Mortality and Growth of Residual Whitebark Pine in High Elevation Variable Retention Harvest Sites in Southeastern British Columbia

by
Jenny M. Berg
B.Sc., University of Victoria, 2014

A Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Geography

University of Victoria

Supervisory Committee

Mortality and Growth of Residual Whitebark Pine in High Elevation Variable Retention Harvest Sites in Southeastern British Columbia

by
Jenny M. Berg
B.Sc. University of Victoria, 2014

Supervisory Committee

Dr. Dan J. Smith, Supervisor
(Department of Geography)

Dr. Rene Alfaro, Departmental Member
(Department of Geography)

Abstract

The rapid decline of whitebark pine (*Pinus albicaulis*) throughout its range is a pressing conservation issue. This keystone species endures multiple pressures toward local extirpation including forest health agents, forest succession, and climate change. Currently, silviculture practices are categorized as a stand-level strategy aimed at effective whitebark pine restoration/conservation. In this thesis I retrospectively evaluated the mortality and growth of whitebark pine at five low-retention ESSF silviculture treatments located in southeastern British Columbia, Canada. I found that whitebark pine reserve trees in low retention silviculture prescriptions were prone to elevated post-harvest mortality due to windthrow within the initial five-year post-harvest interval. Post-harvest growth rates indicated that mature reserve trees were likely to demonstrate increased radial growth after disturbance and that pre-harvest growth rates due to suspected forest health agents can minimize these increases. A two sample Welch t-test found no significant difference between the resistance index of control and reserve trees one year after harvest in three of the four sites examined, suggesting that radial growth reduction was negligible for surviving trees. Visual examination of the post-harvest reserve tree chronologies, however, showed a common two to three-year growth lag. Reserve trees indicated a significant difference in the recovery period for the harvest event year with a one-year lag in two of the four sites. However, this result was confounded by the following: (1) one of the sites showed a negative radial growth trend pre-harvest; and, (2) a pointer year analysis identified an inflated growth response in the control trees for the same year for the second site. These growth-climate relationships indicated that whitebark pine tree chronologies in closed-canopy forests were energy-limited systems with a significant negative correlation to July SPEI.

Table of Contents

List of Tables

List of Figures

Acknowledgements

I would like to thank my supervisor, Dr. Dan Smith, for the opportunity to be a member of the University of Victoria Tree Ring Lab (UVTRL). Thank you for your support throughout my master's program. I would also like to extend my gratitude to my committee member, Dr. Rene Alfaro, who has encouraged me from the beginning of my interest in dendrochronology.

A special mention to the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development for providing the funding for this research. Thank you to Dr. Michael Murry for your support for my fieldwork, by helping with logistics and providing a great crew of field assistants, Katy Fraser, Paul Mosin and Marnie Duthie-Holt. These were truly important learning and career building moments.

My time at UVic was also shaped by my co-operative education experiences, and I am thankful for my time with the Silviculture Branch, at the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development. Thank you to Jodi Axelson who has been a great mentor for helping me remain curious and refine my thinking about forest health.

Thank you to the wonderfully supportive individuals at the Pacific Forestry Centre that have continued to encourage me throughout this process. A special mention to Gurp Thandi for his help with mapping my field sites.

Dedication

The following thesis is dedicated to my mother. You have been my greatest supporter throughout my academic journey. Your encouraging words have helped me persevere. I am eternally grateful to have you as my guide.

Chapter 1: Introduction

1.1 Introduction

There has been growing global acceptance in the last 30 years towards implementing partial harvest silvicultural practices. Today, partial harvest practices are seen as an opportunity to help support the conservation and restoration of whitebark pine. Traditional clearcut logging practices are understood to result in less diverse and complex stands with respect to unmanaged stands. Variable retention (VR), also known as partial harvest, is a recognized silvicultural practice that aims to retain some portion of the original stand structure and function (e.g., Franklin et al., 1997; Thorpe and Thomas, 2007). This management practice aligns with conservation and restoration efforts as it aims to balance other values of forest use and function over the dominating paradigm of maximizing timber profit values (Gustafsson et al., 2012). For example, there is an increasing effort to retain whitebark pine (WPB) amongst subalpine cutblocks in southeastern British Columbia (B.C.) as it is an endangered tree species. However, the success of such efforts as they pertain to the survivorship and resilience of this specific species of reserve trees is still largely unknown. This study will examine the success of such practices by quantifying tree mortality and radial growth response of retained WBP trees in southeastern B.C.

1.1.1 Whitebark Pine

Whitebark pine (*Pinus albicaulis*) is an ecologically significant tree in subalpine forests in western Canada and the United States. Tomback and Kendall (2001) describe WBP as a keystone species because of its cornerstone attributes as a food source for wildlife and its influence on structural aspects such as plant species assemblage. WBP plays an essential role at high elevations as an early successional species because it can establish on sites that are often characterized as being hard, cold and with poor soils. Fifty-six percent of the global population of WBP is located within B.C. and is often found within the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone (ECCC, 2017).

Mature old-growth forests at high elevations are increasingly becoming a part of the commodity market as lower accessible valley bottoms have been harvested. The implications for old-growth WBP in these high-elevation stands have an important bearing on both conservation and timber supply efforts as the ESSF covers approximately 14 million ha in B.C. (Brang et al., 2003). Furthermore, the decline of WBP due to cumulative pressures such as white pine blister rust (Arno and Hoff, 1989; Kendall and Keane, 2001), mountain pine beetle (Logan and Powell, 2001; Wong and Daniels, 2017), successional replacement (Arno, 1980; Murray et al., 2000) and climate change (McKenney et al., 2007; Logan et al., 2010) have placed this species into the spotlight as a conservation priority. WBP is the only tree species in Canada to obtain COSEWIC endangered status and in 2012 was placed under the Species at Risk Act (ECCC, 2017). Thus, there is an increased interest in examining the outcomes of VR for WBP as a tool for conservation/restoration. The success of VR practices are crucial for all managed forests, but are of particular interest for sensitive ecosystems and/or vulnerable species.

1.1.2 Variable Retention

VR harvesting methods allow for structural heterogeneity in managed stands, with the rationale of mimicking the spatial variability akin to natural disturbances. Reserve trees are analogous to biological legacies that remain after natural disturbances, as in the case of fire (Franklin et al., 2002). Legacy trees are considered to be ‘lifeboats’ since they provide habitat to a host of small mammals, birds, and insects (Aubury et al., 1999; Matveinen-Huju et al., 2006). Moreover, legacy trees serve as a connection to the past, representing an early seral state if dominant, mature trees are retained (Franklin et al., 2002; Rudolphi et al., 2014). Often late-successional features such as old-growth trees are prioritized by land managers in VR as the decrease of large, old trees is expressed as a global concern (Carter et al., 2017). The cones from these mature trees provide a seed source for regeneration. However, if reserve trees fail to survive after harvest or have drastically reduced vigor to support stem function or support cone production, the success of such silviculture practices is questionable. The literature indicates that reserve trees are at a higher risk of mortality in the time frame directly after harvest, an interval known for elevated post-harvest mortality (Jonson et al., 2007) or pulse mortality (Olson et al., 2015). To date the most cited rate of mortality associated with failure to meet land management objectives is reported in Coates' (1997) seminal paper, suggesting that mortality rates greater than 10% should constitute a failure in VR harvest practices. Therefore, quantifying mortality is an integral part of VR assessment.

