spike tops (up to 3–4" diameter) and charred bark were acceptable.

Diameter of each subject tree was measured at 1.3m and a photograph showing the crown and bole was taken for reference. Forest inventory was recorded in 3–5 fixed-radius plots along each sampling transect. Trees greater than or equal to 15cm DBH were

measured in  $1/40^{\text{th}}$  ha plots while smaller trees were measured in  $1/250^{\text{th}}$  ha plots. All data were scaled to a per-hectare basis.



Figure 3.2: Study sites in the context of Douglas-fir leading stands and permanent old growth management areas (OGMAs).

#### 3.3.2. Laboratory Preparation

Increment cores were air dried, glued to individual wooden mounts, and sanded with a progression from 240 to 400 to 600 grit sanding belts (Stokes & Smiley, 1968). Automotive polishing paper (1,200 and 2,000 grit) was used where necessary to discern miniscule rings. Visual crossdating was performed on all cores under an Olympus<sup>®</sup> SZ-61 microscope using a combination of the list method and the memorization method (Speer, 2010). The list method was used to identify marker years in the first several sites to be crossdated until a number of regionally consistent marker years were identified then used for visual crossdating of all samples.

Crossdated increment cores were scanned at 1,200 DPI using an Epson 1640XL flatbed scanner. Ring width and latewood width measurements were made using the computer program Windendro<sup>®</sup> (Regent Instruments 2014). Batches of 8–20 cores were scanned and processed together so that crossdating could be examined using the in-program ring width index display. Crossdating was verified at the site level using the program COFECHA (Holmes, 1983). Cores or sections that were excessively damaged or otherwise impossible to crossdate reliably were discarded from the study, leaving 1,693 cores from 907 trees at 46 sites (Figure 3.2).

### 3.3.3. Statistical Analysis

I defined a drought event as a year in which the mean ring width index calculated among all cores in the study (detrended with a 10-year cubic smoothing spline) was in the 10<sup>th</sup> percentile. Previous work (Lloret *et al.*, 2011) used Cook's tree-ring reconstruction of Palmer's Drought Severity Index (PDSI; Cook & Krusic, 2004) in addition to narrow ring

width to identify drought years. I did not use PDSI directly because visual inspection of the plotted PDSI reconstruction and the detrended ring width indices revealed a lag in which a low reconstructed PDSI value sometimes preceded a narrow ring by one year while in other cases both the index value and PDSI value were remarkably low in the same year. Dendroclimatic work in the region identified the total precipitation from the previous June through current May, not PDSI, as having the greatest correlation value with Douglas-fir ring width (Watson & Luckman, 2002). Previous-June through current-June (pJJ) precipitation total provided the highest pairwise correlation with detrended ring width indices in my work (r = 0.58, n = 76, P < 0.0001), and narrow rings often occurred in years with below-average pJJ values.

While low-growth events are attributed to drought and referred to throughout this chapter by the year in which a sharp growth reduction occurred, it is acknowledged that this reduction may be attributable or partly attributable to low precipitation in the previous summer or an unidentified non-drought factor such as a late frost. One event (1988/89) lasted two years and all values were calculated based on the mean of the two years, but the event is referred to exclusively by the first year. Longer-term droughts are understood to have occurred in the region (Hart *et al.*, 2010), but this analysis is focused only on those which lasted one or two years.

Drought resistance was calculated by dividing the basal area increment in the drought year by the mean basal area increment over the five previous years (Lloret *et al.*, 2011). Drought resilience was calculated by dividing the five year mean basal area increment after the event by the five-year mean basal area increment before (Figure 3.3).



Figure 3.3: Increment cores BLU 17A ("17"; release) and BLU 15A ("15"; no release). Drought resistance equals Y/X; drought resilience equals Z/X. Core 17 shows an example of a false ring in 1931, followed by continued growth that accounts for more than half of the ring width and a high drought resistance score. Black dots indicate decade years, from the left: 1910, 1920, and 1930.

Growth releases were identified using the package TRADER in the open-source statistical program R (Version 3.3.1; script in Appendix A). Growth release criteria used by Hadley & Veblen (1993; 250% increase in mean ring width in subsequent vs. previous five years)to identify Douglas-fir beetle mortality were tested and modified by averaging the growth over a longer period (20 years) to eliminate false positives that commonly occurred following ~10 year periods of growth suppression corresponding to known regional droughts (Wolfe *et al.*, 2001; Hart *et al.*, 2010). Ring widths were converted to basal area increments to reflect as accurately as possible the actual growth of the tree (as in Lloret *et al.*, 2011). The criteria ultimately used to define growth release were:

- Period length: 20 years before and after each year
- Minimum rate of basal area increment increase: 50%
- Minimum time elapsed before another release can be identified: 15 years
- Minimum duration: one year

These criteria were further tested against the data from Chapter 2, where the date of disturbance was known. For those data, growth release was identified in 80% of trees located on the edge of skid trails and 38% of the trees growing in the matrix between skid trails. Individual-tree plots of the interior trees showing release were reviewed, and there was in fact an increase over that period of time in these cores, so the criteria were accepted.

Growth releases were consolidated to a per-decade rate and the percentage of the trees recording release in each decade was calculated by dividing the number of releases by the number of trees present at the end of each decade. Initiation dates at coring height were estimated based on the oldest ring among the paired cores for each tree. Initiation dates at coring height were consolidated to a per-decade basis for comparison against release dates on the basis of the percentage of the total sample initiated in any given decade.

Each tree was assigned to an age class (at coring height) at the time of each drought to compare resistance values by age. The age classes were 5–49, 50–149, 150–249, and 250+, roughly representing young, mature, old, and very old trees. As the data could not be transformed to meet the assumption of normality, the nonparametric Kruskall-Wallis rank-sum test (CI 95%; Stata<sup>®</sup> 12.1) was used to assess the differences between age classes and to perform a post-hoc test when the fit of the overall model was significant.

As a point of reference for individual-tree growth trends, mean basal area increments across the entire study area were plotted for 50-year age classes based on the current age

(at coring height) of specimens: 200–249 (n=175), 250–299 (n=169), 300–349 (n=132), 350–399 (n=101), and 400+ (n=84). These data were smoothed with a 50-year spline prior to averaging to visualize long-term trends at the expense of annual and decadal variability (see Figure 3.10). To further describe trends apparent in the data, diameter at breast height in the years 1800 and 1840 was calculated by doubling the sum of accumulated ring widths at each date. The resulting diameter distributions were graphed by 5cm DBH classes, with trees in 1840 separated into ingrowth (trees not present in 1800) and accretion (trees present in 1800).

All trees over the age of 50 were classified as having an ongoing growth release or not. Drought resistance values were compared in a two-way ANOVA considering release/no release and site code as explanatory variables, including an interaction term. Resistance values were transformed as noted in the output table and residuals were tested for heteroscedasticity to confirm that residuals had equal variance across the predicted range. Conformity of the residuals to the normal distribution was visually assessed using histograms.

Multinomial logistic regression was used to assess the resilience of individual trees (mlogit, Stata 14). I placed each tree into one of three equally populated categories based on resilience scores. Low resilience trees were those with the lowest 33.3% of values, mid resilient trees included those in the middle third of resilience scores, and high resilience trees included those with the top third of scores. These categorical scores were regressed against a set of independent variables that described site and growth factors for each tree (Table 3.1).

ClimateWNA (http://www.climatewna.com/, accessed 2016) was used to generate

annual heat-moisture (AHM) indices for each site. Elevation data (1:50,000 scale) (http://ftp.geogratis.gc.ca/pub/nrcan\_rncan/elevation/geobase\_cded\_dnec/50k\_dem/ accessed 2016) were used to calculate total solar radiation at each study site using the Area Solar Radiation tool in ArcGIS. Elevation data were assigned to sites, and the projected easting and northing values were calculated in ArcGIS.

Age and basal area at the time of each drought, and average percent latewood over the life of the tree, were calculated from Windendro<sup>®</sup> measurements. Multinomial logistic regression in Stata 14 was used to assess the influence of each of these variables (Table 3.1) on the probability of a given tree falling into one of the higher resilience categories vs. the lowest category. Tolerance scores with a threshold of 0.1 were used to identify multicollinearity in model structure.

An information theoretic approach was used to identify the most parsimonious multinomial logistic regression model (Burnham & Anderson, 2004). I used the Akaike Information Criterion for small sample sizes (AIC*c*) to identify the best model of the set of models that I tested. Models with AIC*c* differences <2 were considered to be similar and are reported. In total, nine candidate models were assessed (Table 3.2), and standard errors were adjusted within the mlogit model to account for clustering at the site level (Rogers, 1993). Three models consisted of the complete model less one variable or conceptually-related pair of variables (northing/easting). Resistance was expected to be a powerful variable based on previous work (Lloret *et al.*, 2011); a model excluding that variable was included to screen for changes in coefficient sign. A model excluding elevation was included to screen for cases of coefficients changing sign as elevation has had an overwhelming influence on some model fits (Chris Johnson, UNBC, personal

communication 2017). A model excluding northing/easting was included to assess the importance of geographic location. Models using exclusively site-level and tree-level variables were included to test whether one category or the other best explained the observed variation alone. Two models including a subset of site and tree level variables were included to assess the explanatory power of more limited combinations in comparison to the full model. One model included only elevation to test whether that variable alone could provide the most parsimonious explanation for the variation observed.

AIC*c* scores were used to evaluate the explanatory ability of each model in the context of its complexity, accounting for sample size, using the formula

# $(LL^{*}-2)+(2^{*}k)+((2^{*}k(k+1))/(n-k-1))$

where k is the number of parameters in the model, n is the sample size, and LL is the maximised log likelihood of each model from the mlogit output. Table 3.1: Description of variables used in multinomial logistic regression models used to explain the drought resilience of subject trees.

Dependent Variable Resilience = 5-year post-drought/5-year pre-drought growth					
ResilCD	1 = 10000000000000000000000000000000000				
Independent Variables					
LW	Mean latewood % as a decimal, over the full life of the tree				
AHM	Annual Heat-Moisture Index (ClimateWNA)				
Solar	Total annual solar radiation; watt-hours per square meter				
Elev	Elevation; meters above sea level				
Resist	Resistance to the current drought (drought/previous 5-year avg.)				
Prior	Average growth rate over the past 20 years; square mm				
Age	Age at the time of the drought				
BA	Basal area at the time of the drought; square mm				
Easting	Projected easting value in meters (NAD 1983 Albers)				
Northing	Projected northing value in meters (NAD 1983 Albers)				

Table 3.2: Candidate variable sets tested using multinomial logistic regression used to explain the drought resilience of subject trees

Variables
LW+AHM+Solar+Elev+Resist+Prior+Age+BA+Easting+Northing
LW+AHM+Solar+Elev+Prior+Age+BA+Easting+Northing
LW+AHM+Solar+Elev+Resist+Prior+Age+BA
LW+AHM+Solar+Resist+Prior+Age+BA+Easting+Northing
Elev
AHM+Solar+Elev+Easting+Northing
LW+Resist+Prior+Age+BA
LW+AHM+Elev+Resist+Prior+BA
AHM+Solar+Elev+Prior+Age+BA+Easting+Northing

# 3.4. Results

Drought years in 2010, 1988/1989 (referred to as 1988), 1959, 1946, 1938, 1931, 1905, 1869, 1842, 1800, 1772, 1760, 1734 and 1717 were selected for analysis (Figure 3.4).



Figure 3.4: Detrended ring width index (10-year cubic smoothing spline) calculated from all trees in the study. Dotted line indicates 10th percentile (0.7978) used to define drought events. Black boxes indicate drought years selected for analysis.

All of the selected drought years had a negative reconstructed PDSI value in either the preceding or current year (Table 3.3). All years within the period of instrumental record (1936 to 2012) had below average previous June through current June precipitation totals, ranging from a 16 to 28% departure from the average. Growth rings in Jasper and Banff were concurrently narrow in six out of 12 years for which the data overlapped, suggesting these years were regional rather than local droughts.

Table 3.3: Identified drought years and regionally narrow years (negative index values (10year spline) in Jasper and Banff chronologies), low reconstructed PDSI (negative values at Cook's reconstruction point #30) in the current and previous year, and below-average previous June through current June total precipitation (pJJ). Gray cells indicate no data.

		Low	Low	
	Narrow in	PDSI	PDSI	Below
	Jasper and	Current	Previous	Average
Year	Banff	Year	Year	pJJ
2010				Y
1988			Y	Y
1959			Y	Y
1946			Y	Y
1938		Y		Y
1931	Y	Y	Y	
1905		Y	Y	
1869	Y	Y	Y	
1842	Y	Y	Y	
1800	Y		Y	
1772	Y		Y	
1760			Y	
1734		Y		
1717	Y	Y		

Study sites ranged from 645 to 1329m ASL, basal area ranged from 23 to 105 m<sup>2</sup> per hectare in trees >15cm DBH, and trees per hectare <15cm DBH ranged from 337 to 81,330 (Table 3.4).

Table 3.4: Site codes, elevation (meters asl), basal area per hectare in trees over 15cm dbh (BAPH; m<sup>2</sup> per hectare), trees per hectare in trees under 15cm dbh (TPH) and locations (decimal degrees). Inventory data not collected at sites with grayed-out cells.

ABR     1,133     39     12,818     51.74389230     -123.01188846       ACS     1,024     82     2,147     52.06831024     -123.40771210       ALE     959     23     2,147     52.06831024     -123.40771210       ALK     954     51.78347817     -122.18762809     BCA     935     32     443     52.09017948     -123.35763661       BIG     1,261     51.31380538     -122.14872292     BLU     871     50     6,112     52.33392135     -122.24453402       CAL     1,248     53     5,725     52.06929872     -122.61526964       CAM     1,087     53     35,361     51.69793030     -121.61113394       CHI     906	Site	Elevation	BAPH >15cm	TPH <15cm	Latitude	Longitude
ACS   1,024   82   2,147   52.01175487   -123.29969878     ALE   959   23   2,147   52.06831024   -123.40771210     ALK   954   51.78347817   -122.18762809     BCA   935   32   443   52.09017948   -123.35763661     BIG   1,261   51.31380538   -122.4483402   CAL   1,248   53   5,725   52.06929872   -122.61526964     CAM   1,087   53   35,361   51.69793030   -121.61113394     CHI   906   51.90004686   -121.93915042   -122.21572977     DOG   1,136   51   3,220   51.47823126   -122.215729418     ENT   910   51.98366340   -121.87442622   EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.43351471     HAN   1,329   59   2,021   51.96520698   -122.0377503     KCR   831   59   5,999   52.06426670   -121.8822808     LEE   1,031   55<	ABR	1,133	39	12,818	51.74389230	-123.01188846
ALE     959     23     2,147     52.06831024     -123.40771210       ALK     954     51.78347817     -122.18762809       BCA     935     32     443     52.09017948     -123.35763661       BIG     1.261     51.31380538     -122.14807292       BLU     871     50     6,112     52.33392135     -122.61526964       CAL     1,248     53     5,725     52.06929872     -122.61526964       CAM     1,087     53     35,361     51.69793030     -121.61113394       CHI     906     51.90004686     -122.37337676     DCB     947     52     1,957     51.57270984     -122.2259727       DGG     1,136     51     3,220     51.47823126     -122.17934180     DEVIE     122.0134020       FUZ     1,068     47     337     52.28706360     -122.68007984       GAR     1,239     29     3,537     51.7091376     -122.43351471       HAN     1,329     59     2,021     51.96565471     -122.913040419 <td>ACS</td> <td>1,024</td> <td>82</td> <td>2,147</td> <td>52.01175487</td> <td>-123.29969878</td>	ACS	1,024	82	2,147	52.01175487	-123.29969878
ALK     954     51.78347817     -122.18762809       BCA     935     32     443     52.09017948     -123.35763661       BIG     1.261     51.31380538     -122.14807292       BLU     871     50     6,112     52.3392135     -122.24453402       CAL     1.248     53     5,725     52.06929872     -122.61526964       CAM     1.087     53     35,361     51.69793030     -121.61113394       CHI     906     51.90004686     -121.93915042     CTI     11.365     51     3,220     51.47823126     -122.15729418       ENT     910     51.98366340     -121.87442622     EPI     1,262     51     573     51.60443734     -122.01334020       FUZ     1,068     47     337     52.28706360     -122.68007984       GAR     1,239     29     3,537     51.70913776     -122.43351471       HAN     1,329     59     2,021     51.96505471     -122.93040419       JKY     1,136     105     12,692     5	ALE	959	23	2,147	52.06831024	-123.40771210
BCA   935   32   443   52.09017948   -123.35763661     BIG   1,261   51.31380538   -122.14807292     BLU   871   50   6,112   52.33392135   -122.24453402     CAL   1,248   53   5,725   52.06929872   -122.61526964     CAM   1,087   53   35,361   51.69793030   -121.61113394     CHI   906   51.90004686   -121.93915042   CTI   818   52   5,557   52.65916903   -122.37337676     DCB   947   52   1,957   51.57270984   -122.27239727   DOG   1,136   51.98366340   -121.87442622     EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.4351471     HAN   1,329   59   2,021   51.96520698   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.4807884     LEE   1,316   105   12,692   51.69171494   -122.0377503     KCR   831	ALK	954			51.78347817	-122.18762809
BIG   1,261   51.31380538   -122.14807292     BLU   871   50   6,112   52.33392135   -122.21453402     CAL   1,248   53   5,725   52.06929872   -122.61526964     CAM   1,087   53   35,361   51.69793030   -121.61113394     CHI   906   51.90004686   -121.93915042   CTI   818   52   5,557   52.65916903   -122.37337676     DCB   947   52   1,957   51.57270984   -122.15729418   ENT   910   51.98366340   -121.87442622   EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.91335345     HAW   1,306   59   3,199   51.96520698   -122.91335345     HAW   1,306   59   5,999   52.06426670   -121.8822808     LEE   1,031   55   2,526   51.95623186   -123.10607239     MAB   945   47   19,533   51.90773761   -122.2701389     MAQ   931   59	BCA	935	32	443	52.09017948	-123.35763661
BLU     \$71     50     6,112     52.33392135     -122.24453402       CAL     1,248     53     5,725     52.06929872     -122.61526964       CAM     1,087     53     35,361     51.90004686     -121.93915042       CTI     818     52     5,557     52.65916903     -122.37337676       DCB     947     52     1,957     51.57270984     -122.8742622       EPI     1,262     51     573     51.60443734     -122.01334020       FUZ     1,068     47     337     52.28706360     -122.86807984       GAR     1,239     59     2,021     51.98565471     -122.93040419       JKY     1,136     105     12,692     51.69171494     -122.20377503       KCR     831     59     5,999     52.06426670     -121.88228808       LEE     1,031     55     2,526     51.95623186     -123.07392013       LEE     1,031     55     2,526     51.95623186     -123.07392013       LEE     1,031     <	BIG	1,261			51.31380538	-122.14807292
CAL   1,248   53   5,725   52.06929872   -122.61526964     CAM   1,087   53   35,361   51.69793030   -121.61113394     CHI   906	BLU	871	50	6,112	52.33392135	-122.24453402
CAM   1,087   53   35,361   51.69793030   -121.61113394     CHI   906   51.90004686   -121.93915042     CTI   818   52   5,557   52.65916903   -122.37337676     DCB   947   52   1,957   51.57270984   -122.2259727     DOG   1,136   51   3,220   51.47823126   -122.15729418     ENT   910   51.98366340   -121.87442622   EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.43351471     HAN   1,329   59   2,021   51.96520698   -122.93935345     HAW   1,306   59   3,199   51.96565471   -122.0377503     KCR   831   59   5,999   52.06426670   -121.88228088     LEE   1,031   55   2,526   51.95623186   -123.10607239     MAQ   931   59   2,442   52.35246379   -122.18813162     MAY   1,127   43   6,062   51.88406410   -122.19751849	CAL	1,248	53	5,725	52.06929872	-122.61526964
CHI   906   51.90004686   -121.93915042     CTI   818   52   5,557   52.65916903   -122.37337676     DCB   947   52   1,957   51.57270984   -122.2229727     DOG   1,136   51   3,220   51.47823126   -122.15729418     ENT   910   51.98366340   -121.87442622   EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.68007984     GAR   1,239   29   3,537   51.70913776   -122.43351471     HAN   1,329   59   2,021   51.96520698   -122.9037503     KCR   831   59   5,999   52.06426670   -121.8822808     LEE   1,031   55   2,526   51.95623186   -123.0607239     MAB   945   47   19,533   51.90773761   -122.27201389     MAQ   931   59   2,442   52.35246379   -122.51813162     MAY   1,127   43   6,062   51.88406410   -122.19751849 </td <td>CAM</td> <td>1.087</td> <td>53</td> <td>35.361</td> <td>51.69793030</td> <td>-121.61113394</td>	CAM	1.087	53	35.361	51.69793030	-121.61113394
CTI818525,55752.65916903-122.37337676DCB947521,95751.57270984-122.22259727DOG1,136513,22051.47823126-122.15729418ENT91051.98366340-121.87442622EPI1,2625157351.60443734-122.01334020FUZ1,0684733752.28706360-122.68007984GAR1,239293,53751.70913776-122.43351471HAN1,329592,02151.9652698-122.91335345HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.20377503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-122.19751849MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.1889222-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.28627230-122.18609312PTI1,00534 <t< td=""><td>CHI</td><td>906</td><td></td><td>,</td><td>51.90004686</td><td>-121.93915042</td></t<>	CHI	906		,	51.90004686	-121.93915042
DCB     947     52     1,957     51.57270984     -122.22259727       DOG     1,136     51     3,220     51.47823126     -122.15729418       ENT     910     51.98366340     -121.87442622       EPI     1,262     51     573     51.60443734     -122.01334020       FUZ     1,068     47     337     52.28706360     -122.43351471       HAN     1,329     29     3,537     51.70913776     -122.43351471       HAN     1,306     59     3,199     51.96520698     -122.93040419       JKY     1,136     105     12,692     51.69171494     -122.20377503       KCR     831     59     5,999     52.06426670     -121.88228808       LEE     1,031     55     2,526     51.95623186     -123.07392013       LEN     1,268     87     2,463     52.03817036     -122.10607239       MAB     945     47     19,533     51.90773761     -122.27201389       MAQ     931     59     2,442 <t< td=""><td>CTI</td><td>818</td><td>52</td><td>5,557</td><td>52.65916903</td><td>-122.37337676</td></t<>	CTI	818	52	5,557	52.65916903	-122.37337676
DOG   1,136   51   3,220   51.47823126   -122.15729418     ENT   910   51.98366340   -121.87442622     EPI   1,262   51   573   51.60443734   -122.01334020     FUZ   1,068   47   337   52.28706360   -122.68007984     GAR   1,239   29   3,537   51.70913776   -122.43351471     HAN   1,329   59   2,021   51.96520698   -122.93040419     JKY   1,136   105   12,692   51.69171494   -122.0377503     KCR   831   59   5,999   52.0426670   -121.8822808     LEE   1,031   55   2,526   51.95623186   -123.07392013     LEN   1,268   87   2,463   52.03817036   -122.19751849     MAQ   931   59   2,442   52.35246379   -122.51813162     MAY   1,127   43   6,062   51.88406410   -122.19751849     MCL   679   39   2,273   52.42191831   -122.36814577     MEL   939   65   1,452 <td>DCB</td> <td>947</td> <td>52</td> <td>1.957</td> <td>51.57270984</td> <td>-122.22259727</td>	DCB	947	52	1.957	51.57270984	-122.22259727
ENT91051.98366340-121.87442622EPI1,2625157351.60443734-122.01334020FUZ1,0684733752.28706360-122.68007984GAR1,239293,53751.70913776-122.43351471HAN1,329592,02151.96520698-122.91335345HAW1,306593,19951.96520698-122.93040419JKY1,13610512,69251.69171494-122.20377503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.308614577MEL939651,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.720518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,10735 </td <td>DOG</td> <td>1.136</td> <td>51</td> <td>3.220</td> <td>51.47823126</td> <td>-122,15729418</td>	DOG	1.136	51	3.220	51.47823126	-122,15729418
EPI1,2625157351.60443734-122.01334020FUZ1,0684733752.28706360-122.68007984GAR1,239293,53751.70913776-122.43351471HAN1,329592,02151.96520698-122.91335345HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.20377503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-122.1701389MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.36814577MEL939651,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.7308404NRA970401,83152.21898222-122.650518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA	ENT	910		- , -	51,98366340	-121.87442622
FUZ1,0684733752.28706360-122.68007984GAR1,239293,53751.70913776-122.43351471HAN1,329592,02151.96520698-122.91335345HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.20377503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.68814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.7308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES <td>EPI</td> <td>1.262</td> <td>51</td> <td>573</td> <td>51.60443734</td> <td>-122.01334020</td>	EPI	1.262	51	573	51.60443734	-122.01334020
GAR1,239293,53751.70913776-122.43351471HAN1,329592,02151.96520698-122.91335345HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.20377503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.9125910PUD967441,20052.18467036-123.81250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES <td>FUZ</td> <td>1.068</td> <td>47</td> <td>337</td> <td>52.28706360</td> <td>-122.68007984</td>	FUZ	1.068	47	337	52.28706360	-122.68007984
HAN1,329592,02151.96520698-122.91335345HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.2037503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES <td>GAR</td> <td>1 239</td> <td>29</td> <td>3 537</td> <td>51 70913776</td> <td>-122 43351471</td>	GAR	1 239	29	3 537	51 70913776	-122 43351471
HAW1,306593,19951.96565471-122.93040419JKY1,13610512,69251.69171494-122.2037503KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS	HAN	1 329	59	2 021	51 96520698	-122 91335345
JKY1,13610512,69251,69171494-122,20377503KCR831595,99952,06426670-121,88228808LEE1,031552,52651,95623186-123,07392013LEN1,268872,46352.03817036-123,10607239MAB9454719,53351,90773761-122,27201389MAQ931592,44252,35246379-122,51813162MAY1,127436,06251,88406410-122,19751849MCL679392,27352,42191831-122,39560948MON1,127471,45251,18898694-121,19581713NEE1,070741,89452,18793720-122,63864732NOJ1,016541,13752,46709374-122,72308404NRA970401,83152,21898222-122,50518352PTI1,005341,32652,16269145-123,91295910PUD967441,20052,18467036-123,85250382PVA786541,21352,28627230-122,18609312PYP1,107351,31452,03219767-124,13537884REN988641,01152,16901851-123,71319263RES953282,58952,13741314-123,74083106RIS1,259731,64251,94922460-122,63877948SOA6455452,42216492-122,41362522	HAW	1 306	59	3 199	51 96565471	-122 93040419
KCR831595,99952.06426670-121.88228808LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.63877948SOA645541,64251.94922460-122.63877948	JKY	1 1 3 6	105	12 692	51 69171494	-122 20377503
LEE1,031552,52651.95623186-123.07392013LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.2186222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	KCR	831	59	5 999	52.06426670	-121 88228808
LEN1,268872,46352.03817036-123.10607239MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	LEE	1 031	55	2,526	51 95623186	-123 07392013
MAB9454719,53351.90773761-122.27201389MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA6455452.42216492-122.41362522	LEN	1 268	87	2,463	52.03817036	-123 10607239
MAQ931592,44252.35246379-122.51813162MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA6455452.42216492-122.41362522	MAB	945	47	19.533	51 90773761	-122 27201389
MAY1,127436,06251.88406410-122.19751849MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	MAO	931	59	2 442	52 35246379	-122.51813162
MCL679392,27352.42191831-122.36814577MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	MAY	1 127	43	6.062	51 88406410	-122.01010102
MEL939651,45252.25422122-122.39560948MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	MCL	679	39	2,273	52 42191831	-122.36814577
MON1,127471,45251.18898694-121.19581713NEE1,070741,89452.18793720-122.63864732NOJ1,016541,13752.46709374-122.72308404NRA970401,83152.21898222-122.50518352PTI1,005341,32652.16269145-123.91295910PUD967441,20052.18467036-123.85250382PVA786541,21352.28627230-122.18609312PYP1,107351,31452.03219767-124.13537884REN988641,01152.16901851-123.71319263RES953282,58952.13741314-123.74083106RIS1,259731,64251.94922460-122.63877948SOA64552.42216492-122.41362522	MEL	939	65	1 452	52.25422122	-122.39560948
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REN   988   64   1,011   52.16901851   -123.71319263     RES   953   28   2,589   52.13741314   -123.74083106     RIS   1,259   73   1,642   51.94922460   -122.63877948     SOA   645   52.42216492   -122.41362522	РҮР	1 107	35	1 314	52.03219767	-124 13537884
RES   953   28   2,589   52.13741314   -123.74083106     RIS   1,259   73   1,642   51.94922460   -122.63877948     SOA   645   52.42216492   -122.41362522	REN	988	64	1,011	52.05219707	-123 71319263
RIS   1,259   73   1,642   51.94922460   -122.63877948     SOA   645   52.42216492   -122.41362522	RES	953	28	2 589	52 13741314	-123 74083106
SOA 645 52.42216492 -122.41362522	RIS	1 259	73	1 642	51 94922460	-122 63877948
5011 015 52.12210172 122.11502522	SOA	645	15	1,012	52 42216492	-122.03077510
SUG 658 41 1.642 52.10276261 -122.02310368	SUG	658	41	1 642	52 10276261	-122.02310368
TWA 839 52 1 894 52 54848220 -122 63091856	TWA	839	52	1 894	52 54848220	-122.02510500
WEX 1.013 35 1.326 52.06140806 -123.60920120	WFX	1 013	35	1 326	52.04140806	-123 60929129
WHI     857     77     1 515     52 210110000     123.00/20120	WHI	857	77	1 515	52 21711702	-122 32213471
WIL 677 48 674 52 15969659 -122 23387497	WIL	677	48	674	52.15969659	-122.223387497
YUN 996 38 81.330 51 88829296 -123 10229104	YUN	996	38	81.330	51.88829296	-123.10229104

Aside from the spikes to 38% and 34% in 1800–1809 and 1930–1939, the percentage of trees recording growth release in the presettlement era varied between 5 and 25% per decade, averaging 14% from 1600–1609 to 1880–1889. No decade has exceeded 10% of trees recording growth release since the 1930s. Initiation rates (at coring height) of sample trees varied between 5 and 13% per decade after 1600.



Figure 3.5: Percentage of the total sample reaching coring height in a given decade ("Initiation"; grey) and percentage of trees present at the end of each decade showing growth release >50% in each decade (black).

Mean basal area increments among the four older age classes were synchronized ca. 1800–1840, and then separated by age class, with younger cohorts continuing to increase their growth rate and older cohorts remaining steady or falling slightly (Figure 3.6). Growth rate in all cohorts precipitously declined starting ca. 1995.



Figure 3.6: Mean basal area increments by 50-year age class across the entire study area since 1615, smoothed with a 50-year spline prior to averaging to display long-term growth trends.

In 1800 a majority of the sampled trees that had reached breast height were less than 20cm DBH, and 80% were less than 30cm. A shift towards the larger diameter classes is apparent by 1840 (Figure 3.7), with an average diameter growth of 8.7cm or 2.2mm per year in the intervening period. Ingrowth accounted for 102 of the 116 trees less than 10cm DBH in 1840, while several newly initiated trees reached the 20–24.9cm class.



Figure 3.7: Overall diameter distributions in 1800 and 1840, with 1840 trees separated into accretion and ingrowth, respectively those that had and had not reached breast height by 1800.

Visual inspection of cores and plotted series supports the growth trend identified in the analysis, where small, suppressed trees began growing at rates expected of canopy dominants beginning ca. 1800 (e.g. Figure 3.8). The length of the suppressed growth in most cores (more than 100 years in some trees) is too long to be attributed to climatic variation, while 5–10 year periods of more extreme growth reduction correspond to regional droughts inferred from tree ring analyses ca. 1770 and 1790 (Wolfe *et al.*, 2001; Hart *et al.*, 2010), suggesting that competition was responsible for the slow growth and its removal was the cause of the acceleration. Many of the trees showing release ca. 1800 still remain without substantial crown competition (Figure 3.9). Tree JKY10 is one example among hundreds of trees showing this general pattern, having reached 106cm DBH (outside bark) after 213 years without apparent crown competition (Figure 3.10).



Figure 3.8: Core GAR14A from 1740 to 1840 with basal area increment. Single pencil marks indicate decade years, double mark indicates 1750, and triple mark identifies 1800. Radial growth from 1800 to 1840 was 6.5cm, suggesting approximately 13cm diameter growth at an average rate of 3.25mm per year. The widest ring (1820) is 2.9mm, suggesting a diameter growth of 5.8mm on a tree 26cm DBH. Basal area increment continued to increase until 1917, where a period of suppression marks the beginning of a slow decline. The crown was completely isolated when sampled in 2014, with live limbs beginning at 3–4m height.



Figure 3.9: Tree GAR14 (ca. 1609) in 2013. Underexposure of original photograph corrected in GIMP 2.



Figure 3.10: Tree JKY10 (ca. 1723), 106cm DBH (outside bark), apparently isolated since 1800 after being released at the age of 101 ca. 1800 (white triangle at left). Core JKY10C, at left: 1769–1860; at right: 1861–2013. Single dots at decade years, double-dots at 1850/1950, triple dots at 1800/1900, quadruple dots at 2000. Raw and 50-year splined basal area increment (BAI) graphed as solid and dashed lines respectively.

The youngest age class (5–49 years) had significantly higher drought resistance in

nine of 14 years tested (Table 3.5). The oldest age class (250+ years) had significantly

lower drought resistance vs. the next youngest class (150-249 years) in 1931, 1959, and

1988. In 1800 and 1959, the second-youngest age class (50-149 years) had significantly

higher resistance than the next older class (150–249 years).

Р

Table 3.5: Drought resistance by age class. Kruskall-Wallis rank-sum test (95% CI; age classes that do not share a letter within a given year are significantly different in pairwise multiple comparisons. Pairwise comparisons not conducted for 1938 when overall model was insignificant. No trees under 50 in 2010).

Age Class	1717	1734	1760	1772	1800	1842	1869
5–49	0.70a	0.78a	0.88a	0.84a	1.07a	0.77a	0.65a
50-149	0.59b	0.66b	0.75b	0.66b	0.92ac	0.65b	0.52b
150-249	0.57ab	0.71ab	0.69b	0.60b	0.79b	0.62b	0.50b
250+	0.56ab	0.64ab	0.63ab	0.41ab	0.76abc	0.67ab	0.56b
n	302	372	452	501	599	734	784
Chi-squared	8.88	15.25	38.77	35.96	20.04	25.69	38.92
d.f.	3	3	3	3	3	3	3
Р	0.03098	0.00162	0.00010	0.00010	0.00017	0.00010	0.00010
	1005	1021	1020	10.47	1050	1000	2010
Age Class	1905	1931	1938	1946	1959	1988	2010
5–49	0.71a	1.00a	0.92ns	0.92a	0.63abc	0.60a	
50-149	0.62b	0.70b	0.89ns	0.71b	0.62a	0.65a	0.68a
150-249	0.64ab	0.67b	0.86ns	0.69b	0.56b	0.63a	0.64ab
250+	0.61b	0.57c	0.84ns	0.68b	0.43c	0.57b	0.62b
n	845	872	874	879	884	886	878
Chi-squared	12.62	67.46	5.53	34.76	89.35	9.60	8.49
d.f.	3	3	3	3	3	3	3

0.0552 0.0001 0.1371 0.0001 0.0001 0.0223 0.0143

Trees with an ongoing release had higher drought resistance than trees without an ongoing growth release in every year except 1869 (Table 3.6). Site was a significant explanatory variable in every year that a test could be conducted, while growth release status was significant in seven of the 10 years that tests could be conducted. The interaction of site and growth release status was significant in 1842, 1931, and 1946 (p<0.05; Appendix C). The data for the years 1760, 1959, and 1988 did not meet the assumption of normality after transformation. The ANOVA and plot of residual vs. fitted values for 1760, 1959, and 1988 are presented in Appendix C for information.

Table 3.6: Drought resistance in trees with and without ongoing release. Two-way ANOVA; full model outputs in Appendix C. Significant variables in bold;  $\alpha$ =0.05.

	1717	1734	1760	1772	1800	1842	1869
<b>Ongoing Release</b>	0.72	0.72	0.97	0.78	0.99	0.72	0.51
No Release	0.56	0.66	0.68	0.60	0.78	0.63	0.52
Transform	Sqrt	Sqrt		Box-Cox	Box-Cox	Box-Cox	Box-Cox
Release F	6.86	19.95		0.52	12.86	2.56	0.50
Release Prob > F	0.010	<0.001		0.47	<0.001	0.110	0.478
Site F	7.35	8.02		9.21	6.35	14.19	13.03
Site Prob > F	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001
	1905	1931	1938	1946	1959	1988	
<b>Ongoing Release</b>	0.65	0.69	0.88	0.75	0.88	0.64	
No Release	0.62	0.64	0.85	0.68	0.52	0.56	
Transform	Box-Cox	Box-Cox	Box-Cox	Box-Cox			
Release F	17.02	10.91	26.22	19.92			
Release Prob > F	<0.001	0.001	<0.001	<0.001			
Site F	15.62	17.55	12.09	11.43			
Site Prob > F	<0.001	<0.001	<0.001	<0.001			
AICc differences <2 in two models in 1931, two in 1869, and three in 1717 led to 17 top-ranked models from the 13 drought years considered (Table 3.7). Among these, 15 were the full model or its close derivative (seven "Full," five "Less elevation," three "Less easting and northing"). "Mixed 1" (% latewood, annual heat-moisture, elevation, resistance, prior growth and basal area) was among the three top-ranked models for 1717 and was the exclusive top-ranked model for 1772. All output tables and AIC<sub>C</sub> calculations may be found in Appendix B.

Table 3.7: Top-ranked multinomial logistic regression models explaining drought resilience scores for each drought year

Year	Top-Ranked Model
1988	Full model
1959	Full model less elevation
1946	Full model less elevation
1938	Full model
1931A	Full model
1931B	Full model less elevation
1905	Full model less easting and northing
1869A	Full model
1869B	Full model less easting and northing
1842	Full model
1800	Full model less elevation
1772	Mixed 1
1760	Full model less elevation
1734	Full model
1717A	Full model
1717B	Full model less easting and northing
1717C	Mixed 1

Resistance to the current drought had an exclusively positive influence on the probability of higher drought resilience, and was significant in 13 of 17 top-ranked models in the low-resilience vs. mid-resilience categories and 16 of 17 in the low-resilience vs. high-resilience comparisons (Table 3.8). Prior growth rate negatively influenced drought resilience in eight top-ranked models in the low-resilience vs. mid-resilience comparisons and ten in low-resilience vs. high-resilience comparisons. Age at the time of the drought provided several significant negative coefficients: one in the low-resilience vs. mid-resilience vs. mid-resilience and five in the low-resilience vs. high-resilience comparisons. Site-level variables and other tree-level variables were occasionally significant, with inconsistent coefficient signs between years.

Table 3.8: Coefficients of top-ranked models for each drought year. Bold values indicate statistical significance in the original mlogit models (95% CI). Coefficients multiplied by the value at the top of each column for concise display. Gray boxes indicate variables not included in the top-ranking model. "1 vs. 2" indicates the probability of a tree being in the middle 33% vs. the lowest 33%; "1 vs. 3" indicates the probability of a tree being in the highest 33% vs. lowest 33%. Complete outputs can be found in Appendix D.

1 vs. 2	1	1	100,000	100	1	100	100	10,000	10,000	10,000
Year	LW	AHM	Solar	Elev	Resist	Prior	Age	BA	Easting	Northing
1988	0.029	0.053	-0.017	0.356	2.189	-0.050	0.173	-0.008	0.035	0.037
1959	-0.057	0.007	-0.017		3.138	-0.031	-0.074	-0.023	-0.042	0.092
1946	0.024	0.066	0.009		0.604	-0.004	0.031	0.005	-0.083	-0.060
1938	-0.030	-0.057	-0.072	-0.259	2.417	-0.034	-0.298	-0.006	-0.012	-0.082
1931A	-0.012	0.090	0.015	0.098	1.012	-0.086	0.171	0.006	0.084	0.017
1931B	-0.009	0.065	0.018		1.021	-0.085	0.186	0.004	0.057	-0.028
1905	-0.080	-0.051	0.119	-0.198	3.612	-0.064	-0.045	0.006		
1869A	-0.001	-0.074	0.016	-0.258	0.474	-0.067	-0.076	0.024	-0.090	-0.157
1869B	-0.016	-0.002	0.003	-0.015	0.602	-0.079	-0.106	0.035		
1842	0.020	-0.102	0.069	-0.454	3.921	-0.035	0.009	-0.035	-0.005	-0.115
1800	-0.038	-0.074	0.120		1.945	-0.108	-0.397	0.042	-0.069	-0.068
1772	-0.030	-0.057		-0.047	3.758	0.022		-0.099		
1760	-0.094	0.041	-0.027		3.276	-0.197	-0.757	0.128	0.137	-0.198
1734	-0.096	-0.197	-0.029	-0.213	1.633	-0.076	-0.612	0.042	-0.296	-0.109
1717A	0.056	-0.168	0.091	-0.333	5.449	-0.066	-0.860	0.176	-0.159	-0.048
1717B	0.025	-0.065	0.090	-0.141	6.326	-0.065	-0.762	0.172		
1717C	0.007	-0.051		-0.100	6.489	-0.047		0.062		

1 vs. 3	1	1	100,000	100	1	100	100	10,000	10,000	10,000
Year	LW	AHM	Solar	Elev	Resist	Prior	Age	BA	Easting	Northing
1988	0.095	0.020	-0.082	1.932	4.817	-0.066	-0.047	0.016	-0.043	-0.156
1959	-0.021	0.052	-0.039		5.934	-0.107	-0.444	-0.036	-0.025	0.161
1946	0.071	0.084	0.032		0.691	-0.033	0.220	-0.036	-0.137	-0.115
1938	-0.049	-0.120	-0.096	-4.057	6.106	-0.107	-0.393	-0.016	0.029	-0.130
1931A	-0.001	0.045	0.061	-0.722	2.183	-0.150	0.250	-0.055	0.028	-0.089
1931B	-0.003	0.061	0.060		2.180	-0.151	0.240	-0.054	0.046	-0.058
1905	-0.052	-0.058	0.131	-5.186	6.908	-0.159	-0.708	0.018		
1869A	0.010	0.101	0.005	0.405	1.917	-0.163	-0.725	0.042	0.003	0.007
1869B	0.010	0.097	0.004	0.316	1.883	-0.164	-0.730	0.042		
1842	0.034	0.128	0.069	-0.197	9.251	-0.118	-0.155	-0.026	0.306	0.066
1800	-0.055	-0.042	0.173		3.820	-0.257	-0.527	0.033	-0.038	-0.172
1772	-0.035	-0.095		-0.450	7.725	-0.118		-0.104		
1760	-0.067	0.015	-0.103		7.408	-0.401	-1.549	0.263	0.145	-0.363
1734	-0.159	-0.307	-0.091	-6.162	7.163	-0.470	-1.676	0.226	-0.367	-0.321
1717A	0.081	-0.032	-0.048	2.905	11.447	0.010	-0.461	-0.171	-0.072	0.189
1717B	0.064	0.001	-0.045	2.216	12.606	-0.010	-0.329	-0.172		
1717C	0.069	0.016		2.872	12.702	0.008		-0.238		

## **3.5. Discussion**

Drought resistance is higher in trees with ongoing growth release and young trees in general, and higher resistance to drought increases the probability of superior growth resilience. Previous work has shown that exclusion of wildfire from this ecosystem has led to stand densities that exceed historical norms, especially in the understory (Wong & Iverson, 2004). Stand inventory data collected in this study support the conclusion that stands are now largely overstocked, often with extraordinary densities in the understory (Table 3.4, Figure 3.11). This work indicates that besides regulation of the understory and overall stand density, a side-effect of the historical natural disturbance regime of wildfire and bark beetle outbreaks was the alleviation of drought stress in surviving trees.

Limiting the analysis of drought resilience to mature trees (aged >50 years) was intended to avoid confounding the analysis with young trees just initiating within gaps rather than being adjacent to gaps. Age had a negative effect on the probability of higher drought resilience whenever the variable was significant, so the exclusion of trees <50 years old may have suppressed a positive influence of youth on resilience. This study has no bearing on the management of even-aged stands in the region and conclusions about young trees are limited to those growing within uneven-aged stands: only one of the 46 sites considered in this analysis was even-aged (WEX, coring height ca. 1800), and that site contributed very few of the samples in the analysis.



Figure 3.11: Site JKY in 2013, with an average 105m<sup>2</sup>/ha and 12,692 trees per hectare under 15cm. Tree at center dates to 1555; tree behind and to the left dates to 1475, both have charred bark but no open wound.

The mechanism underlying increased drought tolerance in trees adjacent to gaps created by partial disturbances is likely a combination of increased precipitation throughfall supplementing the available moisture in the soil (Bouten *et al.*, 1992; Nadkarni & Sumera, 2004), decreased competition in the rooting zone (Casper & Jackson, 1997), and perhaps increased carbohydrate reserve capacity in faster-growing trees (Waring, 1987). The presence of false rings in some trees, indicating continued growth after a temporary shut-down, is a common pattern in tree rings collected in regions driven by latesummer rains where growth is restarted when moisture becomes available (Griffin *et al.*, 2011). In this context, false rings observed in some samples with ongoing growth release (e.g. Figure 3.3) may have resulted from the reception of moisture later in the season. Latesummer thunderstorms are common in the study area, but the rainfall is often brief and light. It is possible that the effect of these brief summer storms on soil moisture is heavily influenced by canopy interception (Bouten *et al.*, 1992), providing a benefit to trees adjacent to gaps that is unavailable to their interior neighbors.

On average, 14% of trees recorded growth release per decade between 1600–1609 and 1880–1889 (inclusive), varying from 5 to 25% in the presettlement era except for a peak at 38% in 1800–1809. Rates of initiation varied between 5 and 13% per decade after 1600; the drop-off in initiation rates after 1860 is meaningless as older trees were targeted for sampling. This variation in regional growth release and initiation rate is consistent with previous work describing a mixed-severity fire regime with an average 20-year return interval (Daniels & Watson, 2003; Axelson *et al.*, 2010) and periodic mountain pine beetle outbreaks with a 30–40 year return interval (Alfaro *et al.*, 2010). Only one site, WEX in the Chilcotin region, appears to be even-aged with no surviving remnants of the previous

cohort, meeting the definition of a high-severity disturbance used by Heyerdahl *et al.* (2012). Harvey (2017) also reconstructed high-severity disturbances establishing evenaged stands in two of 27 plots in Douglas-fir forests adjacent to grasslands in the Cariboo-Chilcotin, suggesting that these events were a part of the historical ecosystem.

The net effect of a mixed-severity regime is reasonably comparable to the recommendations for management on mule deer winter ranges (Dawson *et al.*, 2007), which constitute the primary management objective in many of the drier managed forests within the study area. These recommendations (Dawson *et al.*, 2007) include a low basal area target in the low-snowpack (drier) areas and intermediate basal area in moderate-snowpack stands. Pole-size trees (12.5–37.5cm) are to be thinned from below. A clumpy distribution of mature trees is encouraged to intercept snow and provide browse through crown abrasion. Some, but not all trees over a certain maximum size are to be retained. The most substantial departure from the historical regime is protection of the youngest regeneration horizon during harvest, as even a light ground fire under historic disturbance regimes would kill a substantial proportion of the regeneration.

A mountain pine beetle outbreak severely affecting much of the Chilcotin region (Erickson, 1992), corroborated by scars and growth releases attributed to beetle mortality by Alfaro *et al.* (2010), offers a partial explanation for the widespread growth release in the 1930–1939 decade. The year 1931 was also known to be dry and prone to wildfire, including human-initiated wildfires (<u>https://catalogue.data.gov.bc.ca/dataset/fire-</u> perimeters-historical accessed 2017). The growth releases in Douglas-fir during the 1930s likely have several causes, including mountain pine beetle and natural wildfires (Alfaro *et al.*, 2010), accidental wildfires may also have played a role.

The effective sample depth at almost all the study sites discussed in Alfaro *et al.* (2010) is exhausted by 1800, but one lodgepole pine series and two Douglas-fir series show growth releases starting ca. 1800 that the authors tentatively attribute to mountain pine beetle. A number of the stands described in the fire history developed by Daniels and Watson (2003) include large cohorts established ca. 1800, but without much evidence of extraordinary fire activity. Several tree ring reconstructions in western Canada for the period 1790-1799 indicate dry conditions, with low streamflow in rivers in Alberta and Saskatchewan to the east (Case & MacDonald, 1995, 2003) and the Chilko River to the west (Hart et al., 2010), increased sand-dune mobilization in southern Saskatchewan (Wolfe et al., 2001), and depressed growth in Douglas-fir in Banff and Jasper National Parks and the trees considered in this study. This prolonged moisture deficit likely predisposed stands to Douglas-fir beetle (Jantz & Rudinsky, 1966), mountain pine beetle (Alfaro et al., 2010), and wildfire (Harvey, 2017; Daniels & Watson 2003), while extreme drought in 1800 may have caused direct mortality in addition to the markedly narrow rings observed in nearly all samples. A combination of all four factors may be responsible for the anomalous peak in growth release in the 1800–1809 decade, but all occurred before the first known European contact in the region (Simon Fraser's 1808 expedition).

This extraordinary growth release event in the beginning of the 19<sup>th</sup> century appears to have had a substantial influence on the long-term growth patterns and stand development in the region. An inflection in average growth rate occurs ca. 1795 in all four established age classes shown in Figure 3.6, and is followed by several decades of similar average growth among the previously distinct groups. A sharp release ca. 1800 and rapid subsequent growth is visually apparent on many cores, and a major shift in diameter

distributions occurred between 1800 and 1840. Though not conclusive, these patterns suggest an event that brought a majority of surviving trees into positions of preeminence within their respective stands. The rapid initial growth of the cohort initiated after 1800 is a further indication of available growing space, further supported by age structure and growth rates described at several nearby sites by Daniels and Watson (2003) and Hawkes *et al.* (2004).

The scale of the series of events starting ca. 1790 and their apparently persistent effects may be applicable to landscape management in the area, as one intense and widespread combination of disturbances shaped forest structure for centuries, establishing the dominance of the large "old veteran" trees that are now considered to be characteristic of old-growth forests in the region. Long-term fire exclusion and its effects on forest composition and structure are not compatible with the mixed-severity disturbance regime identified in this study (see also Harvey, 2017, Heyerdahl *et al.*, 2013, Wong & Iverson, 2004). Preparation of forests for the warmer and effectively drier decades projected under climate change scenarios (Dawson *et al.*, 2008) will require re-establishment of more open-grown forests and a reduction in understory density to enable drought resilience in residual trees.

## **3.6.** Conclusion

Results of this study indicate that adjacency to canopy gaps created by partial disturbance provides significant increases in drought resistance in terms of radial growth, which implies concurrent availability of photosynthate for production of chemicals used to defend against bark beetle attack (Waring, 1987). The historical disturbance regime was such that canopy gaps, inferred by growth release in surviving trees, were more common prior to the exclusion of wildfire ca. 1920 and the subsequent proliferation of a dense understory (Wong & Iverson, 2004). Changes to the moisture regime driven by anthropogenic climate change and development of a dense understory due to wildfire exclusion will likely make hands-off preservation a less viable strategy over time.

Increases in summer temperature are likely to put overstocked stands at a high risk of Douglas-fir beetle attack, which, if severe, would remove many of the older trees from the stand. This would reduce the density of the overstory substantially, but in the absence of low-intensity fire to reduce the density of the lower strata, the result would be a dense young stand. Overstocking is also expected to increase the risk of stand-replacing crown fires as accumulated seedlings and saplings provide a route for flames to reach the main canopy and a fire can then spread easily between closely-packed canopies (Agee & Skinner, 2005). Furthermore, understory seedlings and saplings in multi-storied stands are often heavily utilized by western spruce budworm (Maclauchlan & Brooks, 2009), potentially increasing the pest population affecting older trees.

Application of the silvicultural principles recommended for mule deer winter range (Dawson *et al.*, 2007), particularly the thinning of young trees and basal area targets for larger trees, would provide the kind of structural conditions expected to increase drought

resistance based on the results of this study. Within Community Areas of Special Concern and other areas where harvesting is not a suitable solution, controlled burning could be used to manage understory density and create some canopy gaps, with antiaggregation pheromones used to discourage subsequent utilization of dead or damaged trees by Douglas-fir beetle (Ross & Wallin, 2008). Outside of mule deer winter ranges and special management areas, increased harvest levels in the next planned entry, inspired by the general scale and effect of the disturbances of the 1790s, may help bring production forests smoothly into a warmer and drier 21<sup>st</sup> century.

# 4. Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreak history inferred from tree rings, wood scars and resin pockets in the Cariboo-Chilcotin region of British Columbia

## 4.1. Abstract

Douglas-fir beetle is the primary tree-killing bark beetle attacking mature Douglasfir in central British Columbia, but its contribution to historical stand dynamics is unknown. I used two methods of tree ring analysis to develop a historical timeline of beetle activity. I selected tree-ring data from sites that had low lodgepole pine mortality in the 21<sup>st</sup> century mountain pine beetle outbreak with the goal of creating a chronology of growth release events driven primarily by Douglas-fir beetle. This approach may have been compromised by shifting tree species range margins over the past several centuries. I examined cross-sections of Douglas-fir for scars and resin pockets attributable to failed Douglas-fir beetle attacks, creating a timeline from 1695 to 2014 and providing further evidence for the attribution of these features to Douglas-fir beetle. Abundance of scars and resin pockets was less than would be expected in trees exhibiting growth release due to pheromone mediated mass-attack killing an adjacent competitor, suggesting that Douglasfir beetle has played a secondary role compared to wildfire and mountain pine beetle outbreaks in the stand dynamics of the region. Douglas-fir beetle activity appears to have passed a historical threshold in 2016 and should be monitored for changes in attack patterns.

# 4.2. Introduction

Outbreaks of Douglas-fir beetle in the first decade of the 21<sup>st</sup> century appear to have exceeded the magnitude of previously recorded infestations in central British Columbia, raising concerns about unprecedented attack behavior by this native insect. Douglas-fir beetle is a bark-boring insect that attacks Douglas-fir and western larch in pheromone-mediated mass-attacks that are often fatal to the host tree (Walters, 1956). Walters (1956) estimated that a fully occupied Douglas-fir could contain 11,000 attacking beetles, while Belluschi *et al.* (1965) estimated that up to 3,000 beetles could be rejected by the host's defenses without causing mortality. Eggs are laid beneath the bark and hatch in the same season; the larvae may mature in the same season or overwinter and pupate in the spring (Walters 1956). Maturation time is negatively correlated to temperature (Vité and Rudinsky, 1957), and spring flights are cued by warming temperatures following a cold period (Atkins, 1960). Douglas-fir beetle outbreaks in British Columbia have typically affected trees in clumps or small patches dispersed on the landscape (Erickson, 1992).

Aerial Overview Surveys have identified areas affected by Douglas-fir beetle since 1957, but survey standards changed in 2004 with the addition of Trace (<1% mortality) and Very Severe (>50% mortality) mortality categories. This change in survey standards introduces uncertainty into observations of trends in Douglas-fir beetle impacts. This survey record is also substantially shorter than the lifespan of the host tree species, providing an incomplete picture of the ecology of the host/pest system, which may be driven by stand dynamics or predisposing factors occurring at longer timescales. A longer baseline of Douglas-fir beetle activity, similar to those reconstructed for other bark beetle species using tree ring analysis (Axelson *et al.*, 2010; Sherriff *et al.*, 2011; Hrinkevich &

Lewis, 2011), is desirable to put current events in historical context at timescales more relevant to the long-lived host tree.

Daily, seasonal, annual, decadal, and longer-term climatic trends all have an influence on the physiology of both bark beetles and their host trees, suggesting a cause for changing outbreak behavior as average temperatures in the region have trended upwards over the latter half of the 20<sup>th</sup> century (Dawson *et al.*, 2008). Increased temperatures in spring and summer are expected to accelerate the maturation of Douglas-fir beetle larvae (Vité & Rudinsky, 1957), increasing the proportion of beetles completing development before winter and intensifying the synchronized spring attack in the following year. Increased drought stress resulting from observed and projected increases in temperature (Dawson *et al.*, 2008) and global circulation anomalies leading to prolonged droughts (Mann *et al.*, 2017) are expected to reduce the defensive capacity of the host by increasing water deficit and thereby reducing the pressure of oleoresin that provides the first line of defense against Douglas-fir beetle (Rudinsky, 1966).

While the impacts of Douglas-fir beetle are typically dispersed across the landscape, they are not minor in an economic or ecological sense. Millions of dollars' worth of standing timber has been affected in almost every year since 2000, and unrecovered volume supports extensive recruitment of snags and downed woody debris, providing habitats and resources to animals and understory plants (Hunter, 1990). These impacts are economically and ecologically significant, but relatively dispersed compared to the effects of spruce beetle or mountain pine beetle (Raffa *et al.*, 2008), which have more extensive dendrochronological records (Sheriff *et al.*, 2011; Hrinkevich & Lewis, 2011). I use two methods of dendrochronological reconstruction in this study to account for the typically

dispersed effects of Douglas-fir beetle.

The first method of Douglas-fir beetle outbreak reconstruction follows the wellestablished method of growth-release detection, where synchronous growth releases are attributed to mortality of adjacent trees when some evidence of the insect's presence can be established (Hrinkevich & Lewis, 2011). This approach is limited in this situation by the powerful influences of wildfire and mountain pine beetle on stand dynamics (Alfaro *et al.*, 2004) and the typically patchy nature of Douglas-fir beetle (Negrón *et al.*, 2001). Tree ring series from Chapter 3 are selected from sites that are predominantly Douglas-fir with current and historical evidence of minimal impact from the most recent mountain pine beetle outbreak.

The second line of evidence is the dating of resin pockets and scars left at the location of failed Douglas-fir beetle attacks. Similar scars have been observed in a number of conifer species (Johnson & Shea, 1963; Belluschi *et al.*, 1965), and have been used to support the reconstruction of mountain pine beetle infestations in lodgepole pine in the Chilcotin region of British Columbia (Hawkes *et al.*, 2004), spruce beetle near Hudson Bay, Canada (Caccianiga *et al.*, 2008), and red oak borer (*Enaphalodes rufulus*) in Missouri, USA (Muzika & Guyette, 2004). Resin pockets found in Douglas-fir have been attributed to Douglas-fir beetle since at least 1965, when Belluschi *et al.* (1965) marked the location of each entry wound in a number of attacked trees and waited several years before felling the trees and examining the wood at the attacked locations. They found both resin pockets and scars at the site of the observed attacks, and dated earlier scars to the year of a known spot outbreak in an adjacent patch.

Douglas-fir beetle is only one disturbance agent among many others that individually,

or in combination have shaped the study area over time. Historical wildfires (reconstructed by Daniels & Watson, 2003; Hawkes *et al.*, 2004; Axelson *et al.*, 2010; Harvey, 2017), droughts (reconstructed by Case & MacDonald, 1995; Cook & Krusic, 2004; Wolfe *et al.*, 2001; Case & Macdonald, 2003; Hart *et al.*, 2010), and mountain pine beetle outbreaks (reconstructed by Alfaro *et al.*, 2010 with early surveys summarized by Erickson, 1992), are all potentially involved in the stand dynamics of the old-growth interior Douglas-fir forests under study. The interpretation of both growth release and scar/resin pocket frequency data to address the following research questions must be considered in the context of other disturbances potentially affecting the sampled stands.

- Can the evidence of Douglas-fir beetle attacks account for observed patterns of growth release, especially the widespread growth release described in Chapter
   3 following the regional drought at the beginning of the 19th century?
- 2. Did historical Douglas-fir beetle outbreaks tend to follow periods of drought, or precede periods of growth release?
- 3. Did historical Douglas-fir beetle outbreaks typically affect sites across the region?

# 4.3. Methods

#### 4.3.1. Field and Lab Methods

Local foresters provided locations of Douglas-fir beetle salvage logging operations that they knew to be inactive and accessible. Sites were visited to confirm the presence of cull piles (piled ends of logs that were removed prior to hauling due to undesirable features that would affect processing into wood products) that had not yet been burnt and that were large enough to provide 25 sample trees, without being so large as to pose a safety risk. Six sites that were a minimum of 4 km apart were selected (Figure 4.1).

Cutoffs from the lower end of the first log were abundant at all selected sites, so sampling was focused entirely on sections with evidence that they had come from the bottom section of the tree (i.e. falling cuts or paint) to maintain consistency throughout the sample. Twenty-five cull sections were identified for sampling and two cross sections 5– 10cm thick were recovered from each: one at approximately the breast height of the tree or the highest point available on shorter samples, and the other just above the falling cut or lowest section. Nearly all sampled trees had visible evidence of successful bark beetle galleries and a few contained live beetles.



Figure 4.1: Sampled cull pile locations for Douglas-fir beetle outbreak reconstruction overlaid by a combination of Federal Forest Insect and Disease Survey and Provincial Aerial Overview Survey records of beetle-caused mortality identified by insect surveys from 1957–2013, Provincial helicopter-based mortality surveys from 2007–2014, and forest stands dominated by Douglas-fir. "Trace" severity (<1% mortality) not shown on map to reduce clutter. Five ringwidth chronologies labeled with three-letter codes.

Figure 4.2: Top: sampled cull pile at site H; photograph corrected for underexposure and white balance in Microsoft Office. Bottom: Cross sections collected at site K. Each site filled a midsize pickup truck.

Cross sections were flattened with a power plane to remove gouges from the chainsaw teeth prior to sanding then were sanded using a progression of grits to120 at which point scars and resin pockets could be reliably identified. Further polishing to 600 grit was focused on the locations around identified scars to avoid the time and expense of sanding the entire cookie. 1200 and 2000 grit wet/dry automotive polishing sandpapers were used when the location of the scar within the annual ring was not easily discernable. Cross sections were sanded on each side as resin pockets at the site of Douglas-fir beetle attacks have been demonstrated to be less than 2cm in length in some cases (Belluschi *et al.*, 1965).

Each section was visually crossdated using marker years known from Chapter 3 and the year of death was identified to ensure each cross section came from a recently killed tree. Growth rings with scars or resin pockets were traced to the dated path, and the calendar year of each scar was recorded. Position within the ring was classified into early earlywood (first 33% of earlywood), mid earlywood (second 33%), late earlywood (third 33%), and latewood. Distance to pith was measured to the nearest millimeter using a ruler. Each scar was classified as either a pocket (open, filled with resin) or a true scar (closed, not filled with resin). Scars appear to be formed where the cambium is interrupted by the failed gallery, while resin pockets are found above and below failed galleries and where attacking beetles were rejected before establishing a gallery (Belluschi *et al.*, 1965; Figure 4.7).

Resin pockets bear resemblance to the phenolic lesions formed in conifers inoculated with blue stain fungi associated with bark beetles (diagrammed in Wong *et al.*, 1977). Douglas-fir beetle also carries pathogenic blue stain fungi and the phenolic lesion response

is probably common among related species, but no studies of lesion formation following inoculation could be found in the published literature. With other host species, there is rapid expansion of lesions in the second week following inoculation (Raffa & Smalley, 1988). The formation of necrotic lesions (resin pockets) is a common adaptive response in conifers that occurs in advance of the hyphae of the blue stain fungus (Berryman, 1972). The formation of a necrotic lesion follows both simple wounding and inoculation with blue stain fungi, but the development is faster in the inoculated wounds (Wong *et al.*, 1977).

Further lines of evidence suggesting Douglas-fir beetle as the agent responsible for the scars and resin pockets include observations of brood galleries in the phloem with adjacent scars in the xylem, and alignment of the scar dates with dates of recorded red and green attack in adjacent stands (Figure 4.3 and Figure 4.4). Beetles or parts of beetles were also found and many samples contained partially healed scars in the year preceding death, in some cases with identifiable frass (Figure 4.5). Scars were distinguished from resin pockets by the presence of an open wound subsequently healed over (Figure 4.6).

Every cross section with one or more scars or resin pockets was scanned at 1200 DPI and ring width measurement was performed in the program Windendro (Regent Instruments 2014). Visual crossdating was confirmed using the program COFECHA (Holmes, 1983). Previously crossdated samples from nearby sites were used to corroborate the assignment of calendar years in samples where too few trees were present within the site to build a master chronology. Measurement paths were initiated from the estimated location of pith on trees left hollow by rot so as to provide an estimate of the basal area at particular dates. Ringwidth measurements around rotten sections were allowed to deviate from the master series used for crossdating in order to provide the best possible estimate of

the size of the tree at a particular date despite the rot obscuring the rings.



Figure 4.3: Partially healed injury in the year prior to death of tree D09, photographed before (top) and after (bottom) sanding of the bark to reveal resin saturation of the apparent gallery. Photographs cropped but not manipulated with regards to color or contrast.



Figure 4.4: Injury to tree D09 in the year prior to being killed by DFB. Photograph cropped but not manipulated with regards to color or contrast. White arrows mark the bounds of the apparent gallery in the bark.



Figure 4.5: Progression of scar formation: A: Scar with extensive traumatic resin duct formation (top triangle); apparent resin-filled entry tunnel (middle triangle), and frass (bottom triangle) from a tree at Esler Canyon (an early reconnaissance site not large enough to fully sample). B: Deceased Douglas-fir beetle in current-year gallery, area impregnated with resin, tree D10. C: 2013 scar with apparent gallery tree M23; 2014 ring beginning to close over wound. D: 1990 scar, mirrored in the bark tree K20.



Figure 4.6: A typical scar in the process of formation (A), a typical resin pocket (B), and an empty beetle exoskeleton stuck in a current-year gallery adjacent to a 2010 resin pocket (C and D). The key distinction between a scar and a pocket is that the scar is healing over an open wound (e.g. the arrow at A) while the wood has simply grown around the resin pocket without interruption (e.g. the arrow at B).



Figure 4.7: Mountain pine beetle (black arrow) arrested within the bark of lodgepole pine by defensive resins. A resin pocket would be identified in a cross-section above this point while a scar would be found at the level of the failed gallery. Underexposure of original image corrected in GIMP 2.0.