In addition to monitoring the incidence of reserve tree mortality, the radial growth of reserve trees can be used to evaluate the success of VR objectives. The growth rate of trees is one means to monitor and assess forest health. Surviving reserve trees that demonstrate a return to pre-harvest growth rates are considered resilient individuals (Pimm, 1984; Lloret et al., 2011) and therefore support the intended structure and function adherent with VR objectives. The implications for a negative radial response post-harvest can affect a tree's adaptability to become more wind-firm, increasing the risk of windthrow mortality (Holgén et al., 2003). However, to date, there is some question as to whether or not mature trees have the capacity to respond positively to reduced competition given the general consensus that mature old-growth trees display a decrease in annual radial growth increment due to senesce and, therefore, are less likely to respond positively to removal of competition. Bebber et al. (2004) however, demonstrated that mature white pine in the boreal transition zone in eastern Canada did display significant growth release as a result of reduced competition contradicting the assumptions of age-related decline. The ability of old-growth trees in low retention sites to demonstrate positive radial growth response post-harvest helps to meet land managers' target objectives.

1.2 Thesis Objectives and Outline

To date, there is little evidence that VR practices are succeeding in their attempts to preserve WBP reserve trees in high-elevation ESSF harvest sites. This thesis will address WBP reserve tree survivorship and radial growth by retrospectively sampling VR harvest sites, in southeastern B.C. Research was conducted at VR harvest sites using a multi-level approach, combining forest measurement data with dendrochronological techniques. Chapter 2, reviews the study area and climate of the selected VR harvest sites of southeastern B.C. Chapter 3, describes the methodology used to examine: (1) mortality rates; (2) growth rates of mature whitebark pine reserve trees in low retention harvest sites; and, (3) the growth-climate relationships of this high-elevation tree species. Chapter 4 presents the results of the research. Chapter 5 includes a discussion of the findings and reviews the limitations arising from the research. Chapter 6 includes a summary of the thesis findings, outlines implications and recommendations for forest management and concludes with suggestions for future research.

1.3 Background

1.3.1 Mortality

Survivorship of WBP reserve trees offers an important measure useful for assessing the success of VR strategies. Substantial mortality in reserve trees represents a failure to meet land management objectives (Thorpe and Thomas, 2007). The implications of increased mortality of reserve trees could affect the intended structural objectives of VR including the proportion of green trees, snags and nurse logs (Franklin et al., 2002). For example, windthrow is one of the most cited concerns of VR related mortality and as such an underestimation of the magnitude or persistence of windthrow mortality could lead to excessive coarse woody debris on the landscape. The implications of this underestimation has long-term relevance to high-elevation sites since, as noted by Brown et al. (1998), high-elevation downed tree species can persist in subalpine environments for over 150 years. Therefore, this long-term structural change has the capacity to persist in affecting ecological characteristics including runoff and erosion, seedling establishment, nutrient cycling, and biodiversity (Campbell et al., 2019). Furthermore, forest management strategies recognize that elevated mortality contributes to shifts in forest development, for example, lower stand complexity (Coates, 1997), increased risk of insect outbreaks (Bouget and Duelli, 2004), and altered nitrogen reserves (Mikkelson et al., 2016). Land managers need to be able to quantify post-harvest mortality in terms of how much and how fast in order to meet sustainable forestry objectives.

Elevated mortality rates are an important contributing factor to the long-term achievements of post-harvest structural objectives (Thorpe and Thomas, 2007). For example, elevated mortality rates of mature reserve trees negate the intended structural benefits in post-harvest stands if mortality rates are so exacerbated it does not match the stand regeneration rate (Bladon et al., 2008). The diversity of post-harvest mortality rates are contentious on silviculture prescription, site and species specificity (Caspersen, 2006; Thorpe et al., 2007; Bladon et al., 2008). However, there is a general consensus in the literature that as retention level decreases and dispersion level increases reserve tree mortality due to windthrow will increase (e.g., Maguire et al., 2006; Bladon et al., 2008). Solarik et al. (2012) suggest that elevated mortality response of windthrown trees in low retention sites is likely because reserve trees do not adjust quickly to new environmental conditions. The rate and extent of adaptation have been noted as being dependent on the site quality and level of thinning (Nilsen and Strand, 2008). Increased solar radiation, temperature variability and wind speed are the main contributing factors that dramatically affect microclimatic conditions after clearcut logging practices (Heithhecker and Halpern, 2007). Newly acclimating trees show increased mortality rates vs. background mortality in boreal forests (Bladon et al., 2008, Solarik et al., 2012), coastal forests (Maguire et al., 2006) and eastern hardwood forests (Martin et al., 2014). Thus, reserve trees in VR sites can be impacted by reductions in stand density leading to increased wind penetration causing stem breakage and uprooting (Ruel et al., 1995).

Huggard et al. (1999) note the importance of understanding the relationship between harvesting practices and windthrow in the ESSF as these high-elevation sites endure severe wind events, and frequent summer convective storms elevating the risk of windthrow. In addition, McLaughlin and Dumas (1996) indicated that forest health adds to the vulnerability of wind-induced mortality through pathogen agents that weaken stem function or result in root decay. This is relevant to the proposed study as forest health agents such as mountain pine beetle (*Dendroctonouns ponderosae* Hopkins) and white pine blister rust (*Cronartium ribicola* Fisch.)

can ‘eliminate the less vigorous individuals’ (Campbell and Antos, 2000) that may or may not be well represented in the selected reserve trees.