Figure 4.8: Six of eight scars in tree M23 in 2013; note the relative widths of the scar and the resin-impregnated area in the phloem, the heavy production of resin ducts radiating from all scars in 2013 (circled in E) and 2014 especially in C, and the discoloration of the sapwood especially in A and F. Measurements of B were made on the opposite side of the cookie; pencil slash is a reminder to not count the same scar twice.

## 4.3.2. Selection of ringwidth chronologies for growth release reconstruction

I subsampled the dataset previously used in Chapter 3 by selecting sites with minimal mortality attributed to mountain pine beetle in the 21<sup>st</sup> century outbreak. A 500-meter radius buffer (78.54 ha) was generated around the locations of all sites using ArcGIS. Aerial overview survey records for mountain pine beetle from the years 2001 to 2013 were merged into a pair of individual layers. The site buffer layer and merged aerial overview surveys were overlaid using the intersect tool in ArcMap Desktop 10.2, resulting in a dataset retaining all the records of severity within each buffered area.

British Columbia standards for aerial overview surveys were used to assign mortality coefficients to the severity codes, such that Trace = 1%, Light = 10%, Moderate = 29%, Severe = 40% and Very Severe = 60% mortality of Douglas-fir

(https://www.for.gov.bc.ca/hts/risc/pubs/teveg/foresthealth/assets/aerial.pdf accessed

2017). These mortality coefficients were multiplied by the area affected within the buffer, and extended to the tree level by multiplying by a hypothetical 100 potentially susceptible trees per hectare (coefficient\*area\*100 trees/ha). A pivot table was generated to calculate the sum of the total affected trees at the site level. The process was repeated for Douglas-fir beetle outbreak surveys over the same period for the increment core sites from Chapter 3 and the six sites sampled for this chapter.

Estimates of annual tree mortality attributed to Douglas-fir beetle were made by assessing overview survey data from 1957 to 2013 based on severity codes and area affected. Responsibility for comprehensive forest health surveys passed from the federal government to the provincial government in 1999 following a brief period without data in some regions of British Columbia. The provincial Aerial Overview Survey added two new

severity classes in 2004: "trace" indicating 1% or less current mortality and very severe indicating >50% current mortality. The addition of the "trace" category can exaggerate change over time as far more area is recorded under attack compared to older surveys. The same severity coefficients as above were multiplied by the total area of each polygon, and raw count data from helicopter-based surveys were added where available (https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/ accessed 2017).

## 4.3.3. Analysis: growth releases

Ring width data for the selected sites were exported to the R package TRADER (Altman *et al.*, 2014) for identification of growth releases, and a release event was defined as a year in which the 20-year average basal area increment following the subject year exceeded the 20-year average preceding the subject year by at least 50% (adapted from Nowacki & Abrams, 1997). The selection and validation of these parameters is described in Chapter 3. I used two metrics of growth release: initiation of growth release events, defined as the year in which the maximum increase in growth rate occurred, and ongoing release, defined as years in which the rate of increase was >50%. The latter metric is less conservative as it may include years prior to the actual event due to the length of the periods considered before and after each subject year, the rapid initial growth in young trees, and ongoing growth increase many years after the event that opened the growing space. The value of the metric is that it quantifies the duration of the period where growth was increasing. The same growth release metrics calculated for the increment core data were computed from the ring width series measured from the cross sections.

## 4.3.4. Analysis: scars and resin pockets

Using cross-sections collected from cull piles at the six harvested sites, only scars and resin pockets more than 6.35cm from the pith were considered for analysis. This radius corresponds to the minimum diameter considered in Douglas-fir beetle risk assessment (Hood *et al.*, 2007) and earlier studies of host-finding behavior (Rudinsky, 1966). While smaller trees may be attacked, the 12.7cm diameter (6.35cm radius) was used to avoid counting scars created by other, normally secondary bark beetle species that favor saplings (Walters & McMullen, 1956; McMullen & Atkins, 1962). Every effort was made to avoid counting small sealed fire scars as Douglas-fir beetle scars, and several dozen scars that bore some resemblance to those described by Smith *et al.* (2016) were discarded from the final analysis. Sealed fire scars may be formed by heat damage to the cambium that does not cause an open wound, and I considered a scar to be suspect and discarded it if I found an abundance of traumatic resin ducts after the year of the scar, a misshapen appearance unlike the examples photographed here, or saturation of the wood beneath the scar with resin (Smith *et al.*, 2016).

Sampling for scars and resin pockets is expected to be most effective in cases where the subject tree is showing a growth response to the death of a competitor in a pheromonemediated mass attack: a tree that is close enough to show a growth response to the death of its competitor will fall within the zone of attraction created by the female beetle as she processes the resins of the host tree. Johnson & Pettinger (1961) calculated the average density of Douglas-fir beetle attacks within a radius of an attractive source (a windthrown or felled tree), and found all trees within 1.2 meters of the source were attacked, at an average rate of 33.3 attacks per square meter. At a range of 1.5–4.5 meters not all trees

were attacked, but the rate of attack among all trees averaged 5.6 attacks per square meter.

At a minimum diameter of 12.7cm and a thickness of 6cm, the smallest samples considered in this study have a bark surface area of 239.3cm<sup>2</sup>, accounting for 479.7cm<sup>2</sup> with two samples from each tree. If the average rate of attack is 5.6 per square meter, there will be one attack per 0.178m<sup>2</sup>, or 1,780cm<sup>2</sup>, while a rate of 33.3 attacks per square meter corresponds to one per 300 cm<sup>2</sup>. At these rates of attack, one sampled tree in four should record an attack if it was within 1.5–4.5 meters of an attractive source, and evidence of attack should be left in every tree within 1.2 meters. Extrapolating that rate of attack to a range of diameters, any tree 48cm diameter, represented by two cross-sections each 6cm thick, would be expected to reliably record evidence of that attack (Figure 4.9).



Figure 4.9: Rate of attack expected within the surface area represented by cross-sections of various diameters based on the rates described by Johnson & Pettinger (1961) at a distance of 0–1.2m and 1.5–4.5m from the sampled tree, assuming cookie thickness of 6cm and two samples per tree.

The rate of attack in smaller trees within the 1.5–4.5m radius of an attractive tree suggests that multiple trees would be required to record the event, though the odds are >50% in trees over 24cm diameter. This estimate serves as a minimum, as other work has found that logs with virgin female beetles attract many times more beetles than freshly cut logs without females (maximum 105 (fresh-cut log) vs. 3,259 (log with virgin females); Jantz & Rudinsky, 1966). In a pheromone-mediated mass attack (vs. the windthrown trees studied by Johnson & Pettinger (1961)) that attracted ten times more beetles, a higher rate of attack would be expected in adjacent trees, and these would be more likely to preserve scars or resin pockets. Trees in the immediate vicinity of a windthrown individual are likely to record the event if they are >24cm diameter, while trees close enough to record growth release due to the death of a competitor in a mass-attack organized by pheromone cues will almost certainly contain scars or resin pockets.

I produced a simple timeline at the site level of the total number of scars and resin pockets per year. I also aggregated all six sites by dividing the number of scars or resin pockets by the number of trees >12.7cm diameter in each year to account for changing sample depth over time. Three methods of aggregating data among the six sites were used to compare against previously published records of wildfire, drought, and mountain pine beetle: years where multiple scars or resin pockets were found within a single tree, years in which ten or more scars or resin pockets were found in the complete dataset, and years in which three or more sites each had one or more scars or resin pockets.

# 4.4. Results

Surveys conducted by the Canadian Forest Insect and Disease Survey and British Columbian Aerial Overview Survey and detailed helicopter surveys suggest periods of

Douglas-fir beetle infestation from 1961–1969, 1983–1985, 1989–1996, and 2000–2016 (Figure 4.10). Within the latter period, 2000–2009 and 2014–2016 are most likely distinct events due to the reduction in mortality from 2010–2013. Mortality estimated from the 2016 survey is markedly higher than any preceding year, or the cumulative total of any of the periods outlined in the 20<sup>th</sup> century. Estimated mortality in the "severe" class constituted a small portion of the total in most years in the 21<sup>st</sup> century, while this class was predominant in most years in the 20<sup>th</sup> century.

Every site recorded some level of mountain pine beetle activity, while fixed-wing aircraft surveys identified Douglas-fir beetle mortality at 30 sites and detailed helicopter surveys found patches killed in the vicinity of an additional nine sites (Table 4.2). Five sites with the lowest recorded mountain pine beetle activity (BLU, EPI, GAR, SUG, WIL) were selected for further analysis.

Mountain pine beetle accounted for more mortality than Douglas-fir beetle around all the locations sampled specifically for this study, though site P had very low mountain pine beetle activity compared to the others (Table 4.3).



Figure 4.10: Estimated number of trees killed by Douglas-fir beetle recorded by aerial surveys since 1957. "Trace," "Light," "Moderate," "Severe," and "Very Severe" are codes used in fixed-wing aerial surveys; "AoS Spot" refers to spot attacks identified in the fixed-wing aerial survey, and "Helicopter" accounts for all trees tallied in helicopter-based surveys (helicopter data 2007-2013).

Table 4.1: Estimated mortality within 500m buffer around increment core sites from 2001 to 2013. DFB = Douglas-fir beetle; MPB = mountain pine beetle. "% Total" columns indicate the estimated percentage of the total number of hypothetical trees (n = 7,854) affected. Rows highlighted in gray indicate the sites selected for further analysis.

$\begin{array}{c cccc} \hline Code & (m) & Fixed & Heli & DFB & MPB & Total & Total \\ \hline ABR 1,133 & 0 & 0 & 0 & 2465 & 0.0\% & 31.4\% \\ \hline ACS 1,024 & 597 & 20 & 617 & 9838 & 7.9\% & 125.3\% \\ \hline ALE & 959 & 1330 & 62 & 1392 & 5542 & 17.7\% & 70.6\% \\ \hline ALK & 954 & 9 & 109 & 118 & 1723 & 1.5\% & 21.9\% \\ \hline BCA & 935 & 0 & 10 & 10 & 860 & 0.1\% & 10.9\% \\ \hline BIG 1,261 & 73 & 12 & 85 & 1208 & 1.1\% & 15.4\% \\ \hline BLU & 871 & 25 & 25 & 50 & 432 & 0.6\% & 5.5\% \\ \hline CAL & 1,248 & 809 & 0 & 809 & 8088 & 10.3\% & 103.0\% \\ \hline CAM & 1,087 & 769 & 0 & 769 & 2397 & 9.8\% & 30.5\% \\ \hline CHI & 906 & 94 & 62 & 156 & 1780 & 2.0\% & 22.7\% \\ \hline CTI & 818 & 0 & 0 & 0 & 10403 & 0.0\% & 132.5\% \\ \hline DCB & 947 & 394 & 155 & 549 & 783 & 7.0\% & 10.0\% \\ \hline DCG & 1,136 & 149 & 13 & 162 & 1156 & 2.1\% & 14.7\% \\ \hline ENT & 910 & 161 & 88 & 249 & 2991 & 3.2\% & 38.1\% \\ \hline FUZ & 1,068 & 0 & 24 & 24 & 1371 & 0.3\% & 17.5\% \\ \hline FUZ & 1,068 & 0 & 24 & 24 & 1371 & 0.3\% & 17.5\% \\ \hline GAR & 1,239 & 0 & 52 & 52 & 113 & 0.7\% & 1.4\% \\ \hline HAN & 1,329 & 2 & 0 & 2 & 5172 & 0.0\% & 65.8\% \\ \hline HAN & 1,329 & 32937 & 3366 & 2468 & 42.9\% & 31.4\% \\ \hline HAN & 1,306 & 981 & 16 & 997 & 1917 & 12.7\% & 24.4\% \\ KCR & 831 & 1706 & 29 & 1735 & 3557 & 22.1\% & 45.3\% \\ I EE & 1,031 & 3329 & 37 & 3366 & 2468 & 42.9\% & 31.4\% \\ I EN & 1,268 & 432 & 75 & 507 & 5790 & 6.5\% & 73.7\% \\ \hline MAB & 945 & 2797 & 133 & 2930 & 1305 & 37.3\% & 16.6\% \\ MAQ & 931 & 0 & 0 & 0 & 4887 & 0.0\% & 62.2\% \\ MCL & 679 & 0 & 19 & 19 & 2242 & 0.2\% & 28.5\% \\ MEL & 939 & 0 & 3 & 3 & 5843 & 0.0\% & 74.4\% \\ MON & 1,127 & 0 & 0 & 0 & 4487 & 0.0\% & 62.2\% \\ MCI & 679 & 0 & 19 & 19 & 2242 & 0.2\% & 28.5\% \\ MEL & 939 & 0 & 3 & 3 & 5843 & 0.0\% & 74.4\% \\ MON & 1,127 & 0 & 0 & 0 & 0 & 4887 & 0.0\% & 62.2\% \\ MCI & 679 & 0 & 19 & 19 & 2242 & 0.2\% & 28.5\% \\ MEL & 939 & 0 & 3 & 3 & 5843 & 0.0\% & 74.4\% \\ MON & 1,127 & 0 & 0 & 0 & 0 & 2900 & 0.0\% & 36.9\% \\ NOJ & 1,016 & 0 & 0 & 0 & 2900 & 0.0\% & 37.9\% \\ NRA & 970 & 0 & 31 & 311 & 3323 & 0.0\% & 74.4\% \\ MON & 1,127 & 0 & 0 & 0 & 0 & 106 & 0.0\% & 71.4\% \\ NEK & 1,013 & 589 & 75 & 664 & 4152 & 8.4\% & 62.9\% \\ WH & 857 & 42 & 54 & 96 & 4$		Elevation	DFB	DFB	Total	Total	DFB %	MPB %
ABR         1,133         0         0         0         2465         0.0%         31.4%           ACS         1,024         597         20         617         9838         7.9%         125.3%           ALE         959         1330         62         1392         5542         17.7%         70.6%           ALK         954         9         109         118         1723         1.5%         21.9%           BCA         935         0         10         10         860         0.1%         10.9%           BIU         871         25         50         432         0.6%         5.5%           CAL         1,248         809         0         809         8088         10.3%         103.0%           CAM         1,087         769         0         769         2397         9.8%         30.5%           CHI         906         94         62         156         1780         2.0%         22.7%           DCB         947         394         155         549         783         7.0%         10.0%           DCH         1,262         442         89         531         120         6.8%	Code	(m)	Fixed	Heli	DFB	MPB	Total	Total
ACS $1,024$ $597$ $20$ $617$ $9838$ $7.9\%$ $125.3\%$ ALE $959$ $1330$ $62$ $1392$ $5542$ $17.7\%$ $70.6\%$ ALK $945$ $9$ $100$ $118$ $1723$ $1.5\%$ $21.9\%$ BCA $935$ $0$ $10$ $10$ $860$ $0.1\%$ $10.9\%$ BIG $1,261$ $73$ $12$ $85$ $1208$ $1.1\%$ $15.4\%$ BLU $871$ $25$ $55$ $432$ $0.6\%$ $5.5\%$ CAL $1,248$ $809$ $0$ $809$ $8088$ $10.3\%$ $103.0\%$ CAM $1,087$ $769$ $0$ $769$ $2397$ $9.8\%$ $30.5\%$ CHI $906$ $94$ $62$ $156$ $1780$ $2.0\%$ $22.7\%$ CTI $818$ $0$ $0$ $010403$ $0.0\%$ $132.5\%$ DCB $947$ $394$ $155$ $549$ $783$ $7.0\%$ $10.0\%$ DOG $1,136$ $149$ $13$ $162$ $1156$ $2.1\%$ $14.7\%$ ENT $910$ $161$ $88$ $249$ $2991$ $3.2\%$ $38.1\%$ FUZ $1,068$ $0$ $24$ $24$ $1371$ $0.3\%$ $17.5\%$ GAR $1,239$ $0$ $2$ $5172$ $0.0\%$ $65.8\%$ HAW $1,306$ $9$ $4$ $13$ $8430$ $0.2\%$ $107.3\%$ JKY $1,136$ $981$ $16$ $997$ $1917$ $12.7\%$ $45.3\%$ <t< td=""><td>ABR</td><td>1,133</td><td>0</td><td>0</td><td>0</td><td>2465</td><td>0.0%</td><td>31.4%</td></t<>	ABR	1,133	0	0	0	2465	0.0%	31.4%
ALE9591330621392554217.7%70.6%ALK954910911817231.5%21.9%BCA935010108600.1%10.9%BIG1,26173128512081.1%15.4%BLU8712525504320.6%5.5%CAL1,2488090809808810.3%103.0%CAM1,087769076923979.8%30.5%CHI906946215617802.0%22.7%CTI818000104030.0%132.5%DCB9473941555497837.0%10.0%DOG1,1361491316211562.1%14.7%ENT9101618824929913.2%38.1%EPI1,262442895311206.8%1.5%FUZ1,0680242413710.3%17.5%GAR1,239052521130.7%1.4%HAN1,32920251720.0%65.8%HAW1,306941384300.2%107.3%JKY1,13698116997191712.7%24.4%KCR8311706291735355722.1%45.3%<	ACS	1,024	597	20	617	9838	7.9%	125.3%
ALK954910911817231.5%21.9%BCA935010108600.1%10.9%BIG1,26173128512081.1%15.4%BLU8712525504320.6%5.5%CAL1,2488090809808810.3%103.0%CAM1,087769076923979.8%30.5%CHI906946215617802.0%22.7%CTI818000104030.0%132.5%DCB9473941555497837.0%10.0%DOG1,1361491316211562.1%14.7%ENT9101618824929913.2%38.1%GAR1,239052521130.7%1.4%HAN1,32920251720.0%65.8%HAW1,306941384300.2%107.3%JKY1,13698116997191712.7%24.4%KCR8311706291735355722.1%45.3%LEE1,0313329373366246842.9%31.4%LEN1,2684327550757906.5%73.7%MAB94527971332930130537.3%<	ALE	959	1330	62	1392	5542	17.7%	70.6%
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	ALK	954	9	109	118	1723	1.5%	21.9%
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	BCA	935	0	10	10	860	0.1%	10.9%
BLU $871$ $25$ $25$ $50$ $432$ $0.6\%$ $5.5\%$ CAL         1,248 $809$ 0 $809$ $8088$ $10.3\%$ $103.0\%$ CAM $1,087$ $769$ 0 $769$ $2397$ $9.8\%$ $30.5\%$ CHI $906$ $94$ $62$ $156$ $1780$ $2.0\%$ $22.7\%$ CTI $818$ 0         0 $0$ $10403$ $0.0\%$ $132.5\%$ DCB $947$ $394$ $155$ $549$ $783$ $7.0\%$ $10.0\%$ DOG $1,136$ $149$ $13$ $162$ $1120$ $6.8\%$ $1.5\%$ FUZ $1,068$ $24$ $24$ $13711$ $0.3\%$ $17.5\%$ GAR $1,239$ $0$ $2$ $5172$ $0.0\%$ $65.8\%$ HAW $1,306$ $9$ $4$ $13$ $8430$ $0.2\%$ $1735$ JKY $1,136$ <	BIG	1,261	73	12	85	1208	1.1%	15.4%
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	BLU	871	25	25	50	432	0.6%	5.5%
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CAL	1,248	809	0	809	8088	10.3%	103.0%
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CAM	1,087	769	0	769	2397	9.8%	30.5%
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	CHI	906	94	62	156	1780	2.0%	22.7%
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	CTI	818	0	0	0	10403	0.0%	132.5%
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	DCB	947	394	155	549	783	7.0%	10.0%
ENT910161882492991 $3.2\%$ $38.1\%$ EPI $1,262$ 44289531120 $6.8\%$ $1.5\%$ FUZ $1,068$ 024241371 $0.3\%$ $17.5\%$ GAR $1,239$ 05252113 $0.7\%$ $1.4\%$ HAN $1,329$ 202 $5172$ $0.0\%$ $65.8\%$ HAW $1,306$ 9413 $8430$ $0.2\%$ $107.3\%$ JKY $1,136$ 981169971917 $12.7\%$ $24.4\%$ KCR831 $1706$ 29 $1735$ $3557$ $22.1\%$ $45.3\%$ LEE $1,031$ $3329$ 37 $3366$ $2468$ $42.9\%$ $31.4\%$ LEN $1,268$ $432$ 75 $507$ $5790$ $6.5\%$ $73.7\%$ MAB945 $2797$ $133$ $2930$ $1305$ $37.3\%$ $16.6\%$ MAQ931000 $4887$ $0.0\%$ $62.2\%$ MAY $1,127$ 4 $18$ $22$ $2289$ $0.3\%$ $29.1\%$ MCL $679$ 01919 $2242$ $0.2\%$ $28.5\%$ MEL93903 $3$ $5843$ $0.0\%$ $57.1\%$ NEE $1,070$ 00 $0$ $2900$ $0.0\%$ $36.9\%$ NOJ $1,016$ 000 $3379$ $0.0\%$ $43.0\%$ PTI $1,005$ 0 $36$ $36$ <t< td=""><td>DOG</td><td>1,136</td><td>149</td><td>13</td><td>162</td><td>1156</td><td>2.1%</td><td>14.7%</td></t<>	DOG	1,136	149	13	162	1156	2.1%	14.7%
EPI $1,262$ $442$ $89$ $531$ $120$ $6.8\%$ $1.5\%$ FUZ $1,068$ 0 $24$ $24$ $1371$ $0.3\%$ $17.5\%$ GAR $1,239$ 0 $52$ $52$ $113$ $0.7\%$ $1.4\%$ HAN $1,329$ 202 $5172$ $0.0\%$ $65.8\%$ HAW $1,306$ 94 $13$ $8430$ $0.2\%$ $107.3\%$ JKY $1,136$ $981$ $16$ $997$ $1917$ $12.7\%$ $24.4\%$ KCR $831$ $1706$ $29$ $1735$ $3557$ $22.1\%$ $45.3\%$ LEE $1,031$ $3329$ $37$ $3366$ $2468$ $42.9\%$ $31.4\%$ LEN $1,268$ $432$ $75$ $507$ $5790$ $6.5\%$ $73.7\%$ MAB $945$ $2797$ $133$ $2930$ $1305$ $37.3\%$ $16.6\%$ MAQ $931$ 000 $4887$ $0.0\%$ $62.2\%$ MAY $1,127$ 4 $18$ $22$ $2289$ $0.3\%$ $29.1\%$ MCL $679$ 0 $19$ $19$ $2242$ $0.2\%$ $22\%$ MON $1,127$ 000 $4485$ $0.0\%$ $57.1\%$ NEE $1,070$ 00 $0$ $3379$ $0.0\%$ $42.3\%$ PTI $1,005$ 0 $36$ $36$ $4782$ $0.5\%$ $60.9\%$ NOJ $1,016$ 000 $7106$ $0.5\%$ $69.\%$ NRA <t< td=""><td>ENT</td><td>910</td><td>161</td><td>88</td><td>249</td><td>2991</td><td>3.2%</td><td>38.1%</td></t<>	ENT	910	161	88	249	2991	3.2%	38.1%
FUZ1,0680242413710.3%17.5%GAR1,239052521130.7%1.4%HAN1,32920251720.0%65.8%HAW1,306941384300.2%107.3%JKY1,13698116997191712.7%24.4%KCR8311706291735355722.1%45.3%LEE1,0313329373366246842.9%31.4%LEN1,2684327550757906.5%73.7%MAB94527971332930130537.3%16.6%MAQ93100048870.0%62.2%MAY1,1274182222890.3%29.1%MCL6790191922420.2%28.5%MEL93903358430.0%77.1%NEE1,0700029000.0%36.9%NOJ1,0160033790.0%43.0%NRA9700313133230.4%42.3%PTI1,0050363647820.5%60.9%PUD96706631360.1%39.9%PVA7864033201423487253.9%11.1%PYP1,	EPI	1.262	442	89	531	120	6.8%	1.5%
GAR1,239052521130.7%1.4%HAN1,32920251720.0%65.8%HAW1,306941384300.2%107.3%JKY1,13698116997191712.7%24.4%KCR8311706291735355722.1%45.3%LEE1,0313329373366246842.9%31.4%LEN1,2684327550757906.5%73.7%MAB94527971332930130537.3%16.6%MAQ93100048870.0%62.2%MAY1,1274182222890.3%29.1%MCL6790191922420.2%28.5%MEL93903358430.0%77.1%NEE1,0700044850.0%36.9%NOJ1,0160033790.0%43.0%NRA9700313133230.4%42.3%PTI1,0050363647820.5%60.9%PUD96706631360.1%39.9%PVA7864033201423487253.9%11.1%PYP1,10700071060.0%90.5%REN988<	FUZ	1.068	0	24	24	1371	0.3%	17.5%
HAN         1,329         2         0         2         5172         0.0%         65.8%           HAW         1,306         9         4         13         8430         0.2%         107.3%           JKY         1,136         981         16         997         1917         12.7%         24.4%           KCR         831         1706         29         1735         3557         22.1%         45.3%           LEE         1,031         3329         37         3366         2468         42.9%         31.4%           LEN         1,268         432         75         507         5790         6.5%         73.7%           MAB         945         2797         133         2930         1305         37.3%         16.6%           MAQ         931         0         0         0         4887         0.0%         62.2%           MAY         1,127         4         18         22         2289         0.3%         29.1%           MCL         679         0         19         19         2242         0.2%         28.5%           MEL         939         0         3         35843         0.0%	GAR	1.239	0	52	52	113	0.7%	1.4%
HAW         1,306         9         4         13         8430         0.2%         107.3%           JKY         1,136         981         16         997         1917         12.7%         24.4%           KCR         831         1706         29         1735         3557         22.1%         45.3%           LEE         1,031         3329         37         3366         2468         42.9%         31.4%           LEN         1,268         432         75         507         5790         6.5%         73.7%           MAB         945         2797         133         2930         1305         37.3%         16.6%           MAQ         931         0         0         0         4887         0.0%         62.2%           MAY         1,127         4         18         22         2289         0.3%         29.1%           MCL         679         0         19         19         2242         0.2%         28.5%           MEL         939         0         3         3         5843         0.0%         71.4%           NOI         1,016         0         0         3379         0.0%	HAN	1.329	2	0	2	5172	0.0%	65.8%
JKY         1,136         981         16         997         1917         12,7%         24,4%           KCR         831         1706         29         1735         3557         22,1%         45,3%           LEE         1,031         3329         37         3366         2468         42,9%         31,4%           LEN         1,268         432         75         507         5790         6.5%         73,7%           MAB         945         2797         133         2930         1305         37,3%         16.6%           MAQ         931         0         0         0         4887         0.0%         62,2%           MAY         1,127         4         18         22         2289         0.3%         29,1%           MCL         679         0         19         19         2242         0.2%         28,5%           MEL         939         0         3         3         5843         0.0%         74,4%           MON         1,127         0         0         0         3379         0.0%         36,9%           NOJ         1,016         0         0         3323         0.4%         <	HAW	1.306	9	4	13	8430	0.2%	107.3%
KCR         831         1706         29         1735         3557         22.1%         45.3%           LEE         1,031         3329         37         3366         2468         42.9%         31.4%           LEN         1,268         432         75         507         5790         6.5%         73.7%           MAB         945         2797         133         2930         1305         37.3%         16.6%           MAQ         931         0         0         0         4887         0.0%         62.2%           MAY         1,127         4         18         22         2289         0.3%         29.1%           MCL         679         0         19         19         242         0.2%         28.5%           MEL         939         0         3         3         5843         0.0%         74.4%           MON         1,127         0         0         0         2900         0.0%         36.9%           NOJ         1,016         0         0         3379         0.0%         43.0%           PTI         1,005         0         36         36         4782         0.5%         60	JKY	1,136	981	16	997	1917	12.7%	24.4%
LEE       1,031       3329       37       3366       2468       42.9%       31.4%         LEN       1,268       432       75       507       5790       6.5%       73.7%         MAB       945       2797       133       2930       1305       37.3%       16.6%         MAQ       931       0       0       0       4887       0.0%       62.2%         MAY       1,127       4       18       22       2289       0.3%       29.1%         MCL       679       0       19       19       2242       0.2%       28.5%         MEL       939       0       3       3       5843       0.0%       74.4%         MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%<	KCR	831	1706	29	1735	3557	22.1%	45.3%
LEN         1,268         432         75         507         5790         6.5%         73.7%           MAB         945         2797         133         2930         1305         37.3%         16.6%           MAQ         931         0         0         4887         0.0%         62.2%           MAY         1,127         4         18         22         2289         0.3%         29.1%           MCL         679         0         19         19         2242         0.2%         28.5%           MEL         939         0         3         3         5843         0.0%         74.4%           MON         1,127         0         0         0         4485         0.0%         57.1%           NEE         1,070         0         0         0         2900         0.0%         36.9%           NOJ         1,016         0         0         3379         0.0%         43.0%           NRA         970         0         31         31         3323         0.4%         42.3%           PTI         1,005         0         36         36         4782         0.5%         60.9%	LEE	1.031	3329	37	3366	2468	42.9%	31.4%
MAB         945         2797         133         2930         1305         37.3%         16.6%           MAQ         931         0         0         0         4887         0.0%         62.2%           MAY         1,127         4         18         22         2289         0.3%         29.1%           MCL         679         0         19         19         2242         0.2%         28.5%           MEL         939         0         3         3         5843         0.0%         74.4%           MON         1,127         0         0         0         4485         0.0%         57.1%           NEE         1,070         0         0         0         2900         0.0%         36.9%           NOJ         1,016         0         0         0         3379         0.0%         43.0%           PTI         1,005         0         36         36         4782         0.5%         60.9%           PUD         967         0         6         6         3136         0.1%         39.9%           PVA         786         4033         201         4234         872         53.9%         <	LEN	1 268	432	75	507	5790	6.5%	73 7%
MAQ       931       0       0       0       4887       0.0%       62.2%         MAY       1,127       4       18       22       2289       0.3%       29.1%         MCL       679       0       19       19       2242       0.2%       28.5%         MEL       939       0       3       3       5843       0.0%       74.4%         MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0% <td< td=""><td>MAB</td><td>945</td><td>2797</td><td>133</td><td>2930</td><td>1305</td><td>37.3%</td><td>16.6%</td></td<>	MAB	945	2797	133	2930	1305	37.3%	16.6%
MAY       1,127       4       18       22       2289       0.3%       29.1%         MCL       679       0       19       19       2242       0.2%       28.5%         MEL       939       0       3       3       5843       0.0%       74.4%         MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%	MAO	931	0	0	0	4887	0.0%	62.2%
MCL       679       0       19       19       2242       0.2%       28.5%         MEL       939       0       3       3       5843       0.0%       74.4%         MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2% <td>MAY</td> <td>1 127</td> <td>4</td> <td>18</td> <td>22</td> <td>2289</td> <td>0.3%</td> <td>29.1%</td>	MAY	1 127	4	18	22	2289	0.3%	29.1%
MEL       939       0       3       3       5843       0.0%       74.4%         MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%<	MCL	679	0	19	19	2242	0.2%	28.5%
MON       1,127       0       0       0       4485       0.0%       57.1%         NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3	MEL	939	Ő	3	3	5843	0.0%	74 4%
NEE       1,070       0       0       0       2900       0.0%       36.9%         NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11	MON	1 127	Ő	0	0	4485	0.0%	57.1%
NOJ       1,016       0       0       0       3379       0.0%       43.0%         NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         WA       839       0       5       5       5380       0.1%<	NEE	1 070	Ő	Ő	Ő	2900	0.0%	36.9%
NRA       970       0       31       31       3323       0.4%       42.3%         PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152 <td< td=""><td>NOJ</td><td>1 016</td><td>Ő</td><td>Ő</td><td>0 0</td><td>3379</td><td>0.0%</td><td>43.0%</td></td<>	NOJ	1 016	Ő	Ő	0 0	3379	0.0%	43.0%
PTI       1,005       0       36       36       4782       0.5%       60.9%         PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682 <t< td=""><td>NRA</td><td>970</td><td>Ő</td><td>31</td><td>31</td><td>3323</td><td>0.4%</td><td>42.3%</td></t<>	NRA	970	Ő	31	31	3323	0.4%	42.3%
PUD       967       0       6       6       3136       0.1%       39.9%         PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524 <t< td=""><td>PTI</td><td>1 005</td><td>Ő</td><td>36</td><td>36</td><td>4782</td><td>0.5%</td><td>60.9%</td></t<>	PTI	1 005	Ő	36	36	4782	0.5%	60.9%
PVA       786       4033       201       4234       872       53.9%       11.1%         PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151		967	Ő	6	6	3136	0.1%	39.9%
PYP       1,107       0       0       0       7106       0.0%       90.5%         REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	PVA	786	4033	201	4234	872	53.9%	11.1%
REN       988       1422       127       1549       2717       19.7%       34.6%         RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	РҮР	1 107	0	0	0	7106	0.0%	90.5%
RES       953       347       141       488       5398       6.2%       68.7%         RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	REN	988	1422	127	1549	2717	19.7%	34.6%
RIS       1,259       13       23       36       1927       0.5%       24.5%         SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	RES	953	347	141	488	5398	6.2%	68.7%
SOA       645       0       20       20       1305       0.3%       16.6%         SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	RIS	1 259	13	23	36	1927	0.5%	24 5%
SUG       658       901       32       933       30       11.9%       0.4%         TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	SOA	645	0	20	20	1305	0.3%	16.6%
TWA       839       0       5       5       5380       0.1%       68.5%         WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	SUG	658	901	32	933	30	11.9%	0.4%
WEX       1,013       589       75       664       4152       8.4%       52.9%         WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	TWA	839	0	5	5	5380	0.1%	68 5%
WHI       857       42       54       96       4682       1.2%       59.6%         WIL       677       53       181       234       524       3.0%       6.7%         YUN       996       32       16       48       2151       0.6%       27.4%	WFX	1 013	589	75	664	4152	8 4%	52 9%
WIL         677         53         181         234         524         3.0%         6.7%           YUN         996         32         16         48         2151         0.6%         27.4%	WHI	857	42	, <i>5</i> 54	96	4682	1.2%	59.6%
YUN         996         32         16         48         2151         0.6%         27.4%	WII	677	53	181	234	524	3.0%	6.7%
	YUN	996	32	16	48	2151	0.6%	27.4%
Table 4.2: Summary tabulations of the preceding table: estimated mortality within the 500m buffer around increment core sites from 2001 to 2013. DFB = Douglas-fir beetle; MPB = mountain pine beetle. "% Total" columns indicate the estimated percentage of the total number of hypothetical trees (n = 7,854) affected.

	Elevation (m)	DFB Fixed	DFB Heli	Total DFB	Total MPB	DFB % Total	MPB % Total
Count		30	36	39	46		
Average	1,005	468	44	512	3335	7%	42%
% Total		6.0%	0.6%	6.5%	42.5%		
min	645	0	0	0	30	0.0%	0.4%
max	1,329	4033	201	4234	10403	53.9%	132.5%

Table 4.3: Estimated mortality of trees within the 500m buffer around cookie collection sites. DFB = Douglas-fir beetle; MPB = mountain pine beetle. "% Total" columns indicate the estimated percentage of the total number of hypothetical trees (n = 7,854) affected.

Sita Cada	Elevation	DFB Eived	DFB	Total	Total	DFB %	MPB %
Sile Code	(111)	Fixed	пеп	ЛГР	MIPD	Total	Total
D	1,303	71	25	96	1799	1.2%	22.9%
Н	1,328	0	19	19	6935	0.2%	88.3%
K	967	72	16	88	2674	1.1%	34.0%
М	1,000	831	39	870	3345	11.1%	42.6%
Р	897	63	41	104	311	1.3%	4.0%
W	1,252	0	119	119	1370	1.5%	17.4%
Count		4	6	6	6		
Average	1,125	173	43	216	2739		
% Total		2.2%	0.5%	2.8%	34.9%		
min	897	0	16	19	311	0.2%	4.0%
max	1,328	831	119	870	6935	11.1%	88.3%

The first growth release at site BLU was identified in 1760, during the initiation phase of the population under study, at a time when 100% of trees were accelerating their growth rate (Figure 4.11). Initiation of a growth release was identified in one tree in 1777, one in 1801 and three in 1809, at a time when 75% of trees were in accelerated growth phases. Two trees initiated growth release in 1847 and 1859, while less than 20% of trees were growing faster. Several trees initiated growth release between 1870 and 1910, while 30% of trees were accelerating their growth rate. Growth releases were identified in one tree in a number of years from 1924–1945, and the proportion of trees continuing to increase in growth rate increased over that period. Site BLU was known to have been harvested in the 1960s, and a number of the trees record a growth release at that time.



Figure 4.11: Initiation of growth release and ongoing acceleration of growth in Douglas-fir at site BLU. "Light," "Medium," and "Severe" refer to 50, 100, and 200% rate of increase.

Growth release at site EPI occurred sporadically in no more than one tree per year from 1736 to 1796, except 1786 when two trees recorded release (Figure 4.12). Despite the continued initiation of new trees, only a small fraction experienced an accelerated growth rate prior to 1790. A total of 88% of trees had accelerated growth rates from 1800–1805, and nine of the sixteen trees present at the time recorded a growth release in that period, and an additional four had recorded a release by 1911. A general increase in growth occurred from 1840–1860, and eight trees recorded growth release during that time. Growth rates again accelerated in the 1930s, peaking at 55% of established trees in 1938 and 1939, while 12 of the 20 trees established by that time recorded growth release between 1936 and 1941.



Figure 4.12: Initiation of growth release and ongoing acceleration of growth in Douglas-fir at site EPI. "Light," "Medium," and "Severe" refer to 50, 100, and 200% rate of increase.

Initiation of trees at site GAR was relatively abrupt, beginning around 1600 and completed by 1706 (Figure 4.13). Peaks in growth release and increasing growth rates occurred ca. 1650 and 1690 during this period of initiation. Every tree sampled at this site had accelerated growth from 1809–1811, while 18 of 20 trees recorded growth release between 1800 and 1810 and an additional tree recorded a release in 1812. Ongoing growth acceleration was found only in a small proportion of trees following this event, while two trees recorded initiation of growth release in 1844, 1861, 1867, 1874, and 1876.



Figure 4.13: Initiation of growth release and ongoing acceleration of growth in Douglas-fir at site GAR. "Light," "Medium," and "Severe" refer to 50, 100, and 200% rate of increase.

Site SUG records several periods of increasing growth corresponding to events meeting criteria defining initiation of growth release, beginning ca. 1660, 1680, 1740, 1770, 1800, 1880, 1900, 1940, and 1980 (Figure 4.14). The proportion of trees recording accelerated growth during these events generally decreased with time, as did the number of trees recording initiations.



Figure 4.14: Initiation of growth release and ongoing acceleration of growth in Douglas-fir at site SUG. "Light," "Medium," and "Severe" refer to 50, 100, and 200% rate of increase.

Periods of growth release while stand initiation was ongoing at site WIL occurred beginning around 1675 and 1740, while growth increase affecting more than 50% of the trees at the site occurred ca. 1770 and 1810 after all sampled trees were established (Figure 4.15). Growth acceleration in a fraction of the trees at this site was ongoing from 1840 through 1900, and a number of trees recorded the initiation of growth release during that period. Only a few trees recorded growth release or accelerating growth during the 20<sup>th</sup> century.



Figure 4.15: Initiation of growth release and ongoing acceleration of growth in Douglas-fir at site WIL. "Light," "Medium," and "Severe" refer to 50, 100, and 200% rate of increase.

The first resin pocket at site D was dated in 1718, followed by two in 1746 and one in 1747 (Figure 4.16). Increased frequency of resin pockets was observed in the early 20<sup>th</sup> century, and scar frequency peaked in 1931. Resin pockets were relatively frequent in the 1967–1974 and again in 1987–1992. Some scarring and resin pockets dated to the first decade of the 21<sup>st</sup> century, and many scars were found in 2013 and 2014 before the stand was salvage-logged. Growth releases were recorded throughout the period where new trees were reaching sampling height, with peaks in 1760, 1800–1812, 1860, the 1930s/early 1940s, and the late 1970s/early 1980s.



Figure 4.16: Scars, resin pockets, and growth releases identified in cross sections at Site D. Total count of scars (red) labeled where the bar exceeds the standard Y axis.

Site H recorded the first resin pocket in 1716, but did not record a year with more than one scar or resin pocket until 1909 (Figure 4.17). Six scars and one resin pocket were found in 1920, and one scar in 1921. Four resin pockets were found in 1976. One pocket and four scars were counted in 1999, three scars in 2004, and two in 2010. The final years of the series included 11 scars and one pocket in 2013 and one scar in the process of healing in 2014. Growth releases peaked after 1800, in the 1890s, and the 1930s/early 1940s.



Figure 4.17: Scars, resin pockets, and growth releases identified in cross sections at Site H. Total count of scars (red) labeled where the bar exceeds the standard Y axis.

The first resin pocket at site K was recorded in 1732 (Figure 4.18). Three scars were counted in 1797, two scars and two resin pockets in 1798, two resin pockets in 1799, and six in 1801. Peaks during the 19<sup>th</sup> century ocurred in 1818, 1824, 1827/1828, 1839, 1841, 1843, 1849/1850, 1868, 1873/1874, 1884, and 1898. Three resin pockets were tallied in 1935, 1947, and 1952, two in 1964, five in 1965, six resin pockets plus one scar in 1969, and two scars and one resin pocket in 1971. A peak in scarring occurred in 1990 with a total of 15, followed by five resin pockets in 1991 and five again in 1997. Six scars and one pocket in 2009, followed by 11 scars in 2013 and four scars and one pocket in 2014 before the stand was harvested. Releases peaked in the 1740s, around 1810, and in the 1930s/early 1940s.



Figure 4.18: Scars, resin pockets, and growth releases identified in cross sections at Site K. Total count of scars (red) labeled where the bar exceeds the standard Y axis.

Site M stands out for recording a large number of scars in 1770, two years after the first scar and resin pocket were recorded at the site in 1768 (Figure 4.19). Two resin pockets were recorded in 1836, and one scar and one resin pocket were found in 1854; throughout the rest of the 19<sup>th</sup> century no more than one scar or resin pocket was counted in any single year. Four resin pockets were counted in 1969, two in 1972, and one each in 1971/1973. Scarring in the early 1990s peaked with 22 scars in 1993. Sporadic activity persisted until 2013, when 26 scars were recorded, and 2014, which contained five scars. Growth releases peaked in the 1770s, following 1800, the 1930s/1940s, and around 1980.



Figure 4.19: Scars, resin pockets, and growth releases identified in cross sections at Site M. Total count of scars (red) labeled where the bar exceeds the standard Y axis.

The first scar at site P was counted in 1706 and the second in 1760; two resin pockets and three scars were found in 1794 followed by one scar in 1795 (Figure 4.20). Four scars were tallied in 1802, followed by one each in 1803, 1804, and 1806. Eight scars were located in 1866. Five pockets were found in 1919, four in 1938 and three in 1941. Scars or resin pockets were found in almost every year from 1966–1988, with peaks in 1967, 1975, 1980, 1986, and 1988. Later peaks in frequency occurred 1992–1994 and 2001/2002, but only a few scars and resin pockets were found in the final years of the series. Growth releases were frequent around 1860, the early 20<sup>th</sup> century, and in the 1930s.



Figure 4.20: Scars, resin pockets, and growth releases identified in cross sections at Site P

Site W contains the earliest recorded resin pockets: a pair in 1695 (Figure 4.21). An additional four were tallied in 1750 and 16 scars were found in 1800. The most resin pockets were found in 1992 and these 12 were followed by several years in which one scar or resin pocket was identified. Five scars were dated to 2010, but only two in 2013 and none in 2014. Eight growth releases were identified following 1800, another five around 1860, and 16 between 1920 and 1940.



Figure 4.21: Scars, resin pockets, and growth releases identified in cross sections at Site W. Total count of scars (red) and resin pockets (black) labeled where the bar exceeds the standard Y axis.

Peaks in scar and resin pocket frequency across the six sites combined occurred in the 1740s, 1794–1804, the 1820s and 1880s, 1909–1914, the1920s, and 1964–1977 (Figure 4.22). Scars and resin pockets were frequent from the 1980s through 2010, with peaks in 1988–1994 and again in the stands' final years.



Figure 4.22: Scars and resin pockets at all sites displayed as a ratio to the total number of Douglas-fir >12.7cm diameter, and the percentage of Douglas-fir (of any diameter) with ongoing growth release. Ratio labeled for 2013 where bar exceeded the Y axis.

Periods of increased growth release across the six sites occurred 1720–1760, 1770– 1780, 1800–1820, 1840–1880, and 1920–1940, and particularly high rates of growth release occurred in 1749, 1760, 1772, 1800, 1859/1860, and 1938 (Figure 4.23). The total percentage of the sample initiating growth release within a moving 11-year window reflects the percentage of trees increasing their rate of growth, though slightly fewer trees are meeting the release initiation criteria at any given time.



Figure 4.23: Sampled Douglas-fir trees recording initiation of growth release (above 0% line) and ongoing release (below 0% line) as a percentage of total sample size in each year, displayed by site, with 11-year running total of initiations (total percentage, subject year plus preceding and following five-year periods).

Multiple scars or resin pockets were recorded within a single tree in a given year 114 times between 1695 and 2014 (Figure 4.24).



Figure 4.24: Years where one or more trees recorded multiple scars or resin pockets within a single year. Gray dashed line indicates the proportion accounted for by a single tree.

All drought metrics (Cook & Krusic, 2004; Case & Macdonald, 2003; Daniels & Watson, 2003; Hart *et al.*, 2010) indicate that the last decade of the 18<sup>th</sup> century was drier than average (Figure 4.25), consistent with what has previously been regarded as a prolonged regional drought (Wolfe *et al.*, 2001). Multiple fire scars in Douglas-fir were dated by Daniels & Watson (2003) to 1791, 1797, and 1800, and one scar was dated to 1802 (the two fire chronologies constructed from lodgepole pine do not extend to this period). Evidence of Douglas-fir beetle presence from 1790 through 1802 includes several years with multiple scars or resin pockets within a given year, one year with 10 or more scars or resin pockets (1800), and one year in which three or more sites recorded one or more scars or resin pockets (1794; Figure 4.25). An increased frequency of years with multiple growth releases began at the turn of the 19<sup>th</sup> century and continued over the next two decades.

Multiple sources indicate dry conditions in the study area from the mid–1830s through the late 1840s; three or more sites recorded scars or resin pockets in four of the years within that period and multiple scars within the same tree were found in four of these years (Figure 4.25). Multiple Douglas-fir fire scars were found in three years, and two years had one fire scar (Daniels & Watson, 2003). Hawkes *et al.* (2004) found fire scars in ten or more lodgepole pine during one year within this period, and Axelson *et al.* (2010) recorded fire scars in two of their three lodgepole pine sites. Growth release was recorded in four or more trees during two years within this period, and two or three trees showed growth release in two other years.

Dry conditions in the 1920–1940 period are indicated by all precipitation reconstructions, though the pJJ reconstructions presented by Daniels & Watson (2003)

suggest a longer period of low precipitation beginning in the late 1890s (Figure 4.25). Cook & Krusic's (2004) PDSI reconstruction point 30 indicates several years of negative PDSI in the 1890s and late in the decade of 1900, but does not support a continuous period of drought. Erickson (1992) records a widespread outbreak of mountain pine beetle in the Chilcotin region from 1930–1935, also described by Alfaro *et al.* (2010) on the basis of scars left by failed attacks and growth releases in surviving trees. Growth releases occurred frequently in the 1930s, and 10 or more fire scars were found in 1922 and 1926 (Hawkes *et al.*, 2004). Evidence for Douglas-fir beetle presence in this period includes three or more sites with at least one scar or resin pocket in 1920, 1921, 1923, 1926, 1931, 1935, 1937, and 1938, and multiple scars or resin pockets were found within a single tree in 1919, 1920, 1921, 1923, 1924, 1931, 1935, 1936, 1937, and 1938.

No consistency is found among the reconstructions of drought after 1950 (Figure 4.25), and the frequency of scars attributed to wildfire drops precipitously over the course of the 20<sup>th</sup> century as human settlements expanded and wildfire fighting became more effective (Daniels & Watson, 2003). A severe outbreak of mountain pine beetle was surveyed in the late 1970s and 1980s (Erickson, 1992) and was described by both growth release and scars in lodgepole pine (Alfaro *et al.*, 2010). Scars or resin pockets in Douglas-fir identified in this study were found at multiple sites in the majority of years in the latter half of the 20<sup>th</sup> century, while the number of years with 10 or more scars is more limited. Aerial surveys suggest that Douglas-fir beetle mortality peaked in 1966, a year when three or more sites were affected. Multiple scars or resin pockets were found within one tree in 1967, and every year from 1969 through 1974.

The surveyed Douglas-fir beetle mortality in the late 1980s and early 1990s

coincides with a number of scars and resin pockets, including multiple scars and resin pockets within a single tree in every year from 1983 through 1994 (except 1989), and 10 or more scars or resin pockets in 1986, 1987, 1988, 1990, 1992, and 1993. Three or more sites were affected in every year from 1983 through 1993 except from 1986 and 1989. Lower streamflow in the Chilko River was reconstructed from 1979 through 1988 (Hart *et al.*, 2010), and 1988 and 1989 are two of the driest years in the instrumental record (Chapter 2). Mountain pine beetle populations were rising at the time, but did not reach epidemic levels until the 21<sup>st</sup> century (Shore *et al.*, 2004).



Figure 4.25: Mountain pine beetle, wildfire, and drought histories inferred from tree ring analysis and annual insect surveys compared to scars attributed to Douglas-fir beetle attack. "Growth Release" is coded gray when two or three trees and black for four or more trees were recording growth release in a given year. "DFB Mortality Estimate" (see Figure 4.10) is coded gray when >5,000 and black when >50,000 trees were estimated to have been killed. Cook & Krusic's (2004) PDSI reconstructions are coded gray when between 0 and -0.5, and black when below -0.5. Daniels & Watson JJA = reconstructed June, July and August precipitation total at their site near Williams Lake; Daniels & Watson pJJ = reconstructed previous-July through current-June precipitation total at their site near Williams Lake. All records under the "Drought" heading except Cook's PDSI reconstruction highlight only prolonged periods of low precipitation reconstruction values. Daniels & Watson 2003 fire records coded gray when only one tree at one site recorded a fire and black when two or more trees were affected at a single site or trees at two or more sites were affected. Harvey 2017 indicates years in which >25% of trees at the Churn Creek Protected Area study site recorded a wildfire. Hawkes *et al.* 2004 coded black if 10 or more trees recorded a fire scar. Axelson *et al.* 2010 coded black if two or more sites recorded a fire and gray if fire scars were found at only one site. Erickson 1992 coded gray for localized infestations affecting <10,000 trees and black for larger infestations. Alfaro *et al.* 2010 coded black if two or more scars were attributed to beetle attacks in that year.

## 4.5. Discussion

This study corroborates previous work by Belluschi *et al.* (1965) attributing the scars and resin pockets found in cross-sections of Douglas-fir to failed attacks by the Douglas-fir beetle. In several cases intact or partial Douglas-fir beetles were found within galleries sealed off by defensive resins and there were many examples of apparently failed massattack in years where local beetle populations are known to have been high. The longevity of interior Douglas-fir allowed the development of a chronology of failed attacks into the 18<sup>th</sup> century (not counting the pair of resin pockets dated to 1695), exceeding a similar record established for mountain pine beetle using scars in lodgepole pine in the region (Hawkes *et al.*, 2004) and on par with a chronology of resin pockets attributed to spruce beetle in white spruce near Hudson Bay, Canada (Caccianiga *et al.*, 2008).

The prolonged regional drought at the end of the 18<sup>th</sup> century has previously been established as a critical moment in the history of stands across this million-hectare study area due to widespread growth release implying mortality of competitors between 1790 and 1800 (Chapter 3). Evidence for the regional presence of Douglas-fir beetle populations during this period is strong, though the frequency of scars and resin pockets is substantially less than the frequency of trees experiencing growth release at the beginning of the 19<sup>th</sup> century. Growth release in a survivor implies proximity to a tree that has died. In the case of trees killed by beetles, the survivor would be within the zone of attraction generated by beetle pheromones, suggesting that the survivor should also show signs of unsuccessful attacks. The difference between number of unsuccessfully attacked trees and number of trees experiencing growth release suggests another cause of mortality was driving the

widespread growth release in the early 1800s. This logic extends throughout the period under study, where growth releases affecting substantial fractions of trees at a majority of sites do not correspond to any peaks in scar or resin pocket frequency. The long-term perspective provided by this work suggests that Douglas-fir beetle is more responsive to, than responsible for, the mortality patterns affecting the interior Douglas-fir forest type at landscape scales in central British Columbia.

The frequency of years with multiple scars or resin pockets on a single tree appears to have been increasing over the past century, as does the number of years where three or more sites were affected. There are several explanations for this phenomenon which may interact additively or synergistically. First, there has been an increase in temperature over the past 50 years with a statistically significant trend (Dawson *et al.*, 2008), which may affect the development time of the beetle. An increase of two degrees Celsius, depending on the starting temperature, may allow the beetle to progress from egg to flight-ready adult a week to a month faster (Vité & Rudinsky, 1957). The observed increase in average temperature has been of this magnitude from 1950–2001, with Quesnel Airport increasing at a rate of  $0.34^{\circ}$ C and Tatlayoko Lake increasing at  $0.22^{\circ}$ C per decade, implying a  $1.1-1.7^{\circ}$ C increase over the latter half of the  $20^{\text{th}}$  century.

The second explanation is a demographic wave in the host population, resulting from disturbances that more or less synchronized the development of stands across this landscape, causing a large proportion of forested areas to become vulnerable over the past several decades. A synchronous growth release evident in the 1930s has been attributed to the widespread mountain pine beetle outbreak affecting the region at the time and to a number of natural and accidental wildfires (Alfaro *et al.*, 2010). A disturbance or series of

disturbances at the end of the 18<sup>th</sup> century had a similar effect on tree growth (Chapter 3), and all six sites show a growth response following both of these periods. Ingrowth and crown expansion would have filled many of the gaps created by the 1930s disturbances by the latter half of the 20<sup>th</sup> century, and most mature survivors would have been of a vulnerable size after decades or centuries of free growth. In the sampled stands, very few trees recorded growth release after 1950. The ready supply of mature trees facing heavy competition from below (Wong & Iverson, 2004) would facilitate the steady growth of endemic Douglas-fir beetle populations, which had outbreaks in the late 1980s and early 1990s, mid to late 2000s, and from 2013 to present.

Finally, the transition from a fire-driven disturbance regime to a mountain pine beetledriven disturbance regime described by Axelson *et al.* (2010) in lodgepole pine forests in the Chilcotin region may also be occurring in the region's Douglas-fir forests. Fire frequencies are known to have declined since the early 1900s throughout the region (Daniels & Watson, 2003, Harvey, 2017), and inter-tree competition has increased as a result (Wong & Iverson, 2004). An abundance of mature trees that might otherwise have died in natural wildfires may be fueling increased Douglas-fir beetle outbreak intensity in the same way that mountain pine beetle has been facilitated by abundant mature and overmature host stands.

The sites studied were selected for their lack of mountain pine beetle infestation in the current outbreak due to the lack of available lodgepole pine in the stands. Elimination of other disturbance agents as the origin of the growth release, leaving only mountain pine beetle, suggests that disturbance may have fundamentally altered the species composition of low-elevation stands. Stands in the Chilcotin and Fraser River valleys are presently

dominated by the Interior Douglas-fir very dry-mild ecosystem subzone, which typically has very little lodgepole pine except on glaciofluvial terraces (Steen & Coupé, 1997). Lower temperatures during the Little Ice Age (Bradley & Jonest, 1993) could have permitted the Interior Douglas-fir dry-cool ecosystem subzone (Steen & Coupé, 1997) to extend further downslope. This subzone commonly includes lodgepole pine and was heavily impacted by the mountain pine beetle outbreaks of the 1930s, 1970s, and 2000s (Alfaro *et al.*, 2010; Figure 1.5). An outbreak coming at a time of climatic change may have led to a regeneration failure in lodgepole pine at low elevations, allowing the current Douglas-fir dominated stand structure to become established.

Average summer temperatures in North America and the Northern Hemisphere in general are estimated to have been 0.5-1.5 °C cooler during the  $16^{th}$  and  $17^{th}$  centuries compared to the 1860–1959 baseline (Bradley & Jonest, 1993). Temperatures rose to this baseline between 1760 and 1800 (Bradley & Jonest, 1993), coincident with the widespread growth release of Douglas-fir. Tree species range expansions have been documented at alpine treelines in North America, Europe, and Asia following recovery from local Little Ice Age temperature depressions correlating to the rise in temperature (Lescop-sinclair & Payette, 1995; Bogaert *et al.*, 2010; Kharuk *et al.*, 2010), coincident with growth accelerations in trees within Little Ice Age treelines. Ecosystem change in the valleys of the Chilcotin and Fraser Rivers may parallel these alpine dynamics, though only fine-resolution sediment core analysis could confirm the species shift (e.g. Morris *et al.*, 2017).

### 4.6. Conclusion

The long-term historical baseline of Douglas-fir beetle activity established in this study is consistent with Walters (1956), Johnson & Belluschi (1969), and McGregor (1975), who identified DFB outbreaks following droughts, windthrow, and other predisposing events but not driving mortality or stand dynamics with the same regularity or magnitude as mountain pine beetle or wildfire. There is no evidence in these data that any historical outbreak exceeded the magnitude of the 21<sup>st</sup> century outbreaks. This permits the use of 2000–2015 aerial survey data as a baseline for comparison of 2016 data, which were all collected using consistent survey methods. The magnitude of mortality estimated from 2016 survey data exceeds that of any other year in the 21<sup>st</sup> century by a wide margin, and suggests that the Douglas-fir beetle population is higher than it has been at any point in recent history. Projections of continued regional warming (Dawson et al., 2008), increased stagnation of weather systems due to atmospheric circulation anomalies (Mann et al., 2017), and accumulation of Douglas-fir regeneration providing competition from below (Wong & Iverson, 2004) suggest that outbreaks of DFB in the future may exceed historical limits due to changes in stand structure and climate

# 5. Reconsidering western spruce budworm outbreak history inferred from the annual growth of host and non-host tree species in central British Columbia

### 5.1. Abstract

Western spruce budworm is a common pest of Douglas-fir in western North America, and its historical influence in southern British Columbia is well documented. Outbreak history at the northernmost extent of its present range in British Columbia is less clear. The discrepancy among studies describing outbreak history may stem from the dendrochronological approach used, where the mean ringwidth index of a population of non-host ponderosa pine is subtracted from the ringwidth index of individual host Douglas-fir to compensate for the influence of regional climate. These methods are applied to a collection of Douglas-fir ringwidth chronologies from 45 sites distributed throughout and beyond the range of the recent 800,000-hectare outbreak, using a ponderosa pine chronology from an adjacent region. Periods of relatively low growth in Douglas-fir are identified matching those previously identified as outbreaks, but with a synchrony and spatial distribution that suggests abiotic mechanisms. The growth differential of Douglasfir relative to ponderosa pine that could be interpreted as widespread outbreaks in the 20<sup>th</sup> century and before may be due to differences in precipitation between regions favoring the ponderosa pine population.

## **5.2. Introduction**

Western spruce budworm (WSB; Choristoneura freemani = C. occidentalis) is a defoliating insect native to western North America, where periodic outbreaks affect populations of Douglas-fir (*Pseudotsuga menziesii*), true firs (*Abies spp.*), western larch (Larix occidentalis) and white spruce (Picea glauca) at landscape scales (Nealis, 2016). Adult western spruce budworm moths emerge in July and August and disperse after depositing a portion of their eggs on needles remaining at their original site (Nealis, 2016). They then fly to seek new host material before laying the remainder of their eggs on needles at the new site. The eggs are laid and hatch in the same year. Attraction of the freshly-hatched larvae to light leads to overcrowding on the branch tips where the eggs were laid, causing many larvae to disperse on silken threads (Wellington & Henson, 1947). This dispersal may cause larvae to fall to lower branches or lower canopy horizons, or the larvae may be carried by wind above the canopy to new locations (Wellington & Henson, 1947). When the larvae reach an appropriately rough surface after their initial dispersal, they spin hibernaculae, moult, and overwinter (Nealis, 2016). Emerging second-instar larvae disperse again, moving to branch tips and potentially falling to lower levels or being dispersed on silken threads during windy conditions (Wellington & Henson, 1947). After this second dispersal, the larvae feed by mining into old needles or the swelling buds (Nealis, 2016).

Outbreaks of WSB are driven by temperature trends that promote synchronous budburst (accumulation of degree days after a certain day length) and larval emergence (degree days without regard to day length) (Thomson *et al.*, 1984; Thomson & Benton, 2007). The larvae must emerge early enough to enter the buds as they begin to swell, thus

accessing the foliage while it is still succulent and lacking chemical defenses, without being too early, which could expose the larvae to cold temperatures and starvation (Nealis, 2016). The ideal timing of WSB larval emergence in southern British Columbia has been calculated at 18 days prior to budburst (Thomson *et al.*, 1984). The range of WSB is expected to expand to higher elevations and latitudes under a warmer climate scenario as this temperature shift favors optimal phenological synchrony between larval emergence and budburst in these areas (Marciniak, 2015). A widespread outbreak at the northernmost known extent of the species range in central British Columbia may represent an example of substantial range expansion in the 21<sup>st</sup> century. This region is known as the Cariboo-Chilcotin (alternatively the Cariboo forest district) and is located in the Interior Plateau of British Columbia (Figure 5.3).

Western spruce budworm outbreaks are common throughout southern British Columbia in the 20<sup>th</sup> century, affecting Douglas-fir forests most extensively but also impacting true first, larch, and spruce (Maclauchlan *et al.*, 2006). Severe outbreaks extended to approximately 51° North in the vicinity of Lillooet during the 20<sup>th</sup> century (Erickson, 1987). North of Lillooet, the Cariboo-Chilcotin region has had no recorded infestations except for several patches of defoliation recorded in 1975 near Riske Creek and in 1987 near Quesnel Lake (Erickson, 1992; Figure 5.3). This northern region is ecologically distinct from interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests in southern British Columbia and the Rocky Mountains in the United States. Ponderosa pine (*Pinus ponderosa*) is absent while lodgepole pine (*Pinus contorta*) is abundant, and outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) are especially common and severe (Alfaro *et al.*, 2010).

Ponderosa pine is the typical associate of Douglas-fir on dry aspects in Rocky Mountain forests in Idaho and adjacent British Columbia, while pure ponderosa pine commonly occupies a belt between mixed Douglas-fir/ponderosa pine forests and grasslands where the retention of winter snowpack is insufficient for the survival of Douglas-fir seedlings (Daubenmire & Daubenmire, 1968). Only a small population of ponderosa pine is found in the Cariboo-Chilcotin, in the lowest elevation areas in the Fraser River valley at the southern limit of the study area (Figure 5.1).

Lodgepole pine in the Cariboo-Chilcotin region is less drought resistant than Douglasfir (Brix, 1979). Douglas-fir is found in pure or nearly pure stands in the dry valley bottoms and slopes adjacent to grasslands, while lodgepole pine becomes more abundant with elevation and becomes the dominant species in the uplands, where it is often mixed with spruce. Lodgepole pine in the Cariboo-Chilcotin has one of the most extensive records of mountain pine beetle infestation in the province (Alfaro *et al.*, 2010) and the influence of these outbreaks on the growth of Douglas-fir is substantial where the two species co-occur (Hawkes *et al.*, 2004). Mature lodgepole pine was almost completely eliminated from mixed stands by the mountain pine beetle outbreak of the 2000s, and had previously experienced widespread mortality in the outbreaks of the 1980s and 1930s (Erickson, 1992).



Figure 5.1: Present range of ponderosa pine, lodgepole pine, and Douglas-fir in southern portion of the study area and adjacent regions, overlaid by Chasm Provincial Park and the regional centers of Lillooet and Kamloops. BC VRI data used under Open Government License 2.0.

The extent of the 800,000-hectare WSB outbreak in the Cariboo-Chilcotin region (2001-2015) is without precedent in the written record, but the outbreak was highly variable spatially and temporally. At many locations along the northern and western edges of the outbreak, defoliation was limited to dry valleys and slopes despite an abundance of available host in upland areas. Unfavorable climatic factors may explain the apparent lack of defoliation, for example insufficient degree days for maturation or poor phenological synchrony between budburst and larval emergence preventing feeding. While upland Douglas-fir stands may presently be climatically suboptimal for WSB, they are projected to be at higher risk of infestation by the 2020s (Murdock *et al.*, 2013).

Knowledge of historical outbreak patterns can be used to determine risk of expansion of insect infestations into novel areas due to climate change, forest management practices or other influences on forest and insect dynamics (Ryerson *et al.*, 2003; Flower *et al.*, 2014). Tree growth is affected by defoliation (Alfaro *et al.*, 1982), therefore tree ring analysis can be used to develop long term outbreak chronologies that go beyond the limited extent of historical survey records. Swetnam *et al.* (1985) developed an outbreak reconstruction method for WSB that uses a non-host species as a climate control, which has since been applied in the reconstruction of several spruce budworm species, insect defoliators in hardwoods and softwoods, and fungal diseases of conifers (Case & MacDonald, 2003; Zhang & Alfaro, 2003; Huang *et al.*, 2008; Flower *et al.*, 2014; Welsh *et al.*, 2015).

An important assumption underlying the use of a non-host as a climate control is that both the host species and the non-host respond similarly to climate. A study of the potential use of Douglas-fir and ponderosa pine in tree-ring reconstructions of historical climate in

the southern Cariboo-Chilcotin found that the growth trends of both species growing in the same stands were similar (Watson & Luckman, 2002). They also concluded that there was little evidence of differential growth due to insect infestations in the 20<sup>th</sup> century. Comparison of host and non-host species growing in the same stand should result in an overestimate of the severity of any outbreak as the defoliation of the host gives adjacent non-host trees a competitive advantage (Swetnam *et al.*, 1985).