1.3.2 Growth Rates

The importance of studying growth rates in terms of VR is two-fold. First, the correlation between tree vigor and growth rate indicates that observed losses in radial growth lead to an increased risk of mortality (Bigler and Bugmann, 2003). Secondly, monitoring radial growth response is a valuable tool for assessing tree resilience (Lloret et al., 2011). From a VR perspective, this implies that reserve trees have the potential to recover to pre-disturbance growth rates following harvest (Pimm, 1984; Lloret et al., 2011). It has been well documented that overstorey tree removal results in accelerated succession in the remaining trees, examples of which include both natural thinning disturbance events such as insect outbreaks (e.g., Heath and Alfaro, 1990) and human-induced thinning events (e.g., Abrams and Nowacki, 1992). In such instances, these abrupt release events surpass pre-disturbance growth rates, primarily because the aforementioned studies examined young trees, saplings and suppressed trees (Jones and Thomas, 2004). To date, there are few studies which examine the response of older trees to gap openings in VR practices. Generally, old-growth trees are in a state of gradual tree-ring width decline known as senescence. In the boreal forest, radial growth has been shown to decline with stand age and an increase in stand density (Mailly et al., 2003; Alteyrac et al., 2005). Therefore, there is some question as to whether or not mature reserve trees have the potential to respond to reduced competition.

1.3.3 Growth-Climate Relationships

Through the measurement of tree-ring metrics, researchers can acquire empirical evidence to monitor forest response to climate change. The impact of climate change on forest health is an important consideration in forest management. To date, rising temperatures have been associated with forest dieback globally in some regions due to drought, while other regions have experienced increased insect disturbance (Allen et al., 2010). On the other hand, growth trends for tree species at higher elevations are speculated to increase due to increasing temperatures and/or CO_2 (Silva et al., 2016). This disparity adds to the complexity of understanding whether the growth response of old-growth trees is primarily an artifact of post-harvest disturbance or the additive result of climate warming. According to the linear aggregate model of growth developed by Cook (1987) (equation 1) radial growth is a combination of the following factors:

$$R_t = A_t + C_t + D_t + E_t \qquad (1)$$

where R_t is ring width at time *t,* A_t is the age-associated growth trend, C_t is the climatic signal, D_t is the disturbance signal, and E_t is the error term. In addition to elucidating the potential growth response of old-growth reserve trees post-harvest, the response of high-elevation trees is equally subjected to the implications of rising temperatures, as well as, extreme event years (i.e. drought). To date, the following research has emerged to tackle these complexities. In addition to elucidating the growth of reserve trees to selective harvest, it is important to also consider the influences of rising temperatures in these high-elevation trees, as well as, the effects of extreme events.

Primicia et al. (2015) indicate that not only were older trees more sensitive to climate than younger trees but elevation influenced the growth response in older trees. In addition, Zhang et al. (2018) found that site characteristics also asserted influence on age-related growth-climate sensitivity, whereby older trees in arid locations were generally more sensitive to climate whereas younger trees in mesic locations tended to be more sensitive to climate. In terms of VR thinning, light to moderate treatments were suggested to increase resilience of forests in the face of rising temperatures and increasing drought stress (Voelkeer et al., 2008; D'Amato et al., 2013).

1.4 Works Cited

Abrams, M. D., & Nowacki, G. J. (1992). Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Club*, *119*(1), 19-28.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Hwan Lim, J., Allard, G., Running, S.W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660-684.

Alteyrac, J., Zhang, S. Y., Cloutier, A., & Ruel, J. C. (2007). Influence of stand density on ring width and wood density at different sampling heights in black spruce (*Picea mariana* (Mill.) BSP). *Wood and Fiber Science*, *37*(1), 83-94.

Arno, S. F., & Hoff, R. J. (1989). Silvics of whitebark pine (*Pinus albicaulis*) (Vol. 253). US Department of Agriculture, Forest Service, Intermountain Research Station.

Aubry, K. B., Amaranthus, M. P., Halpern, C. B., White, J. D., Woodard, B. L., Peterson, C. E., Lagoudaki, C. A., & Horton, A. J. (1999). Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. *Northwest Science*, *73*(Special Issue), 12-26.

Bebber, D. P., Thomas, S. C., Cole, W. G., & Balsillie, D. (2004). Diameter increment in mature eastern white pine Pinus strobus L. following partial harvest of old-growth stands in Ontario, Canada. *Trees*, *18*(1), 29-34.

Bigler, C., & Bugmann, H. (2003). Growth-dependent tree mortality models based on tree rings. *Canadian Journal of Forest Research*, *33*(2), 210-221.

Bladon, K. D., Lieffers, V. J., Silins, U., Landhäusser, S. M., & Blenis, P. V. (2008). Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. *The Forestry Chronicle*, *84*(1), 70-75.

Bouget, C., & Duelli, P. (2004). The effects of windthrow on forest insect communities: a literature review. *Biological Conservation*, *118*(3), 281-299.

Brang, P., Moran, J., Puttonen, P., & Vyse, A. (2003). Regeneration of *Picea engelmannii* and *Abies lasiocarpa* in high-elevation forests of south-central British Columbia depends on nurse logs. *The Forestry Chronicle*, *79*(2), 273-279.

Brown, P. M., Shepperd, W. D., Mata, S. A., & McClain, D. L. (1998). Longevity of windthrown logs in a subalpine forest of central Colorado. *Canadian Journal of Forest Research, 28(6)*, 932-936.

Campbell, E. M., & Antos, J. A. (2000). Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Forest Research*, *30*(7), 1051-1059.

Campbell, J. L., Green, M. B., Yanai, R. D., Woodall, C. W., Fraver, S., Harmon, M. E., & Domke, G. M. (2019). Estimating uncertainty in the volume and carbon storage of downed coarse woody debris. *Ecological Applications*, *29*(2), e01844.

Carter, D. R., Seymour, R. S., Fraver, S., & Weiskittel, A. (2017). Reserve tree mortality in two expanding-gap silvicultural systems 20 years after establishment in the Acadian forest of Maine, USA. *Forest Ecology and Management*, *389*, 149-157.

Caspersen, J. P. (2006). Elevated mortality of residual trees following single-tree felling in northern hardwood forests. *Canadian Journal of Forest Research*, *36*(5), 1255-1265.

Coates, K.D. (1997) Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia. *Canadian Journal of Forest Research, 27(*10*)*, 1695-1701.

Cook, E. R. (1987). The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin, 47*, 37-59.

D'Amato, A. W., Bradford, J. B., Fraver, S., & Palik, B. J. (2013). Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, *23*(8), 1735-1742.

Environment and Climate Change Canada. (2017). Recovery Strategy for the Whitebark Pine (*Pinus albicaulis*) in Canada [Proposed], Recovery Strategy Series for the Species at Risk Act, Environment and Climate Change Canada, Ottawa.

Franklin, J. F., Berg, D. F., Thornburg, D., & Tappeiner, J. C. (1997). Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: *Kohm, K.A., Franklin, J.F. (Eds.)*, *Creating a Forestry for the 21st Century.* Island Press, Washington, DC, 111–140.

Franklin, J. F., Spies, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Berg, D. R., & Bible, K. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, *155*(1-3), 399-423.

Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Pastur, M.G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J.A., Wayne, A., & Franklin, J. (2012). Retention forestry to maintain multifunctional forests: a world perspective. *BioScience*, *62*(7), 633-645.