A more recent dendrochronological study of WSB outbreaks in the Cariboo-Chilcotin identified a number of widespread and severe events prior to the 21<sup>st</sup> century, notably ca. 1900–1910 and 1935–1950, both prior to the beginning of aerial forest health surveys in 1957 (Axelson *et al.*, 2015). This study used a tree ring chronology developed from populations of ponderosa pine near Kamloops to account for climatic influences at 11 Douglas-fir sites in the central, southern, eastern and western portions of the 21<sup>st</sup> century outbreak. Periods were identified as budworm outbreaks when the detrended ringwidth index of individual Douglas-fir trees was substantially lower than the mean detrended index of the ponderosa pine populations around Kamloops for at least eight years.

Axelson *et al.* (2015) demonstrated that the Cariboo-Chilcotin region had a history of WSB outbreaks prior to the large scale outbreak starting in 2001. The outbreak history in areas further north and upward in elevation from their study was unknown but of great interest considering the potential for range expansion and increases in severity of outbreaks due to climate change.

The objectives of my study were to:

- Reconstruct outbreak history of western spruce budworm at and beyond the edge of the 21<sup>st</sup> century infestation
- 2. Examine climate factors that contributed to historical outbreaks
- Determine whether the timing of historical outbreaks in the western Chilcotin region is consistent with immigration, as appears to have been the case in the 21<sup>st</sup> century outbreak, or irruption from an endemic population.

Results of preliminary analyses of data collected for the first objective raised questions about the outbreak reconstruction approach, which led to the final research objective:

 Critically reassess regional western spruce budworm outbreak reconstructions by identifying other potential causes of differential growth between the host and non-host populations used to describe outbreak history.



Figure 5.2: Cumulative years of defoliation near the northern extent of surveyed defoliation in the Fraser River valley, with contiguous Douglas-fir forests in the upland region to the west. Contour interval is 25m, with thick contours at 100m. Aerial Overview Survey and Vegetation Resources Inventory data used under BC Open Government License 2.0.
## 5.3. Methods

## 5.3.1. Site Selection and Field Methods

As a point of reference for dendrochronological reconstructions, the annual progression of surveyed western spruce budworm defoliation from 2001 to 2013 (https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/ accessed 2013) was mapped and overlaid by the study site locations. Defoliation records (total years of defoliation, years of medium/severe rated defoliation) and mean annual precipitation data (www.climatewna.com accessed 2016) were attached to each site using a spatial join in ArcGIS.

Sites used for reconstruction of historical outbreaks were selected in the context of their cumulative defoliation history in the current outbreak. Annual defoliation records (2000–2013) were retrieved from the BC Ministry of Forests website

(https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/ accessed 2013) and internal boundaries were dissolved using standard tools in ESRI ArcGIS<sup>®</sup> software, yielding annual boundaries of affected area. The 14 resulting data layers were overlaid using the "Count Overlapping Polygons" plug-in tool

(https://blogs.esri.com/esri/arcgis/2012/11/26/spaghetti\_meatballs\_one\_to\_many/) in ArcGIS<sup>®</sup>, generating a single data layer describing the total number of years that each area had been affected. A final overlay was performed to generate a data layer that identified areas with 6 or more years of surveyed defoliation from 2000–2013, of which at least one year was coded as medium or severe in the survey data. The resulting data layers were used to classify areas as severely affected (6 or more including one medium or severe record), moderately affected (3+ years at any level), lightly affected (1–2 years at any

level), and without any record of defoliation. These layers were exported to Google Earth<sup>®</sup> to inform the site selection process.

Aerial imagery in Google Earth<sup>®</sup> (dated 2005, accessed 2013 and 2014) was used to identify stands that had not been previously logged and were likely to contain old trees. Three main criteria guided the sampling design:

- 1. A number of well-distributed sites covering all four categories of defoliation defined above: heavy, moderate, light, and no record of defoliation.
- 2. Heavy sampling along the Chilcotin River valley, which suffered severe defoliation later than the central area. This delay could be due to immigration rather than an irruption from a ubiquitous endemic population, which may or may not be a regular feature of outbreaks in the region.
- Collection of several sites that escaped 21<sup>st</sup> century defoliation in the higher elevation area west of the northernmost "arm" of the current outbreak in the Fraser River valley and several adjacent sites in the heavily defoliated lower elevation areas for comparison.

A number of suitable candidate sites were identified for each of the categories above. The largest stands were visited first and were sampled immediately if no cut stumps were evident and trees over 250 years old were present. A total of 45 sites were sampled in the 2013 and 2014 field seasons (Figure 5.3).



Figure 5.3: Map of study sites overlying the cumulative defoliation history from 2001–2013 and the range of Douglas-fir leading stands according to the British Columbia Vegetation Resources Inventory (2016). 20<sup>th</sup> century defoliation at Quesnel Lake and Riske Creek indicated in brown. The Chilcotin region is the area west of the Fraser River; the Cariboo is east of the Fraser.

At each site a transect line was established perpendicular to the prevailing slope. Every 20m along the transect line, two trees sampled up to a total of 20 trees. Two 5.1mm increment cores were taken at breast height from opposite sides of each tree, perpendicular to the slope to avoid reaction wood (Speer, 2010). Acceptable trees had no obvious signs of damage to the trunk and no dead branches below approximately 2 meters (an indication of older trees). A photo of each tree was taken for later reference. Tree and stand attributes were measured in 3–5 fixed radius plots along each transect and included diameter at breast height, species, and stand density.

Ponderosa pine chronologies collected near Kamloops, British Columbia, were provided by Lori Daniels of the University of British Columbia Tree Ring Lab in Vancouver. This chronology provides a sample depth of four or more trees from 1677– 2011. Kamloops is 82km from the southernmost site MON near Monkian Lake, and 302 km from the westernmost site PYP near Pyper Lake.

## 5.3.2. Laboratory Preparation

Increment cores were glued to individual wooden mounts and sanded with progressively finer grits to 600 (Stokes & Smiley, 1968). All cores were visually crossdated using a combination of the list method and the memorization method (Speer, 2010). The list method was used to identify marker years in the first several sites to be crossdated until a number of regionally consistent marker years were identified.

Visually crossdated increment cores were scanned in batches of 8–20 at 1200 DPI using an Epson<sup>®</sup> 1640XL flatbed scanner. Ringwidth measurements were made using the computer program Windendro<sup>®</sup> (Regent Instruments 2014) and crossdating was confirmed using the program COFECHA (Holmes, 1983). Cores or sections that were excessively damaged or otherwise impossible to crossdate reliably were discarded from the study, leaving 1,651 series from 886 trees at 45 sites.

## 5.3.3. Outbreak Reconstruction

All ring width series, both host and non-host, were standardized using a doubledetrending process where a modified negative exponential curve was fit to each series, followed by a 50-year cubic smoothing spline (Axelson *et al.*, 2015). The dendrochronological program OUTBREAK (Holmes & Swetnam, 1996) was used to reconstruct historical outbreak periods by correcting detrended individual host-tree series, consisting of the average of two cores from each tree, with the detrended non-host mean chronology to remove the regional climatic trend from the host series. Program default settings were used to define outbreak thresholds: minimum 8 years below-average growth in the corrected series (allowing up to two years of positive deviation) and at least one year

of growth reduction below -1.28 standard deviations from the corrected series mean (as in Axelson *et al.*, 2015). Reconstructed outbreaks were classified based on the percentage of trees recording an outbreak within each site, using the thresholds of 15, 50 and 75% to define light, medium, and severe outbreaks respectively (Axelson *et al.*, 2015). Maps were generated for each regionally-synchronous outbreak period, displaying the maximum percentage of trees meeting outbreak criteria at each site overlaying the cumulative years of defoliation in the 21<sup>st</sup> century and the range of Douglas-fir leading stands.

As there were a large number of sites involved in the study, scripts were developed utilizing the package dplR within the statistical package R (Version 3.2.2.; Bunn *et al.*, 2017) to create the detrended input files for the program OUTBREAK.

Pearson correlation coefficients between detrended site-level chronologies and monthly average temperature and monthly total precipitation measured at the Williams Lake Airport (previous June to current August; <u>http://www.ec.gc.ca/dccha-ahccd/</u>) were calculated for the 1937–2012 period using the package treeclim (version 1.0.16) (Zang & Biondi, 2015) in the open source statistical program R (version 3.2.2; script in Appendix A).

To identify possible alternative explanations for patterns observed from the OUTBREAK results, detrended host and non-host chronologies were plotted for comparison, and periods of regionally synchronous reconstructed outbreaks were isolated from the plotted series for visual assessment. This led to a close re-examination of the nonhost ring width data provided from the Kamloops region, and of available ponderosa pine samples previously collected near Kamloops and stored at the UNBC Tree Ring Laboratory to confirm apparent growth trends. For initial visual analysis, the average

detrended ring width chronology from the ponderosa pine series provided by Lori Daniels and a combined Douglas-fir chronology (all 45 sites) were plotted together.

Individual ring width series making up the ponderosa pine chronology were converted to annual basal area increments in the R package dplR, and growth releases were identified using the R package TRADER (Nowacki & Abrams, 1997; Altman *et al.*, 2014). Growth releases were defined as years in which the 20-year mean basal area increment following a given year exceeded the 20-year mean preceding the subject year by 50% or more. Releases were plotted by both the date of initiation (year of maximum increase) and the dates for which a growth release was ongoing (remaining above 50% rate of increase).

Precipitation totals recorded from the previous June to current June (pJJ) were plotted for the Kamloops weather station from 1897 to 2012 and for the Williams Lake weather station from 1937 to 2012. Adjusted and homogenized monthly climate data for Kamloops (station elevation 345m) and Williams Lake (station elevation 940m) were retrieved from Environment and Climate Change Canada (http://www.ec.gc.ca/dccha-ahccd/ accessed 2017) and pairwise correlations were calculated in Stata 12.1<sup>®</sup> between monthly precipitation totals, seasonal and annual precipitation totals, the sum of previous-June through current-June, and June, July and August precipitation at each weather station. Cook's Palmer Drought Severity Index for the period 1640–1990 for the reconstruction grid points 30 (122.5W 52.5N, 90km north-northwest of Williams Lake) and 42 (120W 50N, 76km south-southeast of Kamloops) were plotted as a point of reference for periods where weather station data were not available for both regions. Reconstructed PDSI values at point 42 were subtracted from those at point 30 to identify periods in which reconstructed drought severity was higher at one grid point than the other.

Forest Insect and Disease Survey data for Douglas-fir beetle infestations (<u>https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/FIDS%20data/</u> accessed 2017) were mapped to confirm the presence of aerial survey crews in the vicinity of study sites during a period when budworm defoliation was reconstructed.

# 5.4. Results

The most recent outbreak was first recorded at four locations in the central Cariboo-Chilcotin in 2001, and defoliation progressed outward from this region in subsequent years (Figure 5.4). Populations reached Alexis Creek in the central Chilcotin in 2004 and became severe in that region in 2005. The outbreak reached its maximum western extent in 2007 and subsequently retreated, though defoliation remained extensive through 2011 (Figure 5.5). Sites in the plateau country immediately east of the Fraser River received the most cumulative years of defoliation, while the highest cumulative medium or severe defoliation occurred at site WIL near Williams Lake with a total of six years (Table 5.1). Basal area per hectare in trees >15cm DBH ranged from 23 m<sup>2</sup>/ha at site ALE to 105 m<sup>2</sup>/ha at site JKY, while the density of trees <15cm DBH ranged from 337 trees per hectare at site FUZ to 81,330 at site YUN. Lodgepole pine and trembling aspen seedlings were present at some sites, but are not included in the totals, which consider only Douglas-fir.



Figure 5.4: Annual progression of surveyed western spruce budworm defoliation, 2001–2008.



Figure 5.5: Annual progression of surveyed western spruce budworm defoliation, 2009–2013; total years of defoliation in the 21st century; maximum severity of defoliation in the 21st century overlaid by site locations; stands with Douglas-fir listed as the leading, secondary, and tertiary species.

Precipitation in the previous summer had a greater number of positive correlations with ring width than current-summer precipitation, though the correlation with current-June precipitation was uniform across all sites but MON, the site closest to the Kamloops region (Table 5.2). All significant precipitation correlations were positive, except for those in February. The Kamloops ponderosa pine chronology had similar correlations with precipitation compared to the rest of the dataset: positive in the previous June, July and August, negative in February, and positive in the current June.

Monthly temperature/ring width correlations were less consistent, but when significant, were negative in both previous and current-summer months (Table 5.3). Growth at several sites showed positive correlations with the temperature of the preceding November and current February, while ring width at site GAR had a negative correlation with the temperature in March.

Only a few correlations for either temperature or precipitation were significant in March, April and May, and none were significant in the current August (Table 5.2, Table 5.3).

Code	21st Cent.	Med/Sev	Elevation (m)	Latitude	Longitude	MAP	BAPH	I TPH
ABR	0	0	1,133	51.7438923	-123.0118885	356	39	12,818
ACS	4	2	1,024	52.0117549	-123.2996988	341	82	2,147
ALE	6	2	959	52.0683102	-123.4077121	334	23	2,147
ALK	10	1	954	51.7834782	-122.1876281	466		
BCA	6	4	935	52.0901795	-123.3576366	325	32	443
BIG	8	1	1,261	51.3138054	-122.1480729	430		
BLU	7	3	871	52.3339213	-122.2445340	480	50	6,112
CAL	7	2	1,248	52.0692987	-122.6152696	477	53	5,725
CAM	7	2	1,087	51.6979303	-121.6111339	480	53	35,361
CHI	7	3	906	51.9000469	-121.9391504	494		
CTI	0	0	818	52.6591690	-122.3733768	497	52	5,557
DCB	10	2	947	51.5727098	-122.2225973	412	52	1,957
DOG	9	1	1,136	51.4782313	-122.1572942	440	51	3,220
ENT	7	2	910	51.9836634	-121.8744262	473		
EPI	9	1	1,262	51.6044373	-122.0133402	474	51	573
FUZ	0	0	1,068	52.2870636	-122.6800798	467	47	337
GAR	6	2	1,239	51.7091378	-122.4335147	381	29	3,537
HAN	3	1	1,329	51.9652070	-122.9133535	459	59	2,021
HAW	5	1	1,306	51.9656547	-122.9304042	457	59	3,199
JKY	9	0	1,136	51.6917149	-122.2037750	509	105	12,692
KCR	8	1	831	52.0642667	-121.8822881	484	59	5,999
LEE	6	2	1,031	51.9562319	-123.0739201	375	55	2,526
LEN	2	0	1,268	52.0381704	-123.1060724	431	87	2,463
MAB	9	1	945	51.9077376	-122.2720139	452	47	19,533
MAQ	0	0	931	52.3524638	-122.5181316	502	59	2,442
MAY	9	0	1,127	51.8840641	-122.1975185	507	43	6,062
MCL	7	1	679	52.4219183	-122.3681458	458	39	2,273
MEL	1	0	939	52.2542212	-122.3956095	459		
MON	6	2	1,127	51.1889869	-121.1958171	357	47	1,452
NEE	1	0	1,070	52.1879372	-122.6386473	487	74	1,894
NOJ	0	0	1,016	52.4670937	-122.7230840	484	54	1,137
NRA	0	0	970	52.2189822	-122.5051835	465	40	1,831
PTI	1	0	1,005	52.1626914	-123.9129591	307	34	1,326
PUD	0	0	967	52.1846704	-123.8525038	317	44	1,200
PVA	9	1	786	52.2862723	-122.1860931	440	54	1,213
РҮР	1	0	1.107	52.0321977	-124.1353788	375	35	1.314
REN	2	0	988	52.1690185	-123.7131926	328	64	1,011
RES	2	0	953	52.1374131	-123.7408311	323	28	2,589
RIS	9	4	1,259	51.9492246	-122.6387795	404	73	1,642
SOA	7	2	645	52.4221649	-122.4136252	423		,
SUG	9	6	658	52.1027626	-122.0231037	415	41	1.642
TWA	0	Ō	839	52.5484822	-122.6309186	461	52	1.894
WHI	7	2	857	52.2171170	-122.3221347	456	77	1.515
WIL	9	6	677	52.1596966	-122.2338750	404	48	674
YUN	6	5	996	51.8882930	-123.1022910	363	38	81,330

Table 5.1: Site attributes;  $21^{st}$  cent. = total years of defoliation; Med/Sev = years in which defoliation was recorded as medium or severe. MAP = mean annual precipitation; BAPH = basal area per hectare (m<sup>2</sup>) in trees >15cm DBH; TPH is trees per hectare <15cm DBH.

Total Monthly Precipitation														
Site	jun	jul	aug	sep	oct	nov	dec	JAN	FEB	MAR AP	R MAY	JUN	JUL	AUG
ABR	0.22	0.29	0.31									0.36		
ACS	0.22	0.25	0.33						-0.25			0.44		
ALE			0.30						-0.23	0.20		0.32		
ALK	0.26	0.21	0.31									0.37	0.27	
BCA			0.32									0.36		
BIG		0.28	0.26		-0.19							0.34		
BLU		0.22	0.28									0.31	0.26	
CAL	0.31		0.25				0.24					0.37		
CAM	0.28		0.36				0.24					0.31	0.30	
CHI			0.38				0.31					0.33	0.27	
CTI	0.26											0.34		
DCB		0.23	0.34									0.37		
DOG	0.24	0.37	0.34									0.41		
ENT	0.30	0.18	0.32									0.42	0.30	
EPI	0.23		0.37									0.34		
FUZ	0.41	0.23	0.28									0.29	0.17	
GAR		0.18	0.38				0.30					0.32		
HAN	0.24	0.43	0.31									0.30	0.29	
HAW		0.34	0.29						-0.25			0.28	0.24	
JKY		0.30	0.30									0.23		
KCR	0.32		0.26								0.43	0.39		
LEE		0.29	0.28						-0.21	0.20		0.44		
LEN	0.24	0.33	0.30						-0.25			0.33	0.27	
MAB	0.21	0.24	0.40				0.24					0.38		
MAO	0.29	0.23										0.27		
MAY	0.36	0.34	0.31				0.20					0.33	0.25	
MCL	0.33		0.27			0.23	0.26				0.27	0.22		
MEL	0.37	0.26	0.30			0.20	0.20				0/	0.26	0 21	
MON	0.31	0.24	0.23						-0.23			0.20	0.21	
NEE	0.28	0.21	0.26						0.20			0 23	0.25	
NOJ	0.33	01	0.20									0.28	0.30	
NRA	0.23	0 22	0 29									0.25	0.21	
PTI	0.22	0	0.39				0 23					0.27	0.26	
PUD	0		0.28				0.29		-0.23			0.29	0.20	
PVA		0.38	0.20				0.27		0.20			0.31	0 33	
РҮР	0.22	0.20	0.30									0.32	0.00	
REN	0.22		0.27			0.26	0.24			0.27		0.34	0.24	
RES			0.25			0.20	0.27	0.21		0.24		0.33	0.25	
RIS	0.27	0.20	0.30				0.26	0.21		0.21		0.33	0.25	
SOA	0.29	0.20	0.50				0.27					0.30	0.23	
SUG	0.33	0 24	0.32				0.24					0.39	0.22	
TWA	0.28	0.32	0.54				0. <i>2</i> r		-0.28			0.26	0.22	
WHI	0.39	0.36	0 33						0.20			0.32	0.26	
WIL	0.30	0.50	0.26				0 24					0.30	0.25	
YUN	0.50	0 21	0.20				0. <i>2</i> r		-0 27			0.30	0.20	
PIPO	0.20	0.22	0.39						-0.27			0.31		
	0.20	·	5.57						·· /			0.01		

Table 5.2: Significant Pearson's correlation coefficients (p<0.05) between detrended ring width indices and monthly precipitation totals. Months in lowercase belong to the preceding calendar year; months in uppercase belong to the current calendar year.

						Μ	ean N	Aonthl	y Tem	peratur	e			
Site	jun	jul	aug	sep	oct	nov	dec	JAN	FEB	MAR	APR	MAY	JUN	JUL AUG
ABR		-0.31	-0.14											
ACS		-0.27											-0.26	-0.29
ALE													-0.23	-0.22
ALK	-0.23												-0.26	-0.16
BCA													-0.28	-0.26
BIG		-0.29												
BLU									0.25				-0.23	
CAL	-0.28	-0.34				0.24								
CAM	-0.24	-0.24											-0.19	-0.19
CHI	-0.30												-0.23	-0.18
CTI		-0.24											-0.35	-0.24
DCB													-0.21	
DOG		-0 29											-0.24	
ENT	-0.31	0>											•	-0.18
EPI	0.21												-0.27	0.10
FUZ	-0.32	-0.38				0 34			0.23				0.27	
GAR	0.52	0.20				0.51			0.25	-0.23				
HAN		-0.33				0.21				0.25				
HAW		-0.24				0.21								
IKY		0.21												
KCR													-0.29	
IFF													-0.25	-0.23
LEL		-0.32				0.27							0.20	0.25
MAR		0.52				0.27							-0.20	
MAO	-0.28	-0.31							0.26				-0.26	
MAY	0.20	-0.32				0.21			0.20				0.20	
MCI	-0.29	0.52				0.21							-0.20	
MEL	-0.29	-0.30							0.30				0.20	
MON	0.27	-0.26				0.23			0.50					
NFF	-0.28	0.20				0.25			0.23					
NOI	-0.29	-0.23				0.22			0.25					
NR A	-0.26	-0.23				0.22			0.27					
PTI	-0.20	-0.25							0.27				-0.26	-0.24
													-0.20	-0.24
DVA													-0.23	-0.24
DVD													-0.24	-0.17
DEN													0.21	-0.24
DES													-0.31	-0.23
RES DIC	0.25	0.20				0.20							-0.51	-0.32
KIS SOA	-0.23	-0.30				0.29							0.22	-0.17
SUA	-0.52		0.22										-0.25	
SUU TWA	-0.20	0.22	-0.23			0.25							-0.28	
1 WA	-0.22	-0.33				0.25			0.22				-0.20	
WIII	-0.31	-0.30				0.22			0.23					
WIL	-0.27	0.20							0.24					
		-0.28							0.24					
PIPU		-0.28							0.25					

Table 5.3: Significant Pearson's correlation coefficients (p<0.05) between detrended ring width indices and monthly average temperature. Months in lowercase belong to the preceding calendar year; months in uppercase belong to the current calendar year.

My WSB reconstructions using the program OUTBREAK are very similar to those of Axelson *et al.* (2015) (Figure 5.6). All sites meet outbreak criteria several times over the course of the tree ring record. Most sites meet outbreak criteria around the turn of the 20<sup>th</sup> century and from 1938-1949, in agreement with Axelson *et al.* (2015) (Figure 5.6). Reconstructions for the 21<sup>st</sup> century often do not match the surveyed values: sites ALE, CAM, ENT, EPI, GAR, JKY, KCR, MON, PVA, SOA, and WHI all survived five or more years of surveyed defoliation, but never pass the threshold of 15% of trees meeting outbreak criteria after 2000. Sites MAQ and TWA, which received no surveyed defoliation, record several years above the 15% threshold in the 21<sup>st</sup> century and site LEN, which received two years of surveyed defoliation, exceeds the 50% threshold for a decade.

Detrended ring width indices for all Douglas-fir in the study area and those of the ponderosa pine non-host are very similar from one year to the next, with differences in magnitude (Figure 5.7). In addition to 1899–1909 and 1938–1940, generally synchronous periods of reconstructed outbreaks were identified ca. 1744–1752, 1770–1786, 1795–1808, 1854–1861, and 1870–1882 (Figure 5.8).



Figure 5.6: Reconstructed outbreaks based on the percentage of trees at each site meeting the defined outbreak criteria. Light gray exceeds the 15% threshold; medium gray 50%, and black 75%.  $21^{st}$ =total years of surveyed defoliation in the  $21^{st}$  century outbreak. Vertical dashed line at 2001 indicates the beginning of the  $21^{st}$  century outbreak.



Figure 5.7: Mean detrended chronology values for all Douglas-fir in the study and ponderosa pine near Kamloops, and the Douglas-fir chronology less the ponderosa pine chronology (host minus non-host) from 1640 to 2011. Areas shaded by gray bars indicate the periods of regionally synchronous reconstructed outbreaks ca. 1744–1752, 1770–1786, 1795–1808, 1854–1861, 1870–1882, 1899–1909, and 1938–1948, the sporadic period of the 1980s and 1990s, and the known outbreak period 2001–2011.



Figure 5.8: Mean detrended chronology values for all Douglas-fir in the study and ponderosa pine, and the Douglas-fir chronology less the ponderosa pine chronology (h-Nh = host minus non-host) for eight periods of regionally synchronous reconstructed outbreak activity ca. 1744–1752, 1770–1786, 1795–1808, 1854–1861, 1870–1882, 1899–1909 and 1938–1940, the sporadic period of the 1980s and 1990s, and the known outbreak period of 2001–2011.

The period of the modern outbreak beginning in 2001 includes five sites in the Chilcotin River valley exceeding the 50% threshold and 17 exceeding the 15% threshold throughout the study area (Figure 5.9). A number of sites in heavily defoliated areas fail to meet any of the outbreak thresholds, while two in the upland area northwest of Williams Lake which has no recorded defoliation, exceed the 15% threshold.



Figure 5.9: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 2001–2011, overlaying the cumulative years of defoliation in the 21st century outbreak and the range of Douglas-fir leading stands

Forest Insect and Disease surveys conducted during the period of sporadic outbreak reconstruction in the 1989s and 1990s identified widespread infestations of mountain pine beetle and pine needle cast in lodgepole pine and Douglas-fir beetle in Douglas-fir. No records were made of western spruce budworm defoliation during this period, but two-year cycle budworm (*Choristoneura biennis*) was mapped northeast of the study area around Quesnel Lake (Figure 5.10).



Figure 5.10: Forest Insect and Disease Survey records from 1985 to 1996 showing data for two-year cycle budworm, mountain pine beetle, pine needle cast, and Douglas-fir beetle, overlaid by site locations displayed by the maximum number of trees meeting outbreak criteria during this period.

A majority of trees met outbreak criteria at all but two sites in the 1938–1948 period (Figure 5.11), and 21 sites exceeded the 75% threshold. Five sites northwest of Williams Lake with no recorded defoliation in the 21<sup>st</sup> century exceeded the 50% threshold.



Figure 5.11: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1938–1948, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

All but two sites had more than 75% of trees meeting the outbreak criteria in the 1899–1909 period, while the remainder surpassed the 50% threshold (Figure 5.12).



Figure 5.12: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1899–1909, overlaying the cumulative years of defoliation in the 21st century outbreak and the range of Douglas-fir leading stands

For the 1870–1882 period, three sites that received no recorded defoliation in the 21<sup>st</sup> century exceeded the 50% threshold in the region northwest of Williams Lake, while sites NOJ and TWA exceeded the 75% threshold (Figure 5.13).



Figure 5.13: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1870–1882, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

Every tree at site NEE met the outbreak criteria in the 1854–1861 period, while this site received only one year of light infestation during the 21<sup>st</sup> century event (Figure 5.14). Three upland sites northwest of Williams Lake and site ABR in the Chilcotin exceeded the 50% threshold in this same period, but had no defoliation recorded in the 21<sup>st</sup> century.



Figure 5.14: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1854–1861, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

The 1795–1808 period includes a number of sites exceeding the 75% threshold in the plateau country immediately east of the Fraser River, and four exceeding the 50% threshold northwest of Williams Lake that received no defoliation recorded in the 21<sup>st</sup> century (Figure 5.15).



Figure 5.15: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1795–1808, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

In the 1770–1786 period, more than 75% of trees met outbreak criteria at two sites northwest of Williams Lake that had no defoliation recorded during the 21<sup>st</sup> century outbreak (Figure 5.16). A number of sites in the Chilcotin River valley exceeded the 50 and 75% thresholds, including sites RES and PUD with two and zero years of defoliation recorded in the 21<sup>st</sup> century.



Figure 5.16: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1770–1786, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

Ten sites exceeded the 75% threshold in the 1744-1752 period, including two sites that had only one year of recorded defoliation in the  $21^{st}$  century (Figure 5.17).



Figure 5.17: Maximum percentage of trees meeting outbreak criteria in a given year at each site in the period 1744–1752, overlaying the cumulative years of defoliation in the 21<sup>st</sup> century outbreak and the range of Douglas-fir leading stands

Peaks in growth release initiations in the non-host chronology occurred ca. 1760, 1800/1801, 1898/1899, 1938/39 and 1976–1990 (Figure 5.18). Peaks in ongoing growth releases correspond to peaks in initiation dates, which is expected as the method of calculating releases identifies the year with the maximum rate of increase, rather than the first year exceeding the threshold (Figure 5.19). Many of these release events appear to represent substantial changes in position within the stand, e.g. ascension to a canopy position from the understory (1899 in "A" or 1731 in "B" and "C" in Figure 5.19) or the death of a competitor (1977 in "D," 1897 in "E," or 1976 in "F" in Figure 5.19).



Figure 5.18: Percent of non-host sample initiating growth release and percent with ongoing release (growth increase >50%) calculated using 20-year periods.



Figure 5.19: Six outputs of the R package TRADER showing growth trends in ponderosa pine, displaying the annual basal area increment in black (left Y axis) and the percent growth change in blue (right Y axis), growth releases marked by dashed vertical lines.

Prolonged periods of below-average total precipitation from the previous June through current June occurred at the Kamloops weather station in 1917–1922, 1929–1938, 1950–1953, 1971–1975, and 2008–2011, and at the Williams Lake weather station in 1941–1951 (excepting 1942 and 1949), 1967–1974, and 1986–1989 (Figure 5.20).



Figure 5.20: Previous June through current June precipitation totals (pJJ) at Kamloops from 1897–2012 and Williams Lake from 1937–2012. Mean lines at 313mm for Kamloops and 548mm for Williams Lake. Periods of below-average precipitation for each site marked in gray.

PDSI was negative both of at Cook's reconstruction points in the periods 1661– 1664, 1717–1722, 1756–1760, 1792–1800, 1839–1843, 1869–1873, 1918–1933, and 1967–1973 (Figure 5.21; Cook & Krusic, 2004). Reconstructed PDSI generally was lower at point 30 (closer to Williams Lake) than point 42 (closer to Kamloops) for nine periods of the length of the record, and higher for six periods (Figure 5.21).



Figure 5.21: Cook's reconstruction of Palmer's Drought Severity Index at grid points 30 (90km northwest of Williams Lake) and 42 (76km south-southeast of Kamloops) for the years 1640–1940. Years of reconstructed outbreaks marked in gray above the 0 line, years where PDSI reconstruction is higher (more moist) at the point nearer Kamloops marked in gray below the 0 line.

Inspection of archived ponderosa pine cores collected near Kamloops consistently revealed a low-growth event corresponding to the period of low precipitation reported at the Kamloops weather station from 1929–1933. As an example, Figure 5.22 shows a core from a tree that was a small sapling at the time of the drought. Growth reduction in this specimen began prior to the drought event, perhaps due to its suppressed or intermediate status in the canopy.



Figure 5.22: Archived ponderosa pine core PP14 from the UNBC Tree Ring Lab showing growth reduction in the late 1920s/early 1930s with growth release beginning ca. 1935

Pairwise correlations between precipitation totals recorded at Williams Lake and

Kamloops weather stations are significant at the annual level and in summer and autumn,

but not in winter or spring, or the months of December, January, February, and March

(Table 5.4). All precipitation means were lower in Kamloops than Williams Lake, but the

differences were more pronounced in the winter months: mean annual precipitation at

Kamloops is slightly less than half that of Williams Lake, but precipitation in winter at

Kamloops is only 15% of that recorded in Williams Lake.

Table 5.4: Mean annual, seasonal, and monthly precipitation total at Williams Lake and Kamloops weather stations from 1937 to 2012, with pairwise correlations and significance score for each variable. Sample size varies due to missing data values excluded from the analysis. pJJ=total precipitation from the previous June to the current June. JJA=total precipitation for the months of June, July and August. All values are in mm. Significant correlations marked by bolded variables names (P<0.05).

	Williams		Pairwise			
Variable	Lake	Kamloops	Correlation	P Value	n	
Annual	489	225	0.42	0.0003	74	
Winter	119	18	-0.15	0.19	75	
Spring	87	50	0.2	0.078	74	
Summer	166	96	0.55	< 0.0001	75	
Autumn	117	60	0.54	< 0.0001	75	
pJJ	548	328	0.4	< 0.0001	75	
JJA	166	96	0.56	< 0.0001	75	
January	44	5	0.12	0.27	75	
February	27	6	-0.12	0.27	75	
March	24	9	0.04	0.74	74	
April	23	15	0.31	0.005	75	
May	40	25	0.38	0.0008	74	
June	62	39	0.61	< 0.0001	75	
July	53	29	0.43	0.0001	75	
August	51	28	0.61	< 0.0001	75	
September	39	26	0.70	< 0.0001	75	
October	38	20	0.42	0.0001	75	
November	40	14	0.26	0.024	75	
December	47	8	-0.08	0.47	75	

Rates of basal area increment increase calculated by comparing the 20-year means preceding and following each year are generally similar between the ponderosa pine and Douglas-fir populations under analysis, except for the period 1890–1905, where a peak occurs in the ponderosa pine but not the Douglas-fir, and from 1840 through 1880 where elevated rates of growth increase are found in Douglas-fir but not ponderosa pine (Figure 5.23).



Figure 5.23: Percent of total ponderosa pine (PIPO, beneath X axis) and Douglas-fir (PSME, above X axis) with ongoing growth release exceeding light (50%), moderate (100%), and severe (200%) thresholds on the basis of 20-year average basal area increase. Black bars indicate growth differentials meeting outbreak reconstruction criteria on a regionally consistent basis.
Peaks in reconstructed western spruce budworm outbreaks tend to coincide with peaks of growth increase in the non-host chronology (Figure 5.24). Reconstructed outbreaks beginning ca. 1899, 1938, and 1980 respectively correspond to peaks in growth increase affecting >35% of trees in the non-host chronology. All of these periods include a number of trees increasing at a rate of over 100% and 10–30% of trees exceeding a 200% rate of increase on the basis of 20-year averages before and after the subject year.



Figure 5.24: Percentage of sites with reconstructed outbreaks exceeding 15, 50, and 75% thresholds, and ponderosa pine trees displaying growth increase exceeding 50, 100, and 200% thresholds on the basis of five-year averages.

## 5.5. Discussion

A majority of the periods when outbreak criteria were met in the host/non-host analysis coincide with a difference in measured or reconstructed precipitation between the locations of the host and non-host populations, and several align with growth increases in the non-host population that are not found in the host populations. Growth increases in the non-host population may be a release from competition due to the death of neighboring trees. This can lead to faster recovery after drought (Erickson & Waring, 2014), leading to higher ring width index values. Finally, the spatial pattern of several reconstructed outbreaks is different than what was observed in the recent outbreak. Sites that received little or no defoliation in the 21<sup>st</sup> century were reconstructed as being more heavily affected than sites that were recently defoliated. It is possible that endemic populations of WSB were not near those sites, or some unknown factors resulted in little or no defoliation during the recent outbreak. It is also possible that these sites, being upslope and/or further north than others, have not experienced WSB outbreaks due to cooler temperatures and asynchronous larva and bud development, and that the reconstructed outbreaks are actually due to some other factor that caused growth differentials between the host and non-host.

Seven periods experienced regionally synchronous growth differentials such that the average detrended growth of the ponderosa pine was greater than the detrended growth of individual Douglas-fir. Each period is discussed below, considering possible confounding factors and other evidence regarding the cause of differential growth between Douglas-fir in the Williams Lake region and ponderosa pine in the Kamloops region.

# 5.5.1. Regionally synchronous periods of differential growth

Aerial surveys of the 21<sup>st</sup> century outbreak (2001–2013) observed medium or severe

defoliation at 28 of 45 sites and several years of light defoliation at two sites, one or two years of light defoliation at seven sites, and no defoliation of any severity at eight sites. This distribution is not reflected in the outputs of the program OUTBREAK: 50% of trees met outbreak criteria at only five sites (implying at least 50% defoliation of those trees; Alfaro *et al.*, 1982), all clustered in the Chilcotin River valley. Each of these sites began meeting outbreak criteria 2–3 years before defoliation surveys identified any infestation. Nine sites that are known to have been severely impacted by the 21<sup>st</sup> century outbreak did not exceed the 15% threshold in any year between 2001 and 2011, while three sites with no record of defoliation did exceed the lowest threshold. This is the only period when a falsenegative result is known to have occurred, where defoliation took place but was not identified in the tree rings.

This difference in surveyed vs. reconstructed defoliation appears to have been caused by a depression in the growth of the non-host trees, apparent in both individual and aggregate plotted chronologies, coincident with the defoliation of the host trees. This growth depression in the non-host may be due to precipitation in Kamloops returning to, and sometimes falling below, the historical average after higher levels from the mid 1970s to the late 1990s. The decades of above-average precipitation may have allowed stands to increase in density beyond the limits of the normal climate, and when precipitation levels returned to the historical average, the abnormally dense stands suffered a reduction in growth beyond what would result from drought alone.

While confirmation of this would require further study, a sharp reduction in growth rate ca. 2000 is apparent in many of the ponderosa pine samples archived at the UNBC Tree Ring Laboratory, and the basal area increment of the ponderosa pine chronology is

generally trending downwards in the final decade (Figure 5.9). This suppression would account for the very poor relationship between the reconstructed values and the observed defoliation because the index value of the non-host would be both lower than average and an inaccurate representation of the climate.

Reconstructed outbreaks **1980s and 1990s** were found in the greatest proportion of trees at host sites in northern and western portions of the study area. If substantial defoliation was occurring in more than half of the trees, the Aerial Overview Survey crews that recorded Douglas-fir beetle, mountain pine beetle, pine needle cast and two-year cycle budworm in the area would probably have observed it. Western spruce budworm was one of eleven pathogens considered to be "major forest insects and diseases" of national relevance in the 1990s (Hall *et al.*, 1994). According to the BC Forest Health Aerial Overview Survey Standards

(https://www.for.gov.bc.ca/hts/risc/pubs/teveg/foresthealth/assets/aerial.pdf accessed 2017) the optimal timing of survey flights for Douglas-fir beetle is mid-June through late-August, while western spruce budworm survey flights should be made from late-June to mid-August, an almost complete overlap. This suggests that these periods of suppression are not attributable to defoliation by the western spruce budworm, and that the reconstruction method has resulted in several false-positives.

Precipitation in Kamloops is substantially above the long-term average in the 1980s and 1990s, while precipitation in Williams Lake remained close to its historical average. This could account for the differential growth patterns meeting outbreak criteria at some sites, but not all the variation within the study area.

Both ponderosa pine and Douglas-fir populations record a peak in growth increase ca.

1980, but a much greater proportion of the ponderosa pine are affected. A mountain pine beetle outbreak was active in the 1980s and 1990s in the study area, and some patches of pine were also killed in the vicinity of Kamloops (Erickson, 1987). It is possible that this resulted in growth release in surviving trees making up the non-host chronology, while simultaneous outbreaks to the north caused growth release in some Douglas-fir growing in mixed stands but not others (Heath & Alfaro, 1990). The impact of this infestation on Douglas-fir would depend very much on the amount of mature lodgepole pine present in the stand at the time. Many sites in the western portion of the study area were heavily affected by the mountain pine beetle outbreak of the 1930s (Erickson, 1992) and would have only been 45 years old in 1980, too young and small to have a major impact on the growth of Douglas-fir even if they were killed by the mountain pine beetle (Heath & Alfaro, 1990). Stand dynamics may be at the root of the difference in the number of trees meeting outbreak criteria among sites: Douglas-fir in the mixed stands heavily affected by the mountain pine beetle in the 1980s and 1990s would have been in a state of growth release at the same time as non-host, reducing the differential between them.

Relatively low growth in Douglas-fir from **1938 to 1948** was recorded across the study area, potentially affecting 100,000 hectares more than the budworm outbreak of the 21<sup>st</sup> century. It comes at a time when detrended ringwidth indices of both Douglas-fir and ponderosa pine chronologies are well above average, but the ponderosa pine index is higher.

Forest health reports from the Cariboo region recorded two-year cycle budworm (*Choristoneura biennis*) defoliating spruce immediately east of the study area in 10 different years from 1926 to 1946 (Erickson, 1992). Forest tent caterpillar (*Malacosoma* 

*disstria*) was recorded as defoliating trembling aspen (*Populus tremuloides*) north of Williams Lake in 1937, and in many locations within the study area in 1941, 1942, and 1943 (Erickson, 1992), during the period identified as an outbreak of WSB (Axelson *et al.*, 2015; Harvey, 2017). Records of western spruce budworm defoliation in Douglas-fir near Lillooet in the 1940s (Erickson, 1987) indicate that the pest and its host were of concern in the interior of the province. It seems unlikely that a severe landscape-scale outbreak of western spruce budworm would go unnoticed by trained surveyors who would have travelled through the affected area on their way to observe defoliation in trembling aspen. While minor defoliation in some areas cannot be ruled out, the landscape-scale event is most likely a false-positive in the tree ring reconstruction of budworm defoliation.

The prolonged difference in precipitation trends between Williams Lake and Kamloops during this period could account for the differential growth between Douglas-fir and ponderosa pine, resulting in the false-positive. Williams Lake is below the long-term average in all years during this period except 1942, while Kamloops falls below average only in 1943 and 1944.

Growth suppression in Douglas-fir from **1899–1909** occurs before any written records from insect survey crews, so budworm defoliation is a possible cause of the growth reduction. As reconstructed, the magnitude of the event is several times that of the 21<sup>st</sup> century outbreak, and the extent would be at least 100,000 hectares greater than the recorded infestation. The near-perfect synchronicity of the suppression period, if caused by budworm, would require an immediate irruption of endemic populations in every affected area. This scale and timing are incongruent with the temperature/elevation gradient which is the basis of projections of future range expansion under climate change (Murdock *et al.*,

2013), and the spread pattern apparent in modern survey records. The temporal synchronicity and severity of the event suggests that some factor other than budworm was at play.

A peak in the proportion of trees showing ongoing growth release in the ponderosa pine chronology ca. 1900 is not matched by a peak in the Douglas-fir population, which is unusual for these chronologies. The 1890s are known to be a period of more frequent groundfire in the Cariboo-Chilcotin region, and the decade is suspected to have been a time of mountain pine beetle outbreaks (Hawkes *et al.*, 2004), but the disturbance history of the ponderosa stand used as the non-host chronology is unknown. Changes in basal area increment in ponderosa pine ca. 1900 are substantial, and appear to represent ascension to the main canopy or release from very strong competition. This may have been a defining event for the stand dynamics of the non-host site, securing the position of many trees that are now canopy dominants. A disturbance of this magnitude affects the hydrology around surviving trees, especially in dry ponderosa pine stands (Erickson & Waring, 2014), and can weaken the climate/growth relationship (Laurent *et al.*, 2003).

The indices of ponderosa pine and Douglas-fir closely parallel one another during this period, suggesting that they are responding to the same weather systems, and the difference in magnitude is what would be expected during a growth release in the ponderosa stand. The observed growth release in the ponderosa pine, and the magnitude of that release, explains the differential between the growth rates of the two species. Defoliation cannot be ruled out as survey records are not available, but the landscape-level growth differential pattern could not have resulted exclusively from budworm defoliation. Flower *et al.* (2014) identified outbreaks in Washington, Idaho, and Montana from the 1890s through the 1920s,

with initiation and maximum defoliation dates varying by location. Campbell *et al.* (2006) also reconstructed outbreaks from the 1890s through the 1910s at many of their sites in the Kamloops region. These outbreaks may have extended to the Chilcotin region, but the synchronicity of initiation and cessation of the reconstructed outbreaks in this chapter are inconsistent with both of these previous studies, suggesting an abiotic component to the tree ring signal.

The ring width indices of both species trend upwards in the **1870–1882** period following a period of suppression in the early 1870s. Cook's reconstruction of Palmer's Drought Severity Index is negative at both points 42 and 30 from 1869–1873 (corresponding to the suppression apparent in both ringwidth indices), but values were lower (indicating drier conditions) at the point north of Williams Lake than the point south of Kamloops from 1875–1881. The upland sites northwest of Williams Lake exceed the higher outbreak criteria in this period but based on the reconstructed PDSI, these sites would have been experiencing unusually dry conditions in the 1870s. The severity of the suppression exceeds the magnitude of the 21<sup>st</sup> century outbreak in marginal sites in the Chilcotin region as well as the upland regions in the north.

The presence of budworm cannot be ruled out, but the difference in reconstructed PDSI between the two regions suggests that moisture was the growth limiting factor in this period. Campbell *et al.* (2006) identified budworm defoliation at only a few of their sites near Kamloops during this period, while Flower *et al.* (2014) reconstructed WSB defoliation at approximately half of their sites in Oregon, Idaho and Montana.

The years **1854–1861** include a depression in the ring width indices of both species that is parallel but of greater magnitude in the Douglas-fir chronology. Most sites only

exceeded the 15% threshold of trees meeting outbreak criteria, except for a cluster meeting the 50 and 75% thresholds in the Chilcotin and northwest of Williams Lake, including sites with little or no recent defoliation. Cook's reconstructed PDSI values vary during this period, and the climate data available do not suggest any cause for differential growth. However, the pattern of reconstructed outbreak severity is inconsistent with the local elevation gradients that seem to have limited the extent of current outbreak.

It is possible that budworm defoliation did occur concurrently with other factors that limited the growth of Douglas-fir at the upland sites, though the nearest WSB reconstruction (Campbell *et al.* 2006) indicates only three of 17 sites experienced defoliation during this period.

Both Douglas-fir and ponderosa pine show sharp growth reduction from 1796–1800 during the **1795–1808** period, most likely caused by the regional drought of the late 18<sup>th</sup> century (Wolfe *et al.*, 2001), but the Douglas-fir average detrended index is much lower than the ponderosa pine index. Cook's reconstructed PDSI is lower (drier) at point 30 (near Williams Lake) than point 42 (near Kamloops) from 1801–1803 and 1806–1814, overlapping with much of the period of differential growth.

The footprint of this differential pattern is again substantially larger and more synchronous than the  $21^{st}$  century budworm outbreak, suggesting an abiotic mechanism. The relatively low (dry) PDSI values at the point nearer Williams Lake provide a plausible explanation for at least a portion of the growth pattern, though defoliation cannot be ruled out for this period. Campbell *et al.* (2006) identified defoliation signatures around this time, but there is substantial variation in the beginning and end dates between their sites. This is also the case in my reconstruction: at some sites, such as KCR, defoliation is

reconstructed as beginning the 1770s and continuing after 1800. This period is not identified as a regional outbreak in the northwestern United States by Flower *et al.* (2014)

Both ponderosa pine and Douglas-fir ring width indices were trending strongly upwards on a parallel trajectory in **1770–1786**, but the ponderosa pine exceeded 1.0 in several years that the Douglas-fir did not. This period also coincided with a period when PDSI values indicate greater moisture deficit in the Williams Lake region, potentially causing the growth differential to meet outbreak criteria. This period is generally quiescent in reconstructions by Flower *et al.* (2014) and Campbell *et al.* (2006).

The final period, **1744–1752**, includes a number of years in which the ponderosa pine ringwidth index was above 1.0 while the Douglas-fir followed a trajectory below 1.0. More than half of the ponderosa pine trees were in a state of growth release at the time, likely due to the initiation of new trees or growth response of surviving trees to the disturbances that opened growing space for that recruitment. The period also overlaps with a differential in Cook's PDSI reconstruction where values were lower (drier) at Williams Lake compared to Kamloops. All three potential confounding factors were present, with the additional influence of young seedlings that may not respond to climate as their established peers would. The spatial pattern of the reconstructed outbreaks was skewed towards the western sites, where five exceeded the 75% threshold and five exceeded 50% in addition to the isolated site ABR, which was also >50%. Several sites in the central area also exceeded both of the higher thresholds, but four sites did not meet the 15% threshold.

Defoliation is recorded by Campbell *et al.* (2006) at most sites following 1750, but only two in the 1740s. Flower *et al.* (2014) identified widespread WSB defoliation beginning in the 1750s and peaking in the 1760s, but less in the 1740s, though some sites

do break with the general trend and record extensive defoliation during this period.

#### 5.5.2. Overview of total record of trees meeting outbreak criteria

Aerial surveys record the 14 sites as collectively defoliated for 231 years between 2001 and 2013, a rate of 39.5% (231/585). For the period 1640-2011, OUTBREAK identified a similar percentage of site-years exceeding the threshold of 15% of trees impacted by WSB (43%). It is unlikely that the same rate of attack has occurred over time without recorded cases after the initiation of the Forest Insect and Disease Survey. Differences in moisture deficit and disturbance histories may have caused at least some of the growth differentials that met OUTBREAK criteria in the host-nonhost procedure.

#### 5.5.3. Limitations of host/non-host defoliation reconstruction method in this study

The use of pure host and non-host stands in geographically separate locations (as in this study), or the use of host and non-host from the same mixed stand both can result in problems. Use of mixed stands in outbreak reconstruction has been discouraged from the earliest development of the host/non-host technique, as defoliation of the host may allow the non-host a competitive advantage, leading to an overestimation of outbreak severity based on the difference between the chronologies (Swetnam *et al.*, 1985). Swetnam *et al.* (1985) also emphasized the importance of selecting host and non-host stands that would be likely to experience the same weather systems and respond in a similar way due to shared topographic situation and underlying soils. Recognizing that host species may not always be available under these conditions, the authors suggest using undefoliated host trees and limiting analyses to the present outbreak where these trees are known to have escaped defoliation. My study explored the alternative approach of using a non-host growing

outside of the immediate study area, but differences in topographic position, soils, and weather systems have the potential to affect results.

## 5.5.4. A note on regeneration as it relates to western spruce budworm

Regeneration surveyed in old-growth stands in this study was often found at extremely high densities, similar to stands described by Wong & Iverson (2004). This overstocking, a historically unprecedented outcome of long-term wildfire exclusion, provides a substantial food source for western spruce budworm outbreaks (Maclauchlan & Brooks, 2009). If historical insect survey records (Erickson, 1992) are taken at face value, then 21<sup>st</sup> century outbreak may represent the range expansion that has been anticipated under the regional warming trend that is already underway, and continued warming will support more outbreaks of similar or greater magnitude (Dawson *et al.*, 2008; Murdock *et al.*, 2013). The abundance of host material in the understory, where larvae falling from the main canopy can find a second chance at feeding, may increase the difficulty of mapping and managing future outbreaks.

# 5.6. Conclusion

No firm support for any extensive western spruce budworm outbreaks prior to the events of the 21<sup>st</sup> century was found in this study. The results of the earlier reconstructions of western spruce budworm outbreaks in the region (Axelson *et al.*, 2015; Harvey, 2017) were broadly replicated using the same host/non-host approach with independent datasets, but the synchronous persistence of these same differential growth patterns, including improbable locations based on budworm biology and spread dynamics, raises the possibility that growth differences in the host-nonhost were actually due to differences in

climate and spatio-temporal variation in disturbance history

Brief and localized events such as the one surveyed at Riske Creek in 1975 (Erickson, 1992) were not identified using the host/non-host method using standard outbreak detection criteria, as differential growth must last at least eight years. The poor description of the 21<sup>st</sup> century outbreak by the host/non-host method, despite the cumulative defoliation record of eight or more years at twelve sites, allows for the possibility of outbreaks not described in this study or others. Mid-20<sup>th</sup> century insect surveys identified small patches of defoliation in species of lower commercial value within the study area, suggesting that had there been major outbreaks between 1930 and 2000, they would have been detected.

These findings are different than those of Flower *et al.* (2014) and Campbell *et al.* (2006) who reconstructed historical outbreaks Oregon, Idaho and Montana and southern interior British Columbia respectively, using the same host-nonhost approach analyzing ponderosa pine from sites near to their Douglas-fir and grand fir sample sites. The defining feature of my reconstructed outbreaks in the 20<sup>th</sup> century is regional synchronicity in dates of initiation and cessation, while both of these studies record wide variation in these dates. The variation described in these studies is consistent with the spatio-temporal variation of the 21<sup>st</sup> century outbreak in the Cariboo-Chilcotin region.

Modeling of budburst and larval emergence dates over the past 100 years indicates that higher effective latitudes (a combination of latitude and elevation) have been experiencing optimal phenological synchrony recently (Marciniak, 2015). The overall effect of the observed warming trend in the study area (Dawson *et al.*, 2008) may act on other stages of the WSB lifecycle as well, including higher temperatures during autumn and spring

dispersal stages facilitating increased movement within and between stands (Wellington & Henson, 1947). Anomalously warm temperatures (average June and July daily temperature of approximately 18 °C and above) combined with low precipitation have preceded several outbreaks southern British Columbia (Thomson *et al.*, 1984). Warmer average temperatures in the study area since 1950 (Dawson *et al.*, 2008) suggest that these warm summer conditions are more likely to occur. Forest insect and disease surveys (Erickson, 1992) show that WSB was present in the study area at low levels as early as 1975; warming temperatures may have created conditions favorable to the expansion of these endemic populations.

Based on my conclusion that it is unlikely that there were major historical outbreaks over the time period and spatial scale studied, the 800,000 hectare outbreak in the first decade of the 21<sup>st</sup> century reflects a range expansion that is probably attributable to the regional temperature increase observed in the late 20<sup>th</sup> century (Dawson *et al.*, 2008). Continued warming is expected to cause further expansion of western spruce budworm range (Murdock *et al.*, 2013), meaning that more naïve populations will likely experience defoliation in the near future.

## 6. Concluding synthesis

## 6.1. Abstract

In this dissertation I consider the history of disturbances in the Cariboo-Chilcotin region of central British Columbia and the effect of canopy gaps created by disturbances on the drought tolerance of surviving interior Douglas-fir. Adjacency to canopy gaps created by natural disturbances or harvesting increased drought resistance of Douglas-fir. My reconstruction of the history of Douglas-fir beetle attacks indicated that the rate of attack has increased in recent decades, but other disturbance agents have been the primary drivers of stand dynamics in the region. My effort to expand western spruce budworm outbreak reconstruction to and beyond the margins of the 21<sup>st</sup> century outbreak revealed spatial patterns that did not appear to be caused by defoliation, but may be attributable to regional differences in precipitation driving differential growth. Widespread disturbance during the drought at the end of the 18<sup>th</sup> century was found to have had a strong influence on stand dynamics, bringing many trees into the position of canopy dominance they still maintain. In this synthesis I review major results and discuss the implications of the work as a whole.

#### 6.2. Summary of chapter results

Chapter 2: Three sampled stands of interior Douglas-fir were partially harvested in the 1970s, leaving the sampled population of residual trees averaging 90 years old and 15cm DBH at the time. Trees that received growing space on all sides grew significantly faster following harvest compared to trees that gained access to growing space on one side, and trees that received no new growing space grew more slowly than either open growing or edge trees. This difference in radial growth is reflected in higher live crown ratios and sapwood basal areas in trees with more growing space, but the relationship does not hold for drought tolerance. Growth reduction during drought, measured relative to the growth rate over the preceding five years, was not significantly different between fully and partially-released trees in most years, though growth reduction in trees with no access to open gaps was more severe than either. The only regular and statistically significant difference between the fully-released trees and partially-released trees with regards to drought tolerance was found when the growth rate during drought was compared to the growth rate prior to harvest: higher growth rate in the open growing trees translated into relatively high growth rate during drought.

Among several interacting mechanisms, the key factor driving drought tolerance in this situation appears to be precipitation throughfall, as reduced canopy interception in open areas allows more rainfall to reach the soil to be taken up by roots. Strong negative correlations between ringwidth and the mean temperature of the current June suggest warmer temperatures projected under anthropogenic climate change scenarios will have a substantial negative effect on tree growth, though the overall detriment to the tree may be mitigated by access to open gaps.

Chapter 3: Trees experiencing a growth release attributed to the death of a neighboring competitor showed higher drought resistance (less relative reduction in growth rate during drought) compared to trees not experiencing growth release, and the relationship was statistically significant in the majority of drought years tested. Drought resilience, or the return to pre-drought growth rate, was positively related to the resistance, and the relationship was almost always statistically significant. As in the previous chapter, precipitation throughfall is the most likely driver of increased drought resistance, with canopy gaps providing areas of higher moisture during the growing season. Resilience was often negatively influenced by both age and basal area of trees at the time of drought, though the relationship was not statistically significant in a majority of cases. Drought resistance of young trees (<50 years old) was found to be significantly higher than that of older trees in many of the drought years tested. Few significant differences were found between older age classes (50-149 vs. 150-249 and 250+), but in the three cases where a difference was significant, the oldest age class (250+) had lower resistance. The average rate of trees showing growth release in a given decade was 14% in the era prior to European settlement in the late 19<sup>th</sup> century, while 38% of trees showed growth release in the first decade of the 19<sup>th</sup> century. This event brought a large number of previously suppressed individuals into positions of canopy dominance that many have retained to the present day. One of the 46 sites appears to have been even-aged, with all 20 trees apparently initiated in the late 18<sup>th</sup> or early 19<sup>th</sup> centuries. The rest were uneven-aged, with the oldest trees initiated between the 14<sup>th</sup> and 18<sup>th</sup> centuries. Density of understory regeneration and basal area of overstory trees in the old-growth remnants sampled was generally high, in some cases far beyond historical levels and silvicultural

recommendations, and may present risk of stand stagnation or catastrophic fire due to the accumulation of ladder fuels.

**Chapter 4:** Failed Douglas-fir beetle attack was quantified temporally based on evidence of attack scars and resin pockets in the annual rings. Scars and resin pockets attributed to failed attacks were identified from the end of the 17<sup>th</sup> century to the death of the sampled Douglas-fir trees in 2014, indicating a regular occurrence that appears to have increased over the 20<sup>th</sup> century. Douglas-fir beetle does not appear to have been a major driver of stand dynamics compared to other common disturbances, especially wildfire and mountain pine beetle. Douglas-fir beetle outbreaks may become more important in the context of rising temperatures, increased stand density, and recent wildfire damage.

**Chapter 5:** My effort to expand upon previous reconstructions of western spruce budworm outbreak history, which were based on the comparison of growth rates between potential host Douglas-fir trees and a non-host ponderosa pine population in an adjacent region, turned into an investigation of confounding factors that became apparent due to the expansion of the study to and beyond the margins of the current outbreak. Growth differentials between the host and non-host tree populations appear to be influenced by differences in climate between the regions where the populations were sampled. The annually surveyed 21<sup>st</sup> century outbreak was poorly described by the same host/non-host comparison due to an unexplained suppression in the growth rate of the ponderosa pine. This suppression may be due to a complex interaction involving prolonged above-average precipitation in the non-host region followed by a return to normal conditions after

extensive ingrowth of trees.

Failure of the host/non-host analysis to accurately describe the known event allows for the possibility that previous outbreaks were also undescribed. However, this study does not contradict earlier work suggesting no history of major outbreaks (Watson & Luckman, 2002). If the historical record from insect surveyors is taken at face value since the 1930s, then the 21<sup>st</sup> century outbreak represents substantial range expansion that is likely attributable to observed warming trends that are expected to continue under anthropogenic climate change.

#### **6.3. Ecological implications and silvicultural applications**

Adjacency to canopy gaps created by disturbances conferred definite benefits in drought tolerance to surviving trees, as measured by radial growth during the drought, whether the canopy gaps were created by natural or anthropogenic disturbances. The dominant mechanism supporting this resistance appears to be access by the roots to areas where precipitation falls directly to the ground without being intercepted by the forest canopy and lost to evaporation. Open space on all four sides does not appear to be a requirement. While Douglas-fir beetle does not seem to have been responsible for the majority of historical canopy gaps, the presence of gaps created by other disturbances likely reduced stand vulnerability to Douglas-fir beetle by increasing the moisture available to potential host trees.

These results all favor the refinement and widespread application of clump-and-gap type silviculture within mule deer winter range (Dawson *et al.*, 2007), balancing needs for gaps allowing precipitation throughfall and clumps preventing that throughfall for the benefit of mule deer mobility and browse. Erring towards smaller clumps (4–6 trees) vs. larger clumps (7–10 trees) would likely favor drought tolerance, especially in combination with thorough application of the spacing and stocking recommendations already established (Dawson *et al.*, 2007). Projections of ecosystem response to climate change predict rapid expansion of the bunchgrass zone into what is presently mule deer winter range. These results suggest widespread application of established density management practices to maintain habitat quality to the greatest extent possible while studies are conducted and decisions are made about adapting range boundaries to match the realized effects of climate change in the 2020s and 2030s (Hamann & Wang, 2006).

Precedent for almost any system of silviculture may be found in the natural history of old-growth stands in the Cariboo-Chilcotin region, including the conservative policy of infrequent removals roughly equaling net growth over the period since the last entry. It is understood that exclusion of natural fires over the past century, both through firefighting efforts and consumption of fine fuels by free range cattle, has resulted in overstocked conditions and growth stagnation across much of the study area (Wong & Iverson, 2004). In the context of overstocking and a warming climate, stand-level growth in recent decades may not be a reliable measure of the productive capacity of the land. Density objectives set relative to current stocking and stand-level growth rates may provide a misleading target. Definition of density objectives and structural goals for each size class under specific moisture regimes (e.g. Dawson *et al.*, 2007), is likely the more sound approach, and some results of this study may inform goals for stands not covered by recommendations for conservation of mule deer winter range.

The series of disturbances affecting stands in the late 18<sup>th</sup> century, which resulted in nearly three times the average decadal rate of growth release, provides a precedent for more substantial harvests in stands outside of mule deer winter ranges that already have some history of harvest. The silvicultural objective would be the rapid growth of small but established trees that was seen between 1800 and 1840, combined with the increased drought tolerance observed after harvest in the 1970s. Accretion on established trees provides the greater benefit to the mid-term timber supply, but where that is impractical, establishment and density management of new regeneration for the long-term timber supply would be a reasonable objective. The utility of this approach is its immediate correction of the overstocking attributed to wildfire exclusion (Wong & Iverson, 2004) in

operations that are generally profitable due to the timber volume extracted. Correction of overstocking would reduce the risk of catastrophic fire and limit the stress of projected climate change in the short to mid-term, mitigating two of the major predisposing factors for Douglas-fir beetle attack.

The events of 1790–1800 allowed a large cohort of previously suppressed Douglas-fir to reach a position of preeminence across the region. The question remains as to why so many suppressed trees were released at this time. Such an extensive wildfire should have left more scarred trees than have been found in previous studies (Daniels & Watson, 2003; Harvey, 2017), and suppressed trees would not be expected to survive a severe fire that killed so many mature Douglas-fir. Windthrow is a possibility, but the region is not known to be prone to hurricanes or tornadoes, and windthrow should have led to more extensive populations of Douglas-fir beetle than are apparent in the scar/resin pocket data. The only serious candidate remaining is mountain pine beetle, which is considered to be responsible for growth release on a similar scale in the 1930s and is known to have affected nearly all mature pine in the area in the 2000s. A complication in this hypothesis is that the geographical footprint of the growth release pattern is greater than could have resulted from the modern distribution of lodgepole pine.

The modern distribution of lodgepole pine follows a gradient from low density in the relatively warm and dry valley bottoms to higher density in the uplands, where Douglas-fir is limited by temperature (Griesbauer & Green, 2010) and is ultimately relegated to small inclusions on advantageous aspects among forests of pine and spruce. If this trend held through the Little Ice Age, the effect of lower temperatures in that era could have been that those forests which are now pure or nearly pure Douglas-fir were then more reminiscent of

stands found at the upland margins of Douglas-fir's realized niche, such as those near Pyper Lake (site PYP; Figure 6.1) or Punti Lake (site PUD; Figure 3.1) in the Chilcotin region. The disturbance at the end of the 18<sup>th</sup> century would have come at the end of the Little Ice Age, and may have been the trigger for a substantial compositional shift with the study area.

There is some support for a species shift in a sediment core sampled in the study area Hansen (1955), which found an increase in Douglas-fir pollen and a reduction in pine pollen in the top 2cm. However there was limited resolution of the dating, and a sample size of only one core in this study.

If lodgepole pine was more dominant in the study area in the late 1700s, then sites at lower elevations presently dominated by Douglas-fir may have resembled sites at the upland margins of the range of Douglas-fir following the mountain pine beetle outbreak of the 2000s (Figure 6.1). Even a light ground fire at any time in the 10–20 years following the mountain pine beetle outbreak could wipe out all lodgepole pine regeneration in the pictured stand (Figure 6.1) before the young trees could form a substantial reserve of serotinous cones. Such a fire would spare most of the mature Douglas-fir, bringing that species into the majority and creating an ideal substrate for seed germination, allowing Douglas-fir to thoroughly occupy the growing space. Given Douglas-fir's longevity, resistance to wildfire, and intermediate shade tolerance, the shade-intolerant lodgepole pine would be slow to re-establish even if it were able to grow under the new climatic conditions. With a mean plot-level fire return interval of 16–36 years, depending on the location (Harvey, 2017), the odds of a fire at an inopportune time for the regenerating lodgepole pine are fair.

Another implication of this hypothesis is that the extensive history of mountain pine beetle in the Chilcotin region (Alfaro et al., 2010) reflects the ebb and flow of the lodgepole pine forest as a viable competitor with interior Douglas-fir according to changes in climate at the margin of its range. In this context, mountain pine beetle would not be displaying cyclic behavior in the way the word is normally used in disturbance ecology (Pickett & White, 1985), but behaving as a consequence of climate change and a facilitator of species migration. This is a plausible scenario as the stands in question are in close proximity to their climatically-limited range margins on several fronts. If this dynamic is supported by future pollen core analyses, it would provide useful information on the future trajectory of stands under anthropogenic climate change, especially if developed in conjunction with an accurate estimate of local temperature change since the Little Ice Age. The combination of temperature change and range margin change reconstructions would support more precise projections of anthropogenic climate change scenarios onto the landscape to identify locations where planners might favor Douglas-fir over lodgepole pine.



Figure 6.1: Tree PYP01, ca. 1619, surrounded by several age classes of lodgepole pine regeneration and Douglas-fir of at least three cohorts.