Heath, R., & Alfaro, R. I. (1990). Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: a case study. *Journal of the Entomological Society of British Columbia*, *87*, 16-21.

Holgén, P., Söderberg, U., & Hånell, B. (2003). Diameter increment in Picea abies shelterwood stands in northern Sweden. *Scandinavian Journal of Forest Research*, *18*(2), 163-167.

Huggard, D. J., Klenner, W., & Vyse, A. (1999). Windthrow following four harvest treatments in an Engelmann spruce-subalpine fir forest in southern interior British Columbia, Canada. *Canadian Journal of Forest Research*, *29*(10), 1547-1556.

Jones, T. A., & Thomas, S. C. (2004). The time course of diameter increment responses to selection harvests in Acer saccharum. *Canadian Journal of Forest Research*, *34*(7), 1525-1533.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgard, M., & Esseen, P.A. (2007). Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management, 242*(2-3), 306-313.

Kendall, K. C., & Keane, R. E. (2001). Whitebark pine decline: infection, mortality, and population trends. *Whitebark pine communities: ecology and restoration. Edited by DF Tomback, SF Arno, and RE Keane.* Island Press, Washington, DC, 221-242.

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: effects of successive low‐growth episodes in old ponderosa pine forests. *Oikos*, *120*(12), 1909-1920.

Logan, J. A., & Powell, J. A. (2001). Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, *47*(3), 160.

Logan, J. A., Macfarlane, W. W., & Willcox, L. (2010). Whitebark pine vulnerability to climate‐driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*, *20*(4), 895-902.

Mailly, D., Turbis, S., & Pothier, D. (2003). Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. *Canadian Journal of Forest Research*, *33*(3), 435-443.

Maguire, D. A., Mainwaring, D. B., & Halpern, C. B. (2006). Stand dynamics after variable-retention harvesting in mature Douglas-fir forests of Western North America. *Allgemeine Forst und Jagdzeitung, 177* (6/7)*,* 120-131.

Matveinen-Huju, K., Niemelä, J., Rita, H., & O'Hara, R. B. (2006). Retention-tree groups in clear-cuts: do they constitute 'life-boats' for spiders and carabids? *Forest Ecology and Management*, *230*(1-3), 119-135.

McKenney, D. W., Pedlar, J. H., Lawrence, K., Campbell, K., & Hutchinson, M. F. (2007). Potential impacts of climate change on the distribution of North American trees. *BioScience*, *57*(11), 939-948.

McLaughlin, J. A., & Dumas, M. T. (1996). Pathological implications of partial cutting in boreal mixedwood stands. *In: Smith, C.R., Crook, G.W. (Compilers)*, *Proceedings of the Advancing Boreal Mixedwood Management in Ontario, Sault Ste. Marie, Ont., October 17–19, 1995. Canadian Forestry Service, Sault Ste. Marie, Ontario,* 167–169.

Mikkelson, K. M., Lozupone, C. A., & Sharp, J. O. (2016). Altered edaphic parameters couple to shifts in terrestrial bacterial community structure associated with insect-induced tree mortality. *Soil Biology and Biochemistry*, *95*, 19-29.

Murray, M. P., Bunting, S. C., & Morgan, P. (2000). Landscape trends (1753–1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range of Idaho/Montana, USA. *Arctic, Antarctic, and Alpine Research*, *32*(4), 412-418.

Nilsen, P., & Strand, L. T. (2008). Thinning intensity effects on carbon and nitrogen stores and fluxes in a Norway spruce (*Picea abies* (L.) Karst.) stand after 33 years. *Forest Ecology and Management*, *256*(3), 201-208.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, *307*(5949), 321-326.

Primicia, I., Camarero, J. J., Janda, P., Čada, V., Morrissey, R. C., Trotsiuk, Bače, R., Teodosiu, M., & Svoboda, M. (2015). Age, competition, disturbance and elevation effects on tree and stand growth response of primary Picea abies forest to climate. *Forest Ecology and Management*, *354*, 77-86.

Rudolphi, J., Jönsson, M. T., & Gustafsson, L. (2014). Biological legacies buffer local species extinction after logging. *Journal of Applied Ecology*, *51*(1), 53-62.

Ruel, J. C. (1995). Understanding windthrow: silvicultural implications. *The Forestry Chronicle*, *71*(4), 434-445.

Silva, L. C., Sun, G., Zhu-Barker, X., Liang, Q., Wu, N., & Horwath, W. R. (2016). Tree growth acceleration and expansion of alpine forests: The synergistic effect of atmospheric and edaphic change. *Science Advances*, *2*(8), e1501302.

Solarik, K. A., Volney, W. J. A., Lieffers, V. J., Spence, J. R., & Hamann, A. (2012). Factors affecting white spruce and aspen survival after partial harvest. *Journal of Applied Ecology*, *49*(1), 145-154.

Thorpe, H. C., & Thomas, S. C. (2007). Partial harvesting in the Canadian boreal: success will depend on stand dynamic responses. *The Forestry Chronicle*, *83*(3), 319-325.

Thorpe, H. C., Thomas, S. C., & Caspersen, J. P. (2007). Residual-tree growth responses to partial stand harvest in the black spruce (*Picea mariana*) boreal forest. *Canadian Journal of Forest Research*, *37*(9), 1563-1571.

Voelker, S. L., Muzika, R. M., & Guyette, R. P. (2008). Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. *Forest Science*, *54*(1), 8-20.

Wong, C. M., & Daniels, L. D. (2017). Novel forest decline triggered by multiple interactions among climate, and introduced pathogen and bark beetles. *Global Change Biology*, *23*(5), 1926-1941.

Zhang, L., Jiang, Y., Zhao, S., Jiao, L., & Wen, Y. (2018). Relationships between tree age and climate sensitivity of radial growth in different drought conditions of Qilian Mountains, northwestern China. *Forests*, *9*(3), 135.

Chapter 2: Study Area

2.1 Study Sites

The study area was located within the Kootenay-Boundary Natural Resource Region of southeastern B.C. (Figure 2.1). A total of 5 VR sites were sampled within the elevation range between 1874 to 2001 m a.s.l. (hereafter m), which is representative of the mid-range of WBP ecosystem (900 to 3660 m).

Paturages Creek (49° 24' 21.96" N, 118° 43' 8.976" W) was located within the Boundary Timber Supply Area (TSA). The Boundary TSA is bounded on the west by the Okanagan Highland Range and Christina Range which is a subrange of the Monashee Mountains (Ministry of Forests, Lands, and Natural Resource Operations, 2014). Paturages Creek (PC) had the highest site elevation of all sites (2001 m) and was the furthest west. In addition, this gently sloping mesic site was predominantly southwesterly facing. Soils are sandy loams with a hard clay layer (Antos and Parish, 2002).

Three sites were sampled within the Invermere TSA, which is bounded on the west by the Purcell Mountains and the Rocky Mountain Trench to the east. Lavington (50° 2'26.15"N, 115°58'58.62"W) had a southwesterly aspect on a well-drained slope. Site elevation averaged around 1884 m. In addition to Lavington (LV), two more sites were sampled with the Invermere TSA. Findlay East (50°11'47.27"N, 116° 4'7.07" W) and Findlay West (50°11'36.924"N, 116°4'0.48" W) were two of the closest site locations among the five sites sampled. These two neighbouring sites were physically separated by ~ 100 m tree buffer and temporarily with different harvest years (Table 1). Topographically the two sites share very similar elevations, Findlay East (FE) had a slightly lower elevation at 1922 m compared with Findlay West (FW) at 1960 m. Slope variability between FW and FW are reported as 19.2 and 32.6, respectively.

A fifth study site, West Elk (49° 50' 44.23" N, 114° 57' 25.56"W) was located in the Cranbrook TSA. The Cranbrook TSA is bounded by the Canadian Rocky Mountains on the east and Purcell Mountains on the west, with the Rocky Mountain trench situated between the two outer ranges. West Elk (WE) had the furthest easting and is most closely associated with the Rocky Mountain trench. The site was located on a north-facing slope with an elevation at 1874 m. WBP found in these eastern and northern ranges typically grows on siliceous soils as opposed to those where limestone bedrock is present (Keane et al., 2012).

Although the sites sampled demonstrate an east-to-west gradient, this distribution doesn't encompass the most westerly ranges of WBP. Whitebark pine ecosystems are represented in the upper submaritime elevations on coastal ranges often associated with the Mountain Hemlock biogeoclimatic zone (Tomback et al., 2001). Reconnaissance travels to the Coastal Range in 2017 disqualified potential sites in this outermost western range due to recent fire disturbance. Therefore, the sampling sites used in this study are reflective of the easternmost ranges of WBP and do not include any sites that represent the coastal range of WBP. All five sites were associated with the Engelmann Spruce–Subalpine Fir biogeoclimatic zone (ESSF). The ESSF zone has an elevation between 1200 and 2300 m, these areas represent the highest forest cover types in B.C. (Meidinger & Pojar, 1991; Banner et al., 1993).

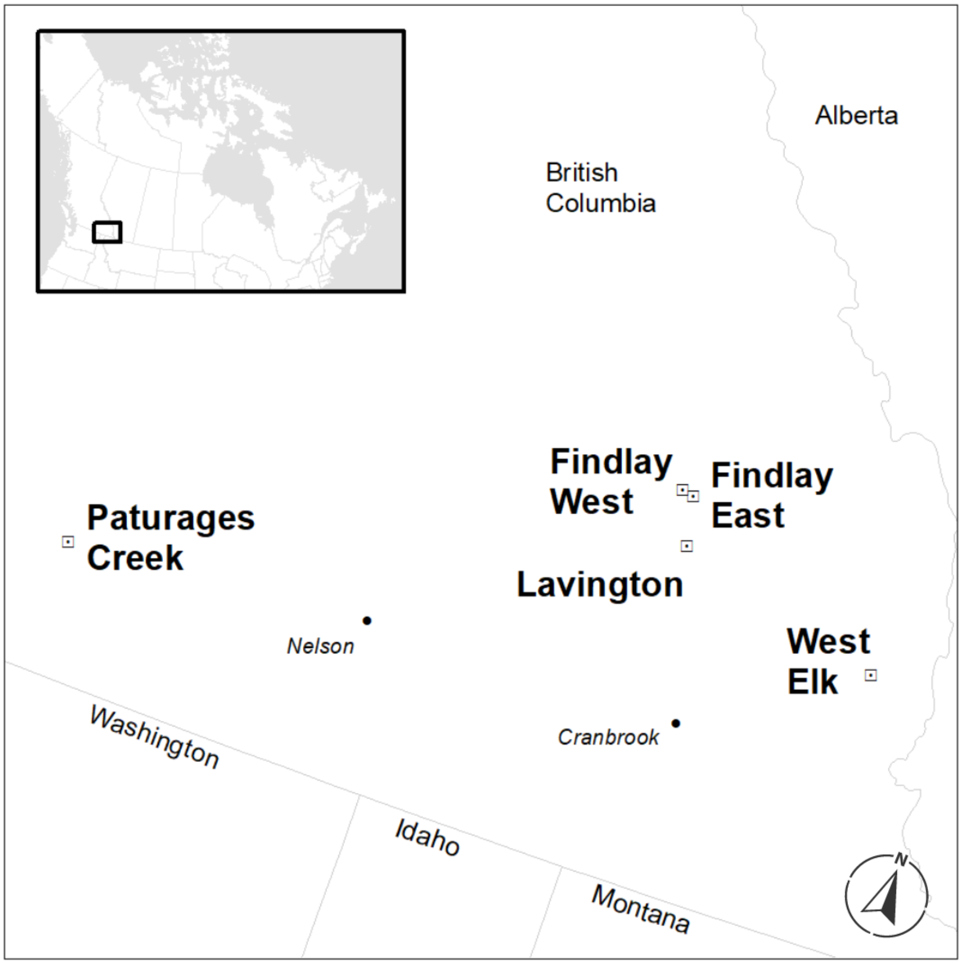


Figure 2.1. Selected variable retention harvest study sites in southeastern British Columbia examining mortality and growth rates of whitebark pine.

Figure 2.2 The Lavington study site (top left) illustrates the level of retention, as well as the amount of debris on the cutblock. The Findlay study site (top right) illustrates brush and debris from logging as well as, regeneration approximately 17 years post-harvest. The West Elk study site (bottom left) illustrates the prominence of the largest reserve trees. The Paturages Creek study site (bottom right) site illustrates regeneration, as well as the variation of slope on the NW corner of the cutblock.

Table 2.1. Characteristics of five high elevation harvest sites sampled in southeastern British Columbia.

Site	Elevation (m a.s.l.)	Lat (degrees)	Long (degrees)	Harvest Unit Size (ha)	Harvest Year
Findlay East (FE)	1922	50.19303	−116.0542	19.9	2006
Findlay West (FW)	1960	50.19359	−116.0668	4.9	2001
Lavington (LV)	1884	50.04018	−115.9787	35.1	2012
Paturages Creek (PC)	2001	49.40264	−118.7187	30.3	2003
West Elk (WE)	1874	49.84562	−114.9571	19.5	2007–2008

2.2. Climate

The Kootenay-Boundary Natural Resource Region has a continental climate. ESSF high elevation forests endure generally relatively cold, moist, and snowy winters (Coupe et al., 1991). PC is the only site located within the Dry Cold ESSF (dc) subzone classification. The remaining four sites are classified as Dry Cool ESSF (dk). Site-specific mean annual climate variables were produced using the software ClimateWNA (Wang et al., 2016) using 1961-1990 climate normals.

PC was also the only ESSF site to have the Dry Cold (dc) subzone classification. General climate patterns illustrated in the climatographs using WNA data modeling suggests that PC endures the driest summer months (Figure 2.3). Although LV and FN with its two composite sites (FE and FW) are less than 100 km apart, the climatograph for LV demonstrates greater monthly variability for precipitation. LV mean annual temperature (1.1℃) were comparable to those at FN (0.8℃).

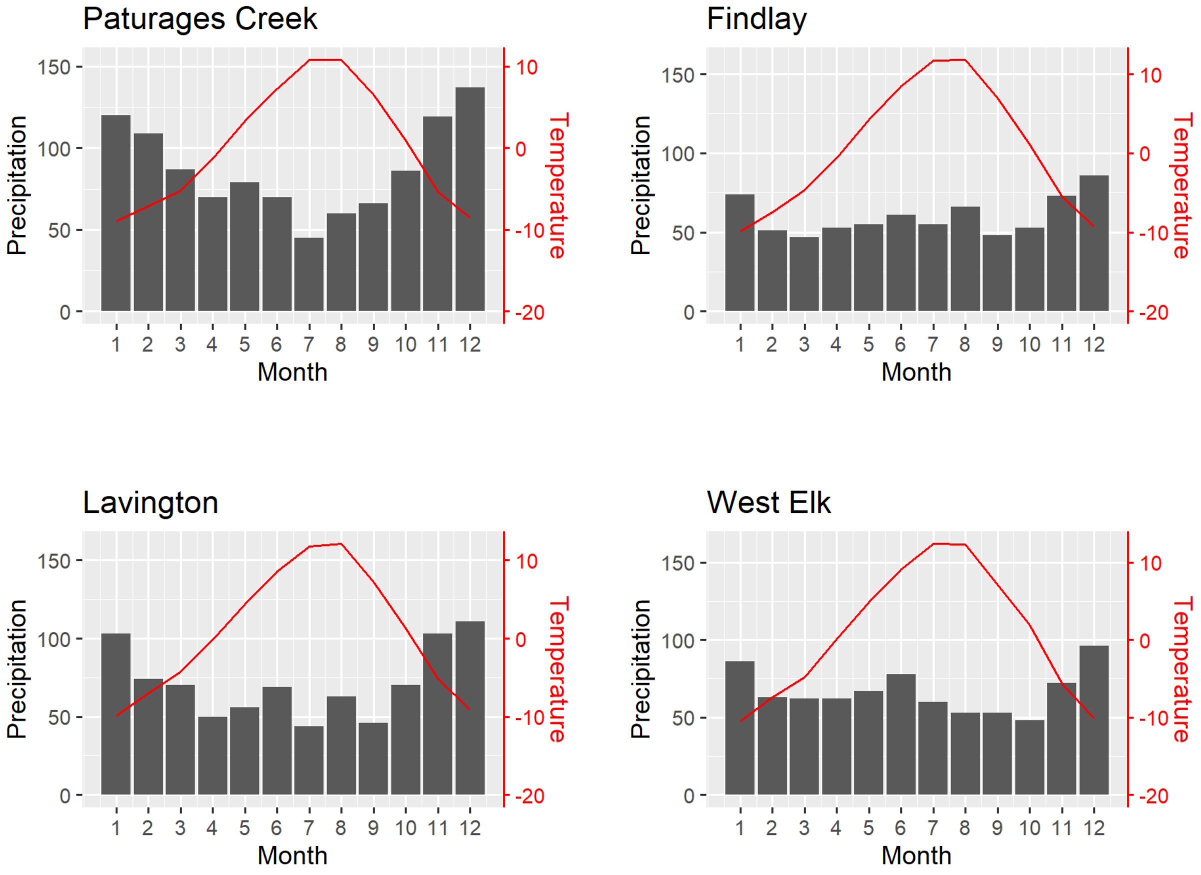


Figure 2.3. Climatogram of mean annual temperature and precipitation for the common time period (1961 - 1990) of four harvest site locations in southeastern British Columbia.

2.3 Forest Cover and Silviculture Practices

The main tree species associated with the ESSF are Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta var. latifolia* Engelm.)*,* alpine Larch *(Larix lyalli* Parl.*),* and whitebark pine (*Pinus albicaulis* Engelm.) (Meidinger and Pojar, 1991). Harvest practices for all five sites focused on the removal of the predominant commercial timber, lodgepole pine. Engelmann spruce and subalpine fir were also present at all sites. Sites were closed canopy forests prior to harvest.

Given the retrospective nature of this study, the following criteria was implemented to examine post-harvest growth and survivorship of reserve trees: a minimum post-harvest age of 5 years: a minimum sample size of 20 trees; and, accessibility (within a one-hour hike). Silviculture prescriptions classify these sites as clearcut with reserves (CCRES) (Kathy Howard, personal communication, April 10, 2019). All the study sites were identified as low retention sites, since each of the selected study sites was characterized as a clearcut with reserve trees. Beese et al. (2019) report that, although this practice doesn't conform to the traditional definition of retention systems because it doesn't meet the >50% forest influence rule, reserve trees within clearcuts can support landscape-level biodiversity strategies as these trees can result in long-term retention. The spatial distribution of reserve trees was highly variable, as all sites adhered more or less to dispersed tree patterns with the exception of FW which had the most notable patch of aggregated trees.

2.4 Works Cited

Antos, J. A., & Parish, R. (2002). Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: tree size, age, and spatial structure. *Canadian Journal of Forest Research*, *32*(11), 1935-1946.

Banner, A., MacKenzie, W., Haeussler, S., Thompson, S., Pojar, J., & Trowbridge, R. (1993). A field guide to site identification and interpretation for the Prince Rupert Forest Region. Land Managers Handbook No. 26. Research Branch, B.C. Ministry of Forests, Victoria

Beese, Deal, J., Dunsworth, B. G., Mitchell, S. J., & Philpott, T. J. (2019). Two decades of variable retention in British Columbia: a review of its implementation and effectiveness for biodiversity conservation. *Ecological Processes*, *8*(1), 1–22.

Coupé, R., Stewart, A. C., & Wikeem, B. M. (1991). Engelmann spruce–subalpine fir zone. *Ecosystems of British Columbia*, 223-236.

Meidinger, D., & Pojar, J. (1991). Ecosystems of British Columbia. *Special Report Series, Research Branch, Ministry of Forests, British Columbia*, *(6)*.

Ministry of Forests, Lands, and Natural Resource Operations. (2014). Boundary Timber Supply Area, Rationale for Allowable Annual Cut (AAC) Determination. Retrieved from https://www2.gov.bc.ca/assets/gov/farming-natural-resources-and-industry/forestry/stewardship/forest-analysis-inventory/tsr-annual-allowable-cut/boundary_tsa_rationale_for_aac.pdf

Keane, R. E., Tomback, D. F., Aubry, C. A., Bower, A. D., Campbell, E. M., Cripps, C.L., Jenkins, M. B. Mahalovich, M. F. Manning, M.McKinney, S. T. Murray, M. P. Perkins, D. L. Reinhart, D. P. Ryan, C. Schoettle, A W. & Smith, C. M. (2012). A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). *General Technical Report. RMRS-GTR-279. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.*

Tomback, D. F., Arno, S. F., & Keane, R. E. (Eds.). (2001). *Whitebark pine communities: Ecology and Restoration*. Island Press

Wang, T., Hamann, A., Spittlehouse, D.L. and Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One, 11*(6): e0156720.

Chapter 3: Methods

3.1 Field Measurements

Fieldwork was conducted during July and August 2018, and July 2019, The intent was to examine WBP survivorship and radial reserve tree growth of WBP in variable retention harvest sites in southeastern B.C. A full WBP census was conducted at each harvest site by combining forest measurement data with dendrochronological techniques to examine survivorship, radial reserve tree growth in VR harvest sites and growth-climate relationships of control trees in unharvested stands. This approach was selected as the spatial variation of WBP reserve trees was observed to be variable during a site assessment reconnaissance conducted in 2017.

All mature WBP trees with a diameter at breast height (DBH) of 17 cm or greater were included in the census. Trees near the perimeter of the harvest unit were excluded if the tree height was greater than the distance to the nearest forest edge. Each tree was measured for tree height, and height to crown using a TruePulse^{TM} 200 Laser Rangefinder. Diameter at 1.3 m was recorded with Lufkin Executive 6 ft x 1/4 inch D-tape. All trees were tagged and marked with loggers paint. GPS coordinates were recorded with the ‘bad elf’ GPS unit. Finally, the slope and distance to the nearest forest edge were measured for each tree using the TruePulse^{TM}. Direction to the nearest forest edge and aspect was recorded with a compass. Trees were categorized by the following status, either standing or horizontal.

Standing tree classification was categorized as either live or dead. Forest health concerns for live trees include the non-native fungal white pine blister rust *(Cronartium ribicola)* and live trees were inspected for signs of blister rust. Binoculars were used to aid in the inspection of live trees, primarily for evidence of active and inactive cankers, as well as for evidence of red needles and rodent damage.

The crowns of standing live trees were estimated to the nearest 10%. Tree boles, whether standing dead, windthrown or living, were inspected for signs of distinctive “J” shaped beetle galleries. Core samples were subsequently examined for the presence of blue-stain fungi to discern whether individual trees were inoculated via bark beetle after an aggregated attack (Krokene, 2015).

Horizontal trees were categorized as either uprooted (windthrown) or damaged. Trees that appeared to have snapped or broken due to a fallen neighbouring tree were classified as damaged. Finally, the direction of fall for horizontal trees identified as uprooted was recorded with a compass.

3.2 Dendrochronology

Increment cores were collected using a 4 mm Haglof increment borer from all reserve and control trees at approximately 1.3 m above the ground surface. One core was collected from live reserve trees at an angle perpendicular to the slope to avoid compression wood. Two cores were collected from all dead trees, from angles to best avoid compression wood.

Control cores were collected at each study site from nearby reference stands sharing similar elevation, slope, and aspects. Reference conditions represent the range of historical variability in ecological structures and, therefore, reflect the same interplay of abiotic and biotic processes (e.g., Morgan et al., 1994; Landres et al., 1999). Hereafter, the term control sites is used to describe reference stands as the post-harvest surrogate.

Twenty trees with two cores per tree sampled perpendicular to the fall line were collected from the control site. The selection of control trees was based on age class and health status. In order to match the mature reserve tree cohorts in the VR harvest sites, dominant and co-dominant canopy status trees were selected from the control sites. In addition, trees with evidence of blister rust infection, damage from a neighbouring tree, rockfall or avalanches were excluded.

All cores from harvest and control sites were air dried and mounted on slotted boards. Cores were polished with sequentially higher grit sandpaper to obtain annual ring resolution (Stokes and Smiley, 1968). Tree-ring width measurements were obtained using either Velmex or CooRecorder. Samples with exceptionally narrow rings were measured with a Velmex uniSlide digitally encoded traversing table at a precision of 0.01 mm. The remaining cores were digitally scanned at 2400 dpi resolution with an HP flatbed scanner. Digital images were imported into CooRecorder measuring software and exported as ring-width files with the CDendro software package (Larsson, 2014).

To ensure that the appropriate calendar date was signed to each measured ring, the program COFECHA (Holmes, 1983) was employed to confirm cross dates for all the increment cores. Raw tree-ring data were detrended with a negative exponential curve to remove the associated biological growth trend. Standardized chronologies with a bi-weighted mean for reserve and control trees were assembled for each site (except FE) using the *dplR* package in the R environment (Bunn, 2008). FE did not have enough surviving reserve trees to compile a site chronology (Table 3.3).

Dead trees required a visual assessment with a microscope to determine if any additional growth followed the last complete growth ring. In cases where earlywood cell development was observed beyond the last complete growth ring, an additional year was added to the final death date.

3.3 Data Analysis

3.3.1 Windthrow Mortality

Post-harvest windthrown reserve trees were isolated from those that died either before harvest or due to forest agents like mountain pine beetle. The distinction was based on field observations and the use of dendrochronology methods. In addition, trees were removed if mortality was suspected to have been influenced by mountain pine beetle based on field observations (i.e. beetle galleries) and/or laboratory observations (i.e. blue stain fungus). These trees included those observed in the field with beetle galleries (n = 30). WE trees appeared to be most impacted by beetle outbreaks, with 17 cores removed due to the presence of blue-stain fungus.

Table 3.1 Summary of cores selected for windthrow analysis (PC= Paturages Creek, FE= Findlay East, FW= Findlay West, LV= Lavington, WE= West Elk)

Site	Total Live	Live Crossdated	Total Dead	Total Dead Crossdated	Total Windthrow	Windthrow Crossdated	Total Standing Dead	Blue stain fungus	Standing Dead Crossdated
PC	22	21	81	51	49	32	32	NA	19
FE	3	3	17	13	15	12	2	NA	1
FW	27	25	7	6	3	3	4	NA	3
LV	16	14	112	77	107	77	5	NA	0
WE	66	53	104	87	76	70	28	17	17

3.3.1.1 Rate of Mortality

The post-harvest mortality rate for each site was expressed as the percent of surviving reserve trees from the time of harvest to sampling date. The length of the time-course varied for each site due to different harvest dates. All reserve trees that were alive and standing a year before harvest become the denominator for the percent of surviving reserve trees.

3.3.1.2 Direction of Windthrow

The dominant direction of windthrown trees for each site was calculated using a circular histogram. The direction of fall was evaluated at each site separately and tested for statistical significance with Rayleigh's test for circular uniformity (Greenwood and Durand, 1955) using the *circular* package (Agostinelli and Lund, 2017) in R (R Core Team, 2018).

3.3.2 Growth Rates

3.3.2.1 Radial Growth Chronologies

The standardized reserve and control site chronologies were compared both visually and using the Pearson correlation coefficients for overlapping time periods. Standardization allowed for growth trend comparisons, as the resulting chronologies are in a dimensionless index format which permits comparisons across samples (Fritts, 1976)**.**

Pointer year analysis was implemented on all crossdated and detrended trees to detect inter-annual growth anomalies, both positive and negative, from 1901-2018 (with exception of FN control trees 1901-2017). The analysis was performed using the *pointRes* package in R (van der Maaten-Theunissen et al., 2015). A moving window of 3 years was selected, as the individual tree-ring series were already detrended. The function *point.norm* calculated the

Cropper values for each detrended tree-ring series to provide a dimensionless index where each tree-ring series has a standard deviation of one and a mean of zero (Neuwirth et al., 2007). Radial growth anomalies, both wide and narrow, that indicated at least a 60% change in growth were recorded as being significant when at least 60% of the trees responded to this threshold for that year. Positive pointer years were limited to the respective post-harvest interval at each site for both reserve and control trees. Negative pointer years were also selected to compare the radial growth response between control and reserve trees in section 3.3.2.3 (Growth Response to Event Years).

3.3.2.2 Pre- and Post-harvest Radial Growth Chronologies

Pre- and post-harvest time intervals were examined at harvest sites that had both reserve and control tree chronologies. Pre-harvest time intervals were equivalent to the post-harvest time period at each site. A chronology level assessment of the percent-growth change between the pre- and post-harvest time intervals was calculated using the following formula:

$$(M_2 - M_1)/M_1 \times 100\% \tag{1}$$

Where M_1 equals the average growth over the prior (n) years and M_2 equals the average growth over the subsequent (n) years (Nowacki and Abrams, 1997).

3.3.2.3 Growth Response to Event Years

A total of four event years were selected to analyze the radial growth response for both reserve and control trees. The three most recent synchronous negative event years shared between reserve and control trees were selected for each site based on the results of the pointer year analysis. The fourth event year selected corresponded to the disturbance event of interest, which was defined as harvest year plus a lag of one year. The one year lag ensured that impacts from harvesting would be captured in the tree ring record as radial growth is autocorrelated with growing conditions from the previous year. The resistance index and recovery period was calculated using the *pointRes* package (van der Maaten-Theunnissen et al., 2015). Resistance is the extent to which a system's state changes in response to disturbances (Lloret et al., 2011). A low resistance index indicates a reduction in growth. The recovery period indicates the length of time till growth resumes to pre-disturbance levels. Resistance index means were compared between reserve and control trees using a two sample Welch t-test at all four sites. A two sample Welch t-test was used to compare recovery period means between reserve and control trees.

3.3.3 Growth-Climate Relationship

Although the primary objective of this study was to assess the impacts of variable harvest practices on WBP, climate is an intrinsic variable that needed to be examined in relation to the radial growth of trees pre- and post-harvest. Residual chronologies for the four control chronologies were used in the growth-climate analysis to mitigate the effects of autocorrelation in the tree-ring data. Climate variables corresponding to the four site locations were downloaded as gridded interpolated monthly temperature and precipitation data from ClimateWNA (Wang et al., 2016) for the common time period 1901 – 2018 for each site (with exception of FN control trees the common time period was 1901-2017). Considerations for drought were explored using the standardized precipitation evapotranspiration index (SPEI) calculated with the *SPEI* package in R (Vicente-Serrano et al., 2010). The potential evapotranspiration (PET) was calculated using the Hargreaves function based on Tmin, Tmax, and latitude. SPEI values were calculated on a

6-month timescale. I used a 6 month time scale for my SPEI index because longer time scales have been shown to have better correlations with tree-ring widths (Bhuyan et al., 2017). The *treeclim* package (Zang and Biondi, 2015) was employed in a correlation function analysis using 13 consecutive monthly variables for the following climate parameters: precipitation; temperature average; and, SPEI.

3.4 Works Cited

Agostinelli, C., & Lund, U. (2017). R package ‘circular’: circular statistics (version 0.4-93). *URL https://r-forge. r-project. org/projects/circular*.

Bunn, A.G. (2008). “A dendrochronology program library in R (dplR).” *Dendrochronologia*, *26*(2), 115–124.

Bhuyan, U., Zang, C., & Menzel, A. (2017). Different responses of multispecies tree ring growth to various drought indices across Europe. *Dendrochronologia*, *44*, 1-8.

Fritts, H. C. (1976). Tree Rings and Climate. Academic Press, San Diego, California. 567 pp.

Greenwood, J. A., & Durand, D. (1955). The distribution of length and components of the sum of n random unit vectors. *The Annals of Mathematical Statistics*, 233-246.

Holmes, R.L. (1983). Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin, 43*, 69–78

Krokene, P. (2015). Conifer defense and resistance to bark beetles. In *Bark beetles,* Academic Press, 177-207.

Landres, P. B., Morgan, P., & Swanson, F. J. (1999). Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications*, *9*(4), 1179-1188.

Larsson, L. (2014). CooRecorder and Cdendro programs of the CooRecorder. *Cdendro package version*, *7*.

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: effects of successive low‐growth episodes in old ponderosa pine forests. *Oikos*, *120*(12), 1909-1920.

Meko, D. M., Touchan, R., & Anchukaitis, K. J. (2011). Seascorr: a MATLAB program for identifying the seasonal climate signal in an annual tree-ring time series. *Computers & Geosciences*, *37*(9), 1234-1241.

Morgan, P., Aplet, G. H., Haufler, J. B., Humphries, H. C., Moore, M. M., & Wilson, W. D. (1994). Historical range of variability: a useful tool for evaluating ecosystem change. *Journal of Sustainable Forestry*, *2*(1-2), 87-111.

Neuwirth, B., Schweingruber, F. H., & Winiger, M. (2007). Spatial patterns of central European pointer years from 1901 to 1971. *Dendrochronologia*, *24*(2-3), 79-89.

Nowacki, G. J., & Abrams, M. D. (1997). Radial‐growth averaging criteria for reconstructing disturbance histories from presettlement‐origin oaks. *Ecological Monographs