The history of Douglas-fir beetle attacks apparent in resin pockets and scars indicates that at some points in 18<sup>th</sup> and 19<sup>th</sup> centuries, there were more widespread infestations than were recorded during 20<sup>th</sup> century aerial surveys. There is nothing in this 250-year record that suggests an event equaling the magnitude of the 21<sup>st</sup> century outbreaks. Douglas-fir mortality estimated from the 2016 records is more than twice that recorded in fixed-wing surveys in any of the preceding 15 years. Based on the combination of long-term tree ring evidence and more recent aerial surveys, I conclude that the 2016 mortality is unusual. The unusually high beetle population warrants close monitoring for atypical attack behavior, focusing especially on mass attacks in healthy trees.

The history of western spruce budworm in the region remains unclear. Based on my results, evidence of differential weather patterns that could lead to false positives in outbreak reconstruction, and the lack of recorded evidence of past budworm outbreaks, it is most likely that the 21<sup>st</sup> century outbreak is anomalous in its extent and severity. If that is the case, the stand density allowed to build over a century of fire exclusion, especially in the understory (Wong & Iverson, 2004), warrants re-evaluation as a food source potentially intensifying future budworm outbreaks in an interaction with a warmer climate.

Interior Douglas-fir forests in the dry-belt region of central British Columbia have survived the insect outbreaks of the early 21<sup>st</sup> century mostly intact, and this work suggests several practical steps that may be taken to maintain them despite changes to the climate that are already being realized. Projections based on anthropogenic climate change scenarios forecast conversion of many grassland-margin forests to bunchgrass ecosystems over the course of the 21<sup>st</sup> century, beginning as early as 2025 (Hamann & Wang, 2006). The pace of this conversion is not a foregone conclusion. Characteristics of the

environment around individual trees can modulate the individual tree's response to changes brought about by climate or disturbance, to a degree that silvicultural intervention can prolong the existence of essential habitat features. Most prescriptions would require enough trees to be removed that the interventions would be commercially viable timber harvests. These harvests will provide time for careful study of the realized effects of climate change on the ground, allowing confident long-term planning to meet mule deer winter range and Douglas-fir timber production objectives on the landscape.

#### 6.4. Suggested topics for future research:

In addition to the pollen-core analysis addressing the hypothesis of dynamic range margins driving disturbance patterns over recent centuries, three other topics of future research are suggested:

- Mitigation of drought stress by the creation of persistent canopy gaps during juvenile spacing or early commercial thinning. This dissertation is focused on primary-growth stands and primary-growth stands with large sawtimber removed, and may not be transferable to even-aged stands managed from initiation.
- 2. Extent of Douglas-fir beetle mass-attacks in healthy trees under increased Douglas-fir beetle population pressure, and comparison of brood production between these healthy host trees and dead, diseased, or fire-damaged trees. This study finds that recent mortality is most likely without precedent within the past three centuries, and suggests close attention in the context of climate warming.
- 3. Population genetics of Douglas-fir extending along river valleys from the dry interior Chilcotin region to the Pacific Ocean via the Bute Inlet. The traits selectively retained along this narrow 'bridge' may add to the basic understanding of the effect of climate on the processes of evolution and migration of tree species (Figure 6.2).



Figure 6.2: Continuity of Douglas-fir from the coast to the interior 'dry belt' via the Bute Inlet. Stands containing Douglas-fir (BC Vegetation Resources Inventory; primary, secondary, or tertiary species) overlaying the mean annual precipitation (mm; "MAP") from 1961 to 1990 (www.climatewna.com accessed 2017), showing the 'bridge' of Douglas-fir from the high-precipitation coastal region to the dry interior areas described in this dissertation (study area corresponds to the northeast quadrant of this map

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## 8. Appendix A: R Scripts Used in Analyses

## 8.1. Introduction

The following scripts are those used for the analyses in this dissertation, in some cases modified and noted to be used as examples with data stored in the UNBC Tree Ring Lab folder called "R Scripts for Dendro." If these folders are not available to you and you wish to acquire the example data, write to <u>both nthompso@unbc.ca</u> and <u>neil.thompson@maine.edu</u>, both of which should be monitored for the foreseeable future. These scripts "should" work with any properly formatted ringwidth measurement files in Tucson or Heidelberg format (use the program TRiCYCLE available at <u>http://www.tridas.org/software.php</u> to convert between formats). Substituting [format=c("tucson")] for [format=c("heidelberg")] or vice versa will allow you to use the other format.

# 8.2. Ring width to basal area increments (Chapters 2, 3, and 4)

# This script converts raw ring width measurements from the Tucson format to basal area increments in mm2

# Last edited by Neil Thompson on January 21, 2016

# Please copy this script and examples to your own directory so you do not overwrite the original

# Developed using R 3.2.2.

# Example dataset provided is a subsample of one site from Neil Thompson's Ph.D. dissertation work

# You may need to use the latest version of dplR to use the tree averaging command. The latest version is available here https://r-forge.r-project.org/R/?group\_id=1105

# Load dplR (https://cran.r-project.org/web/packages/dplR/index.html)
library(dplR)

# Set working directory
setwd(choose.dir(default = "", caption = "Select folder"))

# To confirm successgetwd()# It won't take you to the directory the first time, so you will have to navigate manually. It will be automatic after the first one.

# Read the raw ring width data file (Tucson format) in as the tag "dro" dro <- read.rwl (file.choose (new = FALSE), format = c("tucson"))

# Read the distance to pith data file, measured in millimeters. Two labeled columns ("series" and "d2pith" in mm) must be present and match the above format d2p <- read.csv(file.choose (new = FALSE))</pre>

# Calculate the annual BAI of each series droB <- bai.in(rwl = dro, d2pith = d2p) # If no d2pith file is available, then substitute "d2pith = NULL"

# To average the cores within a tree (example COL01B)
droB.ids <- read.ids(droB, stc = c(3, 2, 1))
# where 3 is the number of characters defining site (COL)
# 2 is the number of characters defining the tree (01)
# 1 is the character defining core within tree (B)</pre>

View(droB.ids) # Confirm that there are the correct number of trees, cores, sites # Calculate the tree level mean across cores, retaining years with missing values droB.treeMean <- treeMean(droB, droB.ids, na.rm=TRUE) # Tree names are dropped but order is retained, will have to add in later

# Write a CSV file of the output
write.csv(droB.treeMean, file = "droB.csv")

# Convert mm2 to cm2 if desired

# Manually check your output: calculate the basal area increment of a single ring using a ruler and the area formula (pi\*r2)

# Calculate the total basal area in Excel by summing each annual increment.

# Reverse the above area calculation to calculate the diameter [2\*(sqrt(area/pi))]. This better look something like your field DBH measurements.

# 8.3. Climate correlations and response functions (Chapters 2 and 5)

# COPY THE EXAMPLE FOLDER TO YOUR OWN DIRECTORY so that you do not overwrite or clutter the original

# This script will take you through climate correlations and response functions using the latest R package as of January 2016

# Prepared by Neil Thompson, 12 January 2016 for use in the UNBC Dendrochronology lab

# Download R and packages dplR and treeclim

# http://cran.us.r-project.org/

# http://www.r-bloggers.com/installing-r-packages/

# https://cran.r-project.org/web/packages/treeclim/index.html

# https://cran.r-project.org/web/packages/dplR/index.html

# Materials (examples provided in this folder):

# 1. Crossdated ring width measurements in Tucson format

# 2. Monthly temperature data in column format (see example; columns are Year, jan, feb, mar, etc.)

# 3. Monthly precipitation data in column format (see example; columns are Year, jan, feb, mar, etc.)

# Monthly data for BC are available here: http://www.ec.gc.ca/dccha-ahccd/ but will require some curation to meet the format (no heading labels or extra columns)

# To use these scripts, copy them to the R command console in the order that they appear # My notes are indicated by #hashtags and are ignored by the program; they may be copied with commands

# The following line is a command, having no hashtag 2+2

# The following line stores the mathematical argument "2+2" as "y" using the < and - (<-) characters

y <- 2+2 y

# This method is used to store complex equations and datasets as simple characters throughout the script

# Copy and paste everything from here to #######Correlation###### to the command console and follow the prompts

# Set the working directory interactively (the version of this folder that you copied to your own directory)

setwd(choose.dir(default = "", caption = "Select folder"))

# Clear the workspace
rm(list=ls())

# Load dplR and bootRes
library(dplR)
library(treeclim)

# Load temperature and precipitation tables interactively
temp <- read.table (file.choose (new = FALSE))
prec <- read.table (file.choose (new = FALSE))</pre>

# Load site interactively
X1<- read.rwl (file.choose (new = FALSE), format = c("tucson"))</pre>

# Detrending, 50 year cubic smoothing spline (to change spline length to X, set"nyrs=X" below) X2 <- detrend(X1, y.name = names(X1), make.plot = TRUE, method = c("Spline"), nyrs=50, f = 0.5, verbose = FALSE, return.info = FALSE)

# Build a residual chronology using a biweight mean X3 <- chron(X2, prefix="xx", biweight = TRUE, prewhiten = TRUE)</pre>

X <- dcc (chrono=X3, climate = list(temp, prec), selection = -6:9, method = "correlation", moving = FALSE, var\_names = c("temp", "prec")) plot(X)

XX <- dcc (chrono=X3, climate = list(temp, prec), selection = -6:9, method = "correlation", moving = TRUE, win\_size=35, win\_offset = 5, var\_names = c("temp", "prec")) plot(XX)

plot(XX)
dev.off()

XXStat <- dcc (chrono=X3, climate = list(temp, prec), selection = -6:9, method = "correlation", moving = TRUE, win\_size=35, win\_offset = 5, var\_names = c("temp", "prec"), ci = 0.05, boot = "stationary") plot(XXStat)

#### 

X1 <- dcc (chrono=X3, climate = list(temp, prec), selection = -6:9, method = "response", moving = FALSE, var\_names = c("temp", "prec")) plot(X1)

XX1 <- dcc (chrono=X3, climate = list(temp, prec), selection = -6:9, method = "response", moving = TRUE, win\_size=35, win\_offset = 5, var\_names = c("temp", "prec")) plot(XX1)

## 8.4. Generation of .tre files (Chapter 5)

This script repeats for each of the 45 sites, but only two iterations are shown for brevity.

# Load dplR (https://cran.r-project.org/web/packages/dplR/index.html)
library(dplR)

# Set working directory
setwd(choose.dir(default = "", caption = "Select folder"))

# To confirm successgetwd()# It won't take you to the directory the first time, so you will have to nagivage manually. It will be automatic after the first one.

# Read the raw ring width data file (Heidelberg format) in as the tag "X1" X1 <- read.rwl ("ABR(01).fh", format = c("heidelberg"))

# Detrending, modnegexp X1a <- detrend(X1, y.name = names(X1), make.plot = TRUE, method = c("ModNegExp"), verbose = FALSE, return.info = FALSE)

# Detrending, 150 year cubic smoothing spline (to change spline length to X, set"nyrs=X"
below)
X2 <- detrend(X1a, y.name = names(X1a), make.plot = TRUE, method = c("Spline"),
nyrs=50, f = 0.5, verbose = FALSE, return.info = FALSE)</pre>

# To average the cores within a tree (example COL01B) X2.ids <- read.ids(X2, stc = c(3, 2, 1)) # where 3 is the number of characters defining site (COL) # 2 is the number of characters defining the tree (01) # 1 is the character defining core within tree (B)

View(X2.ids) # Confirm that there are the correct number of trees, cores, sites

# Calculate the tree level mean across cores, retaining years with missing values X2.M <- treeMean(X2, X2.ids, na.rm=TRUE) # Tree names are dropped but order is retained, will have to add in later # Write a tre file of the output
write.tucson(X2.M, fname = "ABR.tre")

## #######END########

## 

# Read the raw ring width data file (Heidelberg format) in as the tag "X1" X1 <- read.rwl ("ACS(01).fh", format = c("heidelberg"))

# Detrending, modnegexp X1a <- detrend(X1, y.name = names(X1), make.plot = TRUE, method = c("ModNegExp"), verbose = FALSE, return.info = FALSE)

# Detrending, 150 year cubic smoothing spline (to change spline length to X, set"nyrs=X"
below)
X2 <- detrend(X1a, y.name = names(X1a), make.plot = TRUE, method = c("Spline"),
nyrs=50, f = 0.5, verbose = FALSE, return.info = FALSE)</pre>

# To average the cores within a tree (example COL01B)
X2.ids <- read.ids(X2, stc = c(3, 2, 1))
# where 3 is the number of characters defining site (COL)
# 2 is the number of characters defining the tree (01)
# 1 is the character defining core within tree (B)</pre>

View(X2.ids) # Confirm that there are the correct number of trees, cores, sites

# Calculate the tree level mean across cores, retaining years with missing values X2.M <- treeMean(X2, X2.ids, na.rm=TRUE) # Tree names are dropped but order is retained, will have to add in later

# Write a tre file of the output write.tucson(X2.M, fname = "ACS.tre")

#######END########

#### 9. Appendix B: AIC Calculation and Top Ranked Models for Chapter 3

Calculation tables of Akaike's Information Criterion for small sample sizes (AIC*c*) from the log likelihood and sample size in each drought year. Models with AIC*c* differences ("AIC DIFF") <2 were considered to be ties and are full outputs of the multinomial logistic regression are reported in the tables following the AIC*c* calculation.

**1988** minAICc= 1768.4

-912.74

-898.13

16

16

Mixed 2

Mixed 2

n=907 AIC Log exp(-Likelihood DIFF Κ AIC **AIC**<sub>C</sub> 1/2delta) w Full 20 -863.72 1767.43 1768.4 0.0 0.87 1.0000 Less resistance -909.06 1854.9 < 0.01 18 1854.13 86.5 0.0000 Less coordinates 16 -870.31 1772.61 1773.2 4.8 0.08 0.0887 Less elevation 18 -868.58 1773.15 1773.9 5.5 0.05 0.0627 Elevation 2 -964.33 1932.66 1932.7 164.3 < 0.01 0.0000 Site level -924.29 10 1868.58 1868.8 100.4 < 0.01 0.0000 Tree level -904.74 1829.47 1829.7 < 0.01 0.0000 10 61.3 Mixed 1 -879.44 1782.88 1783.2 14.8 < 0.01 0.0006 12

1959 minAICc= 1692.0 n=904 AIC Log exp(-Κ Likelihood AIC AIC<sub>C</sub> DIFF W 1/2delta) Full 20 1696.0 3.9 0.1397 -827.50 1695.00 0.12 Less resistance -895.96 1827.91 1828.7 136.7 < 0.01 0.0000 18 Less coordinates 16 -839.66 1711.32 1711.9 19.9 < 0.01 0.0000 Less elevation -827.62 1691.24 1692.0 0.0 0.87 1.0000 18 Elevation 2 -981.36 1966.72 1966.7 274.7 < 0.01 0.0000 Site level 10 -952.62 1925.25 1925.5 233.5 < 0.01 0.0000 22.9 Tree level 10 -847.31 1714.62 1714.9 < 0.01 0.0000 Mixed 1 12 -843.89 1711.78 1712.1 20.1 < 0.01 0.0000

1857.48

1858.1

89.7

< 0.01

0.0000

0.0000

1828.25

1828.9

136.8

< 0.01

minAICc=	1886.5

```
n=896
```

1946

		Log			AIC		exp(-
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-924.59	1889.18	1890.1	3.6	0.11	0.1651
Less resistance	18	-926.48	1888.95	1889.7	3.2	0.18	0.2023
Less coordinates	16	-932.89	1897.79	1898.4	11.9	< 0.01	0.0026
Less elevation	18	-924.88	1885.76	1886.5	0.0	0.87	1.0000
Elevation	2	-983.28	1970.55	1970.6	84.0	< 0.01	0.0000
Site level	10	-941.68	1903.36	1903.6	17.1	< 0.01	0.0002
Tree level	10	-965.66	1951.33	1951.6	65.0	< 0.01	0.0000
Mixed 1	12	-934.68	1893.35	1893.7	7.2	0.02	0.0277
Mixed 2	16	-930.17	1892.35	1893.0	6.4	0.03	0.0401

1938

n=893

minAICc= 1785.8

	K	Log Likelihood	AIC	AIC <sub>C</sub>	AIC DIFF	w	exp(- 1/2delta)
				-			
Full	20	-872.43	1784.87	1785.8	0.0	0.97	1.0000
Less resistance	18	-943.77	1923.55	1924.3	138.5	< 0.01	0.0000
Less coordinates	16	-881.46	1794.93	1795.5	9.7	0.01	0.0078
Less elevation	18	-878.35	1792.70	1793.5	7.6	0.02	0.0218
Elevation	2	-974.48	1952.97	1953.0	167.1	< 0.01	0.0000
Site level	10	-964.16	1948.32	1948.6	162.7	< 0.01	0.0000
Tree level	10	-908.38	1836.77	1837.0	51.2	< 0.01	0.0000
Mixed 1	12	-893.08	1810.16	1810.5	24.7	< 0.01	0.0000
Mixed 2	16	-944.57	1921.14	1921.8	135.9	< 0.01	0.0000

minAICc= 1832.0

n=890

	К	Log Likelihood	AIC	AICc	AIC DIFF	w	exp(- 1/2delta)
Full	20	-896.32	1832.65	1833.6	1.6	0.29	0.4456
Less resistance	18	-911.52	1859.04	1859.8	27.8	< 0.01	0.0000
Less coordinates	16	-903.94	1839.87	1840.5	8.5	0.01	0.0143
Less elevation	18	-897.61	1831.21	1832.0	0.0	0.64	1.0000
Elevation	2	-977.49	1958.98	1959.0	127.0	< 0.01	0.0000
Site level	10	-963.51	1947.02	1947.3	115.3	< 0.01	0.0000
Tree level	10	-908.96	1837.92	1838.2	6.2	0.03	0.0458
Mixed 1	12	-906.91	1837.82	1838.2	6.2	0.03	0.0456
Mixed 2	16	-911.73	1855.47	1856.1	24.1	< 0.01	0.0000

1905

minAICc= 1617.3

	Log				AIC		
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-791.34	1622.68	1623.7	6.4	0.04	0.0410
Less resistance	18	-858.38	1752.76	1753.6	136.3	< 0.01	0.0000
Less coordinates	16	-792.32	1616.65	1617.3	0.0	0.96	1.0000
Less elevation	18	-801.37	1638.75	1639.6	22.3	< 0.01	0.0000
Elevation	2	-928.94	1861.89	1861.9	244.6	< 0.01	0.0000
Site level	10	-903.14	1826.29	1826.5	209.3	< 0.01	0.0000
Tree level	10	-838.42	1696.84	1697.1	79.8	< 0.01	0.0000
Mixed 1	12	-815.36	1654.71	1655.1	37.8	< 0.01	0.0000
Mixed 2	16	-862.46	1756.93	1757.6	140.3	< 0.01	0.0000

minAICc= 1620.0

n=794

	K	Log Likelihood	AIC	AIC <sub>C</sub>	AIC DIFF	w	exp(- 1/2delta)
Full	20	-789.47	1618.94	1620.0	0.0	0.47	1.0000
Less resistance	18	-796.29	1628.58	1629.5	9.4	0.01	0.0089
Less coordinates	16	-793.84	1619.68	1620.4	0.4	0.80	0.8374
Less elevation	18	-793.49	1622.97	1623.9	3.8	0.14	0.1473
Elevation	2	-928.94	1861.89	1861.9	241.9	< 0.01	0.0000
Site level	10	-843.13	1706.27	1706.5	86.5	< 0.01	0.0000
Tree level	10	-808.50	1637.00	1637.3	17.3	< 0.01	0.0002
Mixed 1	12	-800.26	1624.52	1624.9	4.9	0.08	0.0865
Mixed 2	16	-796.62	1625.24	1625.9	5.9	0.05	0.0519

1842

minAICc= 1305.7

	Log			AIC			exp(-
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-632.26	1304.52	1305.7	0.0	1.00	1.0000
Less resistance	18	-704.43	1444.85	1445.8	140.1	< 0.01	0.0000
Less coordinates	16	-669.24	1370.49	1371.2	65.5	< 0.01	0.0000
Less elevation	18	-640.55	1317.11	1318.1	12.4	< 0.01	0.0021
Elevation	2	-792.18	1588.35	1588.4	282.7	< 0.01	0.0000
Site level	10	-731.76	1483.52	1483.8	178.1	< 0.01	0.0000
Tree level	10	-691.11	1402.21	1402.5	96.8	< 0.01	0.0000
Mixed 1	12	-671.40	1366.81	1367.2	61.5	< 0.01	0.0000
Mixed 2	16	-707.07	1446.14	1446.9	141.2	< 0.01	0.0000

n=588							
		Log			AIC		exp(-
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-529.63	1099.26	1100.7	2.9	0.19	0.2319
Less resistance	18	-585.78	1207.55	1208.8	110.9	< 0.01	0.0000
Less coordinates	16	-537.19	1106.38	1107.3	9.5	0.01	0.0086
Less elevation	18	-530.31	1096.62	1097.8	0.0	0.81	1.0000
Elevation	2	-642.87	1289.75	1289.8	191.9	< 0.01	0.0000
Site level	10	-621.54	1263.07	1263.5	165.6	< 0.01	0.0000
Tree level	10	-551.48	1122.96	1123.3	25.5	< 0.01	0.0000
Mixed 1	12	-549.00	1121.99	1122.5	24.7	< 0.01	0.0000
Mixed 2	16	-586.00	1204.00	1204.9	107.1	< 0.01	0.0000

minAICc= 1097.8

1772

1800

minAICc= 845.6

	Log			AIC			exp(-
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-407.38	854.76	856.6	11.0	< 0.01	0.0042
Less resistance	18	-466.93	969.86	971.4	125.7	< 0.01	0.0000
Less coordinates	16	-408.07	848.14	849.3	3.7	0.13	0.1591
Less elevation	18	-407.96	851.92	853.4	7.8	0.02	0.0205
Elevation	2	-507.84	1019.68	1019.7	174.1	< 0.01	0.0000
Site level	10	-490.51	1001.02	1001.5	155.8	< 0.01	0.0000
Tree level	10	-414.18	848.36	848.8	3.2	0.16	0.2032
Mixed 1	12	-410.49	844.97	845.6	0.0	0.81	1.0000
Mixed 2	16	-467.14	966.28	967.5	121.8	< 0.01	0.0000

n=438							
	K	Log Likelihood	AIC	AICo	AIC DIFF	142	exp(- 1/2delta)
	K	Likelinood	me	mee	DITT	VV	1/200110)
Full	20	-417.31	874.62	876.6	97.2	< 0.01	0.0000
Less resistance	18	-417.31	870.62	872.3	92.8	< 0.01	0.0000
Less coordinates	16	-399.91	831.82	833.1	53.7	< 0.01	0.0000
Less elevation	18	-370.90	777.80	779.4	0.0	0.81	1.0000
Elevation	2	-479.51	963.02	963.0	183.6	< 0.01	0.0000
Site level	10	-453.71	927.42	927.9	148.5	< 0.01	0.0000
Tree level	10	-405.30	830.60	831.1	51.7	< 0.01	0.0000
Mixed 1	12	-407.32	838.64	839.4	59.9	< 0.01	0.0000
Mixed 2	16	-421.40	874.80	876.1	96.7	< 0.01	0.0000

minAICc= 779.4

1734

1760

minAICc= 614.8

		Log			AIC		
	Κ	Likelihood	AIC	AIC <sub>C</sub>	DIFF	W	1/2delta)
Full	20	-286.14	612.28	614.8	0.0	0.87	1.0000
Less resistance	18	-320.21	676.42	678.5	63.7	< 0.01	0.0000
Less coordinates	16	-300.78	633.56	635.2	20.4	< 0.01	0.0000
Less elevation	18	-290.24	616.49	618.5	3.7	0.13	0.1547
Elevation	2	-382.77	769.54	769.6	154.8	< 0.01	0.0000
Site level	10	-354.57	729.14	729.8	115.0	< 0.01	0.0000
Tree level	10	-307.16	634.31	635.0	20.2	< 0.01	0.0000
Mixed 1	12	-306.36	636.71	637.6	22.8	< 0.01	0.0000
Mixed 2	16	-323.07	678.15	679.8	65.0	< 0.01	0.0000

1717
------

minAICc= 473.6

	K	Log Likelihood	AIC	AIC	AIC DIFF	w	exp(- 1/2delta)
							//
Full	20	-215.42	470.84	473.9	0.3	0.27	0.8634
Less resistance	18	-262.02	560.03	562.5	88.9	< 0.01	0.0000
Less coordinates	16	-219.83	471.66	473.6	0.0	0.31	1.0000
Less elevation	18	-219.04	474.09	476.6	2.9	0.07	0.2288
Elevation	2	-311.30	626.60	626.6	153.0	< 0.01	0.0000
Site level	10	-275.15	570.30	571.1	97.4	< 0.01	0.0000
Tree level	10	-227.58	475.16	475.9	2.3	0.10	0.3157
Mixed 1	12	-224.51	473.03	474.1	0.5	0.24	0.7776
Mixed 2	16	-266.23	564.45	566.4	92.8	< 0.01	0.0000

	Robust					
resilcd1988	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base outcome)					
2						
lwmean	0.029419	0.03091510	0.95	0.341	-0.0311736	0.0900116
ahm	0.053303	0.03672830	1.45	0.147	-0.0186831	0.1252893
solar	0.000000	0.0000039	-0.45	0.652	-0.0000009	0.0000006
elev	0.003558	0.00125330	2.84	0.005	0.0011011	0.0060138
resist1988	2.188537	0.79328470	2.76	0.006	0.6337273	3.7433460
prior1988	-0.000497	0.00023660	-2.10	0.036	-0.0009604	-0.0000329
age1988	0.001735	0.00189490	0.92	0.360	-0.0019794	0.0054484
ba1988	-0.000001	0.00000244	-0.33	0.739	-0.0000056	0.0000040
easting	0.000003	0.00000581	0.60	0.550	-0.0000079	0.0000149
northing	0.000004	0.00000854	0.44	0.663	-0.0000130	0.0000205
_cons	-13.904640	14.21691000	-0.98	0.328	-41.7692800	13.9600000
3						
lwmean	0.094984	0.03359190	2.83	0.005	0.0291456	0.1608232
ahm	0.019592	0.07805370	0.25	0.802	-0.1333905	0.1725743
solar	-0.000001	0.00000062	-1.32	0.187	-0.0000020	0.0000004
elev	0.001932	0.00232020	0.83	0.405	-0.0026160	0.0064790
resist1988	4.817027	1.08506300	4.44	< 0.0001	2.6903420	6.9437110
prior1988	-0.000658	0.00027130	-2.43	0.015	-0.0011900	-0.0001267
age1988	-0.000469	0.00227540	-0.21	0.837	-0.0049282	0.0039910
ba1988	0.000002	0.00000300	0.52	0.605	-0.0000043	0.0000074
easting	-0.000004	0.00000794	-0.54	0.592	-0.0000198	0.0000113
northing	-0.000016	0.00001490	-1.04	0.296	-0.0000448	0.0000136
_cons	10.989060	24.26692000	0.45	0.651	-36.5732400	58.5513500

		Robust				
resilcd1959	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base outcome)					
2						
lwmean	-0.056653	0.02541890	-2.23	0.026	-0.1064731	-0.0068330
ahm	0.007371	0.03312190	0.22	0.824	-0.0575471	0.0722885
solar	0.000000	0.00000043	-0.39	0.694	-0.0000010	0.0000007
resist1959	3.138056	0.59780630	5.25	< 0.0001	1.9663770	4.3097350
prior1959	-0.000313	0.00021970	-1.42	0.154	-0.0007434	0.0001177
age1959	-0.000742	0.00120850	-0.61	0.539	-0.0031109	0.0016264
ba1959	-0.000002	0.00000180	-1.30	0.192	-0.0000059	0.0000012
easting	-0.000004	0.00000370	-1.13	0.260	-0.0000114	0.0000031
northing	0.000009	0.00000414	2.23	0.026	0.0000011	0.0000173
_cons	-1.192390	6.87437400	-0.17	0.862	-14.6659200	12.2811400
3						
lwmean	-0.020750	0.03386960	-0.61	0.540	-0.0871330	0.0456335
ahm	0.052262	0.04395850	1.19	0.234	-0.0338948	0.1384195
solar	0.000000	0.00000059	-0.66	0.512	-0.0000015	0.0000008
resist1959	5.933811	0.77739240	7.63	< 0.0001	4.4101500	7.4574720
prior1959	-0.001067	0.00034140	-3.12	0.002	-0.0017357	-0.0003974
age1959	-0.004443	0.00223280	-1.99	0.047	-0.0088190	-0.0000667
ba1959	-0.000004	0.00000209	-1.72	0.085	-0.0000077	0.0000005
easting	-0.000002	0.00000545	-0.45	0.652	-0.0000131	0.0000082
northing	0.000016	0.00000579	2.77	0.006	0.0000047	0.0000274
cons	-10.675210	10.70599000	-1.00	0.319	-31.6585700	10.3081500

		Robust				
resilcd1946	Coef.	Std. Err.	Z	P>z	[95% Conf.	Interval]
1	(base outcome)					
2						
	0.002026	0.02457120	0.60	0.490	0.0429225	0.001(020
Iwmean	0.023936	0.0345/120	0.69	0.489	-0.0438225	0.0910939
ahm	0.066024	0.02958000	2.23	0.026	0.0080481	0.1239996
solar	0.000000	0.0000034	0.27	0.788	-0.0000006	0.0000008
resist1946	0.603534	0.41210240	1.46	0.143	-0.2041714	1.4112400
prior1946	-0.000044	0.00024730	-0.18	0.859	-0.0005285	0.0004407
age1946	0.000312	0.00188680	0.17	0.869	-0.0033860	0.0040102
ba1946	0.000000	0.00000218	0.21	0.833	-0.0000038	0.0000047
easting	-0.000008	0.00000298	-2.77	0.006	-0.0000141	-0.0000024
northing	-0.000006	0.00000370	-1.63	0.104	-0.0000133	0.0000012
_cons	11.820400	5.36835100	2.20	0.028	1.2986300	22.3421800
3						
lwmean	0.071153	0.03432550	2.07	0.038	0.0038764	0.1384301
ahm	0.084156	0.03686400	2.28	0.022	0.0119040	0.1564080
solar	0.000000	0.00000044	0.72	0.474	-0.0000006	0.0000012
resist1946	0.691093	0.49570910	1.39	0.163	-0.2804790	1.6626650
prior1946	-0.000333	0.00022240	-1.50	0.134	-0.0007690	0.0001029
age1946	0.002199	0.00195790	1.12	0.261	-0.0016384	0.0060364
ba1946	-0.000004	0.00000222	-1.61	0.107	-0.0000079	0.0000008
easting	-0.000014	0.00000386	-3.55	< 0.0001	-0.0000213	-0.0000061
northing	-0.000012	0.00000517	-2.22	0.027	-0.0000216	-0.0000013
_cons	21.054490	7.47548000	2.82	0.005	6.4028200	35.7061600

resilcd1938	Coef.	Robust Std. Err.	Z	P>z	[95% Conf.	Interval]
1	(base outcome)					
	(					
2						
lwmean	-0.030118	0.02701030	-1.12	0.265	-0.0830571	0.0228211
ahm	-0.056953	0.05371610	-1.06	0.289	-0.1622350	0.0483282
solar	-0.000001	0.00000035	-2.07	0.038	-0.0000014	0.0000000
elev	-0.002594	0.00156390	-1.66	0.097	-0.0056586	0.0004716
resist1938	2.416910	0.66871360	3.61	< 0.0001	1.1062550	3.7275650
prior1938	-0.000337	0.00032530	-1.04	0.300	-0.0009743	0.0003007
age1938	-0.002982	0.00189560	-1.57	0.116	-0.0066972	0.0007335
ba1938	-0.000001	0.00000196	-0.31	0.755	-0.0000045	0.0000032
easting	-0.000001	0.00000575	-0.21	0.832	-0.0000125	0.0000100
northing	-0.000008	0.00000842	-0.97	0.332	-0.0000247	0.0000083
_cons	13.006570	15.10658000	0.86	0.389	-16.6017800	42.6149200
3						
lwmean	-0.048869	0.03268240	-1.50	0.135	-0.1129254	0.0151871
ahm	-0.120137	0.05914320	-2.03	0.042	-0.2360551	-0.0042180
solar	-0.000001	0.00000052	-1.86	0.063	-0.0000020	0.0000001
elev	-0.004057	0.00194910	-2.08	0.037	-0.0078775	-0.0002370
resist1938	6.106275	0.74073510	8.24	< 0.0001	4.6544610	7.5580890
prior1938	-0.001065	0.00042090	-2.53	0.011	-0.0018904	-0.0002405
age1938	-0.003928	0.00255640	-1.54	0.124	-0.0089382	0.0010826
ba1938	-0.000002	0.00000297	-0.55	0.581	-0.0000075	0.0000042
easting	0.000003	0.00000679	0.43	0.668	-0.0000104	0.0000162
northing	-0.000013	0.00001130	-1.16	0.247	-0.0000351	0.0000091
cons	13.590990	18.67833000	0.73	0.467	-23.0178700	50.1998400

А		Robust				
resilcd1931	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base outcome)					
	``´´´					
2						
lwmean	-0.012383	0.02634530	-0.47	0.638	-0.0640190	0.0392527
ahm	0.089744	0.05002070	1.79	0.073	-0.0082946	0.1877829
solar	0.000000	0.00000045	0.33	0.742	-0.0000007	0.0000010
elev	0.000976	0.00148320	0.66	0.510	-0.0019307	0.0038835
resist1931	1.011700	0.46614560	2.17	0.030	0.0980716	1.9253290
prior1931	-0.000862	0.00023720	-3.64	< 0.0001	-0.0013273	-0.0003974
age1931	0.001713	0.00190230	0.90	0.368	-0.0020158	0.0054412
ba1931	0.000001	0.00000221	0.27	0.784	-0.0000037	0.0000049
easting	0.000008	0.00000486	1.73	0.083	-0.0000011	0.0000180
northing	0.000002	0.00000798	0.22	0.830	-0.0000139	0.0000174
_cons	-15.594400	13.21523000	-1.18	0.238	-41.4957700	10.3069600
3						
lwmean	-0.001115	0.03133570	-0.04	0.972	-0.0625314	0.0603023
ahm	0.044860	0.05945640	0.75	0.451	-0.0716724	0.1613923
solar	0.000001	0.00000059	1.03	0.305	-0.0000006	0.0000018
elev	-0.000722	0.00204500	-0.35	0.724	-0.0047302	0.0032861
resist1931	2.182757	0.53656200	4.07	< 0.0001	1.1311140	3.2343990
prior1931	-0.001502	0.00040940	-3.67	< 0.0001	-0.0023049	-0.0007000
age1931	0.002503	0.00227400	1.10	0.271	-0.0019544	0.0069594
ba1931	-0.000006	0.00000246	-2.26	0.024	-0.0000104	-0.0000007
easting	0.000003	0.00000607	0.46	0.646	-0.0000091	0.0000147
northing	-0.000009	0.00001040	-0.86	0.390	-0.0000292	0.0000114
cons	2.236028	18.06747000	0.12	0.902	-33.1755600	37.6476200

В		Robust				
resilcd1931	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base outcome)					
2						
lwmean	-0.008932	0.02674990	-0.33	0.738	-0.0613611	0.0434964
ahm	0.065470	0.05078140	1.29	0.197	-0.0340598	0.1649995
solar	0.000000	0.00000046	0.40	0.693	-0.0000007	0.0000011
resist1931	1.020697	0.46718520	2.18	0.029	0.1050306	1.9363630
prior1931	-0.000846	0.00023360	-3.62	< 0.0001	-0.0013034	-0.0003876
age1931	0.001858	0.00184020	1.01	0.313	-0.0017491	0.0054643
ba1931	0.000000	0.00000219	0.17	0.866	-0.0000039	0.0000047
easting	0.000006	0.00000466	1.23	0.219	-0.0000034	0.0000149
northing	-0.000003	0.00000502	-0.56	0.574	-0.0000127	0.0000070
_cons	-7.095796	9.13467700	-0.78	0.437	-24.9994300	10.8078400
3						
lwmean	-0.002931	0.03279180	-0.09	0.929	-0.0672014	0.0613400
ahm	0.061290	0.04865020	1.26	0.208	-0.0340631	0.1566421
solar	0.000001	0.00000060	0.99	0.321	-0.0000006	0.0000018
resist1931	2.179971	0.54427840	4.01	< 0.0001	1.1132050	3.2467370
prior1931	-0.001513	0.00040750	-3.71	< 0.0001	-0.0023115	-0.0007143
age1931	0.002395	0.00218900	1.09	0.274	-0.0018954	0.0066854
ba1931	-0.000005	0.00000241	-2.23	0.026	-0.0000101	-0.000007
easting	0.000005	0.00000463	0.99	0.320	-0.0000045	0.0000137
northing	-0.000006	0.00000505	-1.15	0.252	-0.0000157	0.0000041
cons	-3.619915	9.06618800	-0.40	0.690	-21.3893200	14.1494900

resilcd1905	Coef.	Robust Std. Err.	Z	P>z	[95% Conf.	Interval]
1	(base outcome)					
2						
lwmean	-0.079674	0.02784780	-2.86	0.004	-0.1342549	-0.0250935
ahm	-0.051085	0.03274720	-1.56	0.119	-0.1152686	0.0130981
solar	0.000001	0.00000045	2.63	0.008	0.0000003	0.0000021
elev	-0.001980	0.00078470	-2.52	0.012	-0.0035177	-0.0004418
resist1905	3.612302	0.69772640	5.18	< 0.0001	2.2447830	4.9798210
prior1905	-0.000638	0.00026700	-2.39	0.017	-0.0011614	-0.0001148
age1905	-0.000451	0.00227290	-0.20	0.843	-0.0049055	0.0040041
ba1905	0.000001	0.00000249	0.23	0.820	-0.0000043	0.0000054
_cons	2.837433	1.98128300	1.43	0.152	-1.0458100	6.7206760
3						
lwmean	-0.051762	0.03751540	-1.38	0.168	-0.1252913	0.0217664
ahm	-0.058098	0.04932430	-1.18	0.239	-0.1547723	0.0385755
solar	0.000001	0.00000080	1.63	0.102	-0.0000003	0.0000029
elev	-0.005186	0.00131280	-3.95	< 0.0001	-0.0077586	-0.0026124
resist1905	6.907991	1.19821700	5.77	< 0.0001	4.5595290	9.2564520
prior1905	-0.001586	0.00039300	-4.04	< 0.0001	-0.0023566	-0.0008160
age1905	-0.007084	0.00292880	-2.42	0.016	-0.0128238	-0.0013432
ba1905	0.000002	0.00000330	0.55	0.580	-0.0000046	0.0000083
_cons	4.889696	2.84491700	1.72	0.086	-0.6862394	10.4656300

А		Robust				
resilcd1869	Coef.	Std. Err.	Z	P>z	[95% Conf.	Interval]
1	(base out	come)				
	(********	)				
2						
lwmean	-0.001019	0.03927100	-0.03	0.979	-0.0779889	0.0759508
ahm	-0.073960	0.06315590	-1.17	0.242	-0.1977433	0.0498233
solar	0.000000	0.00000043	0.37	0.714	-0.0000007	0.0000010
elev	-0.002582	0.00199900	-1.29	0.196	-0.0065001	0.0013360
resist1869	0.474111	0.61583050	0.77	0.441	-0.7328950	1.6811160
prior1869	-0.000673	0.00030950	-2.18	0.030	-0.0012799	-0.0000668
age1869	-0.000756	0.00272770	-0.28	0.782	-0.0061023	0.0045899
ba1869	0.000002	0.00000335	0.71	0.477	-0.0000042	0.0000089
easting	-0.000009	0.00000714	-1.26	0.206	-0.0000230	0.0000050
northing	-0.000016	0.00001030	-1.53	0.126	-0.0000358	0.0000044
_cons	28.431750	19.28659000	1.47	0.140	-9.3692750	66.2327700
3						
lwmean	0.009676	0.04153380	0.23	0.816	-0.0717285	0.0910808
ahm	0.100954	0.08113240	1.24	0.213	-0.0580621	0.2599709
solar	0.000000	0.00000045	0.11	0.914	-0.0000008	0.0000009
elev	0.000405	0.00253060	0.16	0.873	-0.0045546	0.0053652
resist1869	1.917497	0.90732760	2.11	0.035	0.1391673	3.6958260
prior1869	-0.001625	0.00043010	-3.78	< 0.0001	-0.0024680	-0.0007820
age1869	-0.007247	0.00347900	-2.08	0.037	-0.0140654	-0.0004278
ba1869	0.000004	0.00000435	0.96	0.338	-0.0000044	0.0000127
easting	0.000000	0.00000828	0.03	0.975	-0.0000160	0.0000165
northing	0.000001	0.00001530	0.04	0.965	-0.0000294	0.0000307
cons	-3.869999	25.39381000	-0.15	0.879	-53.6409600	45.9009600

В		Robust				
resilcd1869	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base out	come)				
1	(buse but	conic)				
2						
lwmean	-0.015949	0.03948870	-0.40	0.686	-0.0933454	0.0614474
ahm	-0.001669	0.03811590	-0.04	0.965	-0.0763750	0.0730367
elev	-0.000145	0.00092450	-0.16	0.875	-0.0019574	0.0016665
solar	0.000000	0.00000044	0.07	0.947	-0.0000008	0.0000009
resist1869	0.602097	0.64607140	0.93	0.351	-0.6641794	1.8683740
prior1869	-0.000787	0.00033760	-2.33	0.020	-0.0014490	-0.0001258
age1869	-0.001063	0.00283270	-0.38	0.707	-0.0066150	0.0044890
ba1869	0.000003	0.00000356	0.97	0.331	-0.0000035	0.0000104
_cons	0.817651	2.57532900	0.32	0.751	-4.2299000	5.8652020
3						
lwmean	0.010486	0.04059950	0.26	0.796	-0.0690874	0.0900597
ahm	0.097426	0.04403420	2.21	0.027	0.0111206	0.1837314
elev	0.000316	0.00103380	0.31	0.760	-0.0017103	0.0023420
solar	0.000000	0.00000046	0.10	0.923	-0.0000009	0.0000009
resist1869	1.883131	0.85742340	2.20	0.028	0.2026118	3.5636500
prior1869	-0.001636	0.00045220	-3.62	< 0.0001	-0.0025225	-0.0007499
age1869	-0.007298	0.00356520	-2.05	0.041	-0.0142857	-0.0003105
ba1869	0.000004	0.00000441	0.96	0.338	-0.0000044	0.0000129
cons	-2.799774	2.50191000	-1.12	0.263	-7.7034280	2.1038800

resilcd1842	Coef.	Robust Std. Err.	Z	P>z	[95% Conf.	Interval]
1	<i>a i</i>	``				
1	(base out	come)				
2						
lwmean	0.019515	0.03772090	0.52	0.605	-0.0544167	0.0934464
ahm	-0.101725	0.09004310	-1.13	0.259	-0.2782060	0.0747566
solar	0.000001	0.00000050	1.36	0.172	-0.0000003	0.0000017
elev	-0.004536	0.00287140	-1.58	0.114	-0.0101634	0.0010922
resist1842	3.921190	0.96965120	4.04	< 0.0001	2.0207090	5.8216720
prior1842	-0.000349	0.00033240	-1.05	0.294	-0.0010002	0.0003027
age1842	0.000093	0.00361660	0.03	0.979	-0.0069951	0.0071818
ba1842	-0.000004	0.00000471	-0.74	0.458	-0.0000127	0.0000057
easting	-0.000001	0.00000985	-0.05	0.957	-0.0000198	0.0000188
northing	-0.000012	0.00001370	-0.84	0.40	-0.0000383	0.0000153
_cons	14.389920	26.71764000	0.54	0.59	-37.9756800	66.7555300
3						
lwmean	0.033931	0.04281680	0.79	0.428	-0.0499887	0.1178500
ahm	0.128021	0.14322250	0.89	0.371	-0.1526899	0.4087321
solar	0.000001	0.00000066	1.05	0.293	-0.0000006	0.0000020
elev	-0.000197	0.00393660	-0.05	0.96	-0.0079128	0.0075183
resist1842	9.250511	1.30960400	7.06	< 0.0001	6.6837340	11.8172900
prior1842	-0.001181	0.00049230	-2.40	0.016	-0.0021463	-0.0002164
- age1842	-0.001547	0.00426570	-0.36	0.717	-0.0099079	0.0068133
ba1842	-0.000003	0.00000554	-0.47	0.635	-0.0000135	0.0000082
easting	0.000031	0.00001650	1.85	0.064	-0.0000018	0.0000630
northing	0.000007	0.00001610	0.41	0.681	-0.0000250	0.0000382
cons	-53.179050	39.67630000	-1.34	0.18	130.9432000	24.5850700

		Robust				
resilcd1800	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base out	come)				
2						
lwmean	-0.037723	0.03763700	-1.00	0.316	-0.1114905	0.0360437
ahm	-0.074213	0.03862110	-1.92	0.055	-0.1499088	0.0014832
solar	0.000001	0.00000054	2.21	0.027	0.0000001	0.0000023
resist1800	1.945396	0.42645530	4.56	< 0.0001	1.1095590	2.7812330
prior1800	-0.001080	0.00039170	-2.76	0.006	-0.0018478	-0.0003125
age1800	-0.003965	0.00253790	-1.56	0.118	-0.0089395	0.0010090
ba1800	0.000004	0.00000436	0.96	0.338	-0.0000044	0.0000127
easting	-0.000007	0.00000512	-1.34	0.179	-0.0000169	0.0000032
northing	-0.000007	0.00000643	-1.05	0.292	-0.0000194	0.0000058
_cons	15.131330	10.44804000	1.45	0.148	-5.3464570	35.6091200
3						
lwmean	-0.054968	0.05378680	-1.02	0.307	-0.1603883	0.0504522
ahm	-0.041501	0.05284630	-0.79	0.432	-0.1450781	0.0620758
solar	0.000002	0.00000066	2.63	0.008	0.0000004	0.0000030
resist1800	3.820334	0.54304600	7.04	< 0.0001	2.7559830	4.8846840
prior1800	-0.002565	0.00056750	-4.52	< 0.0001	-0.0036772	-0.0014527
age1800	-0.005268	0.00389990	-1.35	0.177	-0.0129111	0.0023762
ba1800	0.000003	0.00000996	0.33	0.742	-0.0000162	0.0000228
easting	-0.000004	0.00000706	-0.54	0.588	-0.0000177	0.0000100
northing	-0.000017	0.00000968	-1.78	0.076	-0.0000362	0.0000018
cons	17.218410	14.25989000	1.21	0.227	-10.7304600	45.1672800

resilcd1772	Coef.	Robust Std. Err.	Z	P>z	[95% Conf.	Interval]
1	(base out	come)				
2						
2	0 020222	0.025207(0	0.96	0.200	0.0005251	0.0200602
Twmean	-0.030333	0.03530760	-0.80	0.390	-0.0995351	0.0388683
ahm	-0.05/36/	0.03599210	-1.59	0.111	-0.1279099	0.0131765
elev	-0.000467	0.00103410	-0.45	0.652	-0.0024939	0.0015599
resist1772	3.758332	0.77101950	4.87	< 0.0001	2.2471610	5.2695020
prior1772	0.000219	0.00047710	0.46	0.646	-0.0007160	0.0011542
ba1772	-0.000010	0.00000466	-2.13	0.034	-0.0000190	-0.0000008
_cons	1.138637	2.06593500	0.55	0.582	-2.9105210	5.1877950
3						
lwmean	-0.034600	0.04672490	-0.74	0.459	-0.1261789	0.0569795
ahm	-0.094993	0.05429260	-1.75	0.080	-0.2014041	0.0114189
elev	-0.000450	0.00154890	-0.29	0.771	-0.0034859	0.0025857
resist1772	7.724760	1.16056100	6.66	< 0.0001	5.4501030	9.9994180
prior1772	-0.001184	0.00087650	-1.35	0.177	-0.0029016	0.0005343
ba1772	-0.000010	0.00000793	-1.31	0.189	-0.0000259	0.0000051
cons	-0.164125	3.60135100	-0.05	0.964	-7.2226430	6.8943920
		Robust				
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resilcd1760	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(1)	``				
1	(base out	come)				
2						
lwmean	-0.093879	0.04237650	-2.22	0.027	-0.1769357	-0.0108227
ahm	0.040846	0.02584590	1.58	0.114	-0.0098114	0.0915026
solar	0.000000	0.00000043	-0.62	0.533	-0.0000011	0.0000006
resist1760	3.276225	0.78583800	4.17	< 0.0001	1.7360110	4.8164390
prior1760	-0.001968	0.00057390	-3.43	0.001	-0.0030928	-0.0008430
age1760	-0.007572	0.00369560	-2.05	0.040	-0.0148151	-0.0003286
ba1760	0.000013	0.00000705	1.82	0.069	-0.0000010	0.0000267
easting	0.000014	0.00000314	4.36	< 0.0001	0.0000075	0.0000198
northing	-0.000020	0.00000592	-3.35	0.001	-0.0000314	-0.0000082
_cons	-0.852170	5.62941600	-0.15	0.880	-11.8856200	10.1812800
3						
lwmean	-0.067336	0.06409600	-1.05	0.293	-0.1929619	0.0582899
ahm	0.015304	0.05951870	0.26	0.797	-0.1013508	0.1319584
solar	-0.000001	0.0000084	-1.23	0.220	-0.0000027	0.0000006
resist1760	7.407947	1.03346500	7.17	< 0.0001	5.3823940	9.4335010
prior1760	-0.004005	0.00067240	-5.96	< 0.0001	-0.0053229	-0.0026873
age1760	-0.015487	0.00507140	-3.05	0.002	-0.0254268	-0.0055472
ba1760	0.000026	0.00000919	2.86	0.004	0.0000083	0.0000443
easting	0.000015	0.00000621	2.33	0.020	0.0000023	0.0000267
northing	-0.000036	0.00001010	-3.60	< 0.0001	-0.0000561	-0.0000165
_cons	9.504638	13.08287000	0.73	0.468	-16.1373200	35.1466000

resilcd1734	Coef.	Robust Std. Err.	Z	P>z	[95% Conf.	Interval]
1	4	``````````````````````````````````````				
1	(base out	come)				
2						
lwmean	-0.096108	0.04631140	-2.08	0.038	-0.1868769	-0.0053395
ahm	-0.196514	0.09787100	-2.01	0.045	-0.3883372	-0.0046900
elev	-0.002129	0.00267750	-0.80	0.427	-0.0073765	0.0031190
solar	0.000000	0.00000066	-0.44	0.661	-0.0000016	0.0000010
resist1734	1.632822	0.74054210	2.20	0.027	0.1813863	3.0842580
prior1734	-0.000762	0.00069580	-1.09	0.274	-0.0021255	0.0006021
age1734	-0.006116	0.00340190	-1.80	0.072	-0.0127831	0.0005522
ba1734	0.000004	0.00000759	0.55	0.58	-0.0000107	0.0000191
easting	-0.000030	0.00001250	-2.38	0.017	-0.0000540	-0.0000052
northing	-0.000011	0.00001160	-0.94	0.347	-0.0000335	0.0000118
_cons	55.870580	27.92960000	2.00	0.045	1.1295670	110.6116000
3						
lwmean	-0.158666	0.06342550	-2.5	0.012	-0.2829776	-0.0343541
ahm	-0.307386	0.13068980	-2.35	0.019	-0.5635336	-0.0512390
elev	-0.006162	0.00399390	-1.54	0.123	-0.0139898	0.0016662
solar	-0.000001	0.00000098	-0.93	0.353	-0.0000028	0.0000010
resist1734	7.162789	1.21212600	5.91	< 0.0001	4.7870660	9.5385120
prior1734	-0.004705	0.00111480	-4.22	< 0.0001	-0.0068894	-0.0025196
age1734	-0.016758	0.00719910	-2.33	0.020	-0.0308684	-0.0026485
ba1734	0.000023	0.00001500	1.51	0.132	-0.0000068	0.0000520
easting	-0.000037	0.00001670	-2.20	0.028	-0.0000695	-0.0000040
northing	-0.000032	0.00001980	-1.62	0.105	-0.0000709	0.0000067
cons	88.211330	39.66616000	2.22	0.026	10.4670900	165.9556000

А		Robust				
resilcd1717	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base out	come)				
2						
lwmean	0.055846	0.04449780	1.26	0.209	-0.0313687	0.1430597
ahm	-0.168046	0.07428980	-2.26	0.024	-0.3136514	-0.0224409
solar	0.000001	0.00000075	1.21	0.228	-0.0000006	0.0000024
elev	-0.003329	0.00239880	-1.39	0.165	-0.0080301	0.0013729
resist1717	5.448682	1.07584500	5.06	< 0.0001	3.3400640	7.5573000
prior1717	-0.000656	0.00065940	-0.99	0.320	-0.0019480	0.0006369
age1717	-0.008596	0.00488160	-1.76	0.078	-0.0181640	0.0009716
ba1717	0.000018	0.00001210	1.45	0.148	-0.0000062	0.0000413
easting	-0.000016	0.00000989	-1.61	0.108	-0.0000353	0.0000035
northing	-0.000005	0.00001420	-0.34	0.736	-0.0000327	0.0000231
_cons	27.324910	25.49037000	1.07	0.284	-22.6352900	77.2851200
3						
lwmean	0.081418	0.05579420	1.46	0.144	-0.0279369	0.1907722
ahm	-0.031985	0.13609200	-0.24	0.814	-0.2987205	0.2347502
solar	0.000000	0.0000087	-0.55	0.58	-0.0000022	0.0000012
elev	0.002905	0.00366090	0.79	0.428	-0.0042705	0.0100800
resist1717	11.446810	2.06430900	5.55	< 0.0001	7.4008410	15.4927800
prior1717	0.000096	0.00124900	0.08	0.939	-0.0023518	0.0025442
age1717	-0.004609	0.00740820	-0.62	0.534	-0.0191285	0.0099111
ba1717	-0.000017	0.00001980	-0.86	0.389	-0.0000559	0.0000218
easting	-0.000007	0.00001180	-0.61	0.541	-0.0000302	0.0000159
northing	0.000019	0.00001810	1.05	0.295	-0.0000165	0.0000544
cons	-15.993710	32.96529000	-0.49	0.628	-80.6045000	48.6170700

В		Robust				
resilcd1717	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base out	come)				
2						
lwmean	0.024911	0.05018340	0.50	0.620	-0.0734469	0.1232683
ahm	-0.065385	0.04671330	-1.40	0.162	-0.1569417	0.0261712
solar	0.000001	0.00000063	1.44	0.151	-0.0000003	0.0000021
elev	-0.001412	0.00088040	-1.60	0.109	-0.0031370	0.0003141
resist1717	6.325952	1.34646300	4.70	< 0.0001	3.6869320	8.9649710
prior1717	-0.000653	0.00071220	-0.92	0.359	-0.0020489	0.0007428
age1717	-0.007621	0.00533410	-1.43	0.153	-0.0180760	0.0028331
ba1717	0.000017	0.00001590	1.08	0.281	-0.0000141	0.0000484
_cons	-0.984830	2.75549300	-0.36	0.721	-6.3854970	4.4158370
3						
lwmean	0.063862	0.06055520	1.05	0.292	-0.0548242	0.1825480
ahm	0.001412	0.07763640	0.02	0.985	-0.1507524	0.1535767
solar	0.000000	0.00000073	-0.62	0.534	-0.0000019	0.0000010
elev	0.002216	0.00170240	1.30	0.193	-0.0011207	0.0055527
resist1717	12.605840	2.16859100	5.81	< 0.0001	8.3554770	16.8562000
prior1717	-0.000096	0.00121180	-0.08	0.937	-0.0024715	0.0022786
age1717	-0.003295	0.00738280	-0.45	0.655	-0.0177646	0.0111755
ba1717	-0.000017	0.00002100	-0.82	0.412	-0.0000583	0.0000239
cons	-10.798790	3.54756600	-3.04	0.002	-17.7518900	-3.8456850

С		Robust				
resilcd1717	Coef.	Std. Err.	Z	$P>_Z$	[95% Conf.	Interval]
1	(base out	come)				
2						
lwmean	0.007133	0.05077830	0.14	0.888	-0.0923912	0.1066562
ahm	-0.050639	0.05192840	-0.98	0.329	-0.1524163	0.0511392
elev	-0.001004	0.00093700	-1.07	0.284	-0.0028407	0.0008323
resist1717	6.489108	1.26563700	5.13	< 0.0001	4.0085060	8.9697110
prior1717	-0.000472	0.00063100	-0.75	0.455	-0.0017085	0.0007649
ba1717	0.000006	0.00000973	0.64	0.524	-0.0000129	0.0000253
_cons	-0.910793	2.66641000	-0.34	0.733	-6.1368600	4.3152730
3						
lwmean	0.069485	0.06571590	1.06	0.290	-0.0593161	0.1982854
ahm	0.016067	0.07481370	0.21	0.830	-0.1305647	0.1626994
elev	0.002872	0.00160280	1.79	0.073	-0.0002697	0.0060133
resist1717	12.702030	2.12768200	5.97	< 0.0001	8.5318530	16.8722100
prior1717	0.000080	0.00115980	0.07	0.945	-0.0021934	0.0023528
ba1717	-0.000024	0.00001320	-1.80	0.072	-0.0000497	0.0000022
_cons	-12.810780	3.81384800	-3.36	0.001	-20.2857800	-5.3357720

# 10. Appendix C: ANOVA output tables from Chapter 3

The following output tables include the output of two-way ANOVA models. Drought resistance is the dependent variable, transformed as noted in the summary output in Chapter 3. Explanatory variables are the growth release status (binary; biyear) and site (sitecd). Outputs proceed from the most recent year backwards. Years 1959 and 1760, which did not meet assumptions of normality and were excluded from the main results table, include scatterplots of residual vs. fitted values for information.

1	Number of obs = Root MSE =	879 25209	5 R-squar 6 Adj R-s	ed = quared =	0.6024 0.5688
Source	Partial SS	df	MS	F	Prob>F
Model	77.599343	68	1.1411668	17.96	0.0000
bi1988 sitecd	.2162829 48.910509	1 44	.2162829	3.40 17.49	0.0654
bi1988#sitecd	1.3969323	23	.06073619	0.96	0.5222
Residual	51.223129	806	.06355227		
Total	128.82247	874	.14739413		

# . anova box bi##sitecd

. hettest

```
Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of box
chi2(1) = 33.94
```

Prob > chi2 = 0.0000



1	Number of obs =			858 R-squared =		
I	Root MSE =		23321 Adj R-s		quared =	0.5887
Source	Partial SS	¢	lf	MS	F	Prob>F
Model	69.713063	ł	55	1.2675102	23.31	0.0000
bi1959	.10177584		1	.10177584	1.87	0.1717
sitecd	51.325274	4	14	1.1664835	21.45	0.0000
bi1959#sitecd	1.006887	1	0.0	.1006887	1.85	0.0487
Residual	43.618386	80	02	.05438702		
Total	113.33145	85	57	.13224207		

. hettest

```
Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of box
chi2(1) = 4.35
Prob > chi2 = 0.0369
```



1	Number of obs =	84	4 R-squa	red =	0.5202
1	Root MSE =	.17679	6 Adj R-	squared =	0.4686
Source	Partial SS	df	MS	F	Prob>F
Model	25.793969	82	.31456059	10.06	0.0000
bi1946	. 6227216	1	.6227216	19.92	0.0000
sitecd	15.723506	44	.35735241	11.43	0.0000
bi1946#sitecd	1.8109009	37	.04894327	1.57	0.0185
Residual	23.786381	761	.03125674		
Total	49.580349	843	.05881417		

. hettest

```
Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of box
chi2(1) = 0.57
Prob > chi2 = 0.4496
```

1	Number of obs = Root MSE =	81 . 17002	.5 R-squa 4 Adj R-	red = squared =	0.5323 0.4764
Source	Partial SS	df	MS	F	Prob>F
Model	23.922597	87	. 27497238	9.51	0.0000
bi1938 sitecd	.75793503 15.372778	1 44	.75793503	26.22 12.09	0.0000
Residual	21.016209	42 727	.03071175	1.06	0.3675
Total	44.938807	814	.05520738		

# . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of box

> chi2(1) = 1.58 Prob > chi2 = 0.2090

## . anova box bi##sitecd

1	Number of obs =	82	23 R-squa	red =	0.6078
1	Root MSE =	.21510	02 Adj R-	squared =	0.5632
Source	Partial SS	df	MS	F	Prob>F
Model	52.920493	84	. 63000587	13.62	0.0000
bi1931	.50477013	1	.50477013	10.91	0.0010
sitecd	35.732801	44	.81210912	17.55	0.0000
bi1931#sitecd	2.7347254	39	.07012116	1.52	0.0243
Residual	34.146356	738	.04626878		
Total	87.066849	822	.10592074		

### . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
 Ho: Constant variance
 Variables: fitted values of box
 chi2(1) = 0.00

Prob > chi2 = 0.9891

1	Number of obs = Root MSE =	76 .15232	7 R-squar 4 Adj R-s	ed = quared =	0.5446 0.5031
Source	Partial SS	df	MS	F	Prob>F
Model	19.480119	64	.30437685	13.12	0.0000
bi1905 sitecd	.39494594 15.948098	1 44	.39494594 .36245676	17.02 15.62	0.0000
Residual	16.288329	702	.02320275	1.55	0.0630
Total	35.768448	766	.0466951		

# . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of box

> chi2(1) = 1.47 Prob > chi2 = 0.2258

#### . anova box bi##sitecd

1	Number of obs =	674	4 R-squar	ed =	0.6276
I	Root MSE =	.159551	1 AdjR-s	quared =	0.5781
Source	Partial SS	df	MS	F	Prob>F
Model	25.487852	79	.32263104	12.67	0.0000
bi1869	.01284311	1	.01284311	0.50	0.4778
sitecd	14.597114	44	.3317526	13.03	0.0000
bi1869#sitecd	1.0326404	34	.03037178	1.19	0.2120
Residual	15.121221	594	.0254566		
Total	40.609073	673	.06034038		

# . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of box

chi2(1) = 3.12 Prob > chi2 = 0.0775

1	Number of obs = Root MSE =	59 .13731	97 R-squar 9 Adj R-s	ed = squared =	0.6227 0.5725
Source	Partial SS	df	MS	F	Prob>F
Model	16.367833	70	.23382618	12.40	0.0000
bi1842 sitecd	.04830292	1 44	.04830292	2.56 14.19	0.1101
bi1842#sitecd	1.2773497	25	.05109399	2.71	0.0000
Residual	9.9184807	526	.01885643		
Total	26.286313	596	.04410455		

### . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of box

> chi2(1) = 2.68 Prob > chi2 = 0.1018

#### . anova box bi##sitecd

1	Number of obs =	44	0 R-squa	red =	0.5104
1	Root MSE =	.35147	2 Adj R-	squared =	0.4030
Source	Partial SS	df	MS	F	Prob>F
Model	46.366313	79	.58691535	4.75	0.0000
bi1800	1.5885022	1	1.5885022	12.86	0.0004
sitecd	32.939752	42	.78427982	6.35	0.0000
bi1800#sitecd	5.8896827	36	.1636023	1.32	0.1064
Residual	44.471725	360	.12353257		
Total	90.838038	439	.20692036		

# . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of box
chi2(1) = 1.87

Prob > chi2 = 0.1716

1	Number of obs = Root MSE =	35 .23540	2 R-squar 4 Adj R-se	ed = quared =	0.6600 0.5884
Source	Partial SS	df	MS	F	Prob>F
Model	31.191312	61	.51133299	9.23	0.0000
bi1772 sitecd	.028934	1	.028934	0.52	0.4705
bi1772#sitecd	.84479418	21	.04022829	0.73	0.8056
Residual	16.070361	290	.05541504		
Total	47.261673	351	.13464864		

#### . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of box

> chi2(1) = 0.14 Prob > chi2 = 0.7111

. anova box bi##sitecd

1	Number of obs = Root MSE =	29 . 23325	8 R-square 7 Adj R-sq	d = puared =	0.6421 0.5533
Source	Partial SS	df	MS	F	Prob≻F
Model	23.22756	59	.39368746	7.24	0.0000
bi1760 sitecd	.3089998 9.0782107	1 37	.3089998	5.68 4.51	0.0180 0.0000
bi1760#sitecd	1.5365282	21	.07316801	1.34	0.1479
Residual	12.94926	238	.05440866		
Total	36.17682	297	.12180748		

# . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of box
chi2(1) = 9.72
Prob > chi2 = 0.0018



```
. anova sqre bi##sitecd
```

1	Number of obs =	232	R-squa:	red =	0.6405
		.001000	, maj r	squarea -	0.0001
Source	Partial SS	df	MS	F	Prob>F
Model	2.0961119	53	.03954928	5.98	0.0000
bi1734	.13189142	1	.13189142	19.95	0.0000
sitecd	1.6968964	32	.05302801	8.02	0.0000
bi1734#sitecd	.09734288	20	.00486714	0.74	0.7848
Residual	1.1766709	178	.00661051		
Total	3.2727828	231	.01416789		

. hettest

```
Breusch-Pagan / Cook-Weisberg test for heteroskedasticity
Ho: Constant variance
Variables: fitted values of sqre
chi2(1) = 0.36
Prob > chi2 = 0.5459
```

### . anova sqre bi##sitecd

1	Number of obs = Root MSE =	19 .09114	5 R-squar 9 Adj R-s	ed = quared =	0.6942 0.5992
Source	Partial SS	df	MS	F	Prob>F
Model	2.7916118	46	.06068721	7.30	0.0000
bi1717 sitecd	.05699735 1.8311086	1 30	.05699735	6.86 7.35	0.0097
bi1717#sitecd Residual	.18094507	15 148	.012063	1.45	0.1308
Total	4.0212109	194	.02072789		

## . hettest

Breusch-Pagan / Cook-Weisberg test for heteroskedasticity Ho: Constant variance Variables: fitted values of sqre

> chi2(1) = 0.97 Prob > chi2 = 0.3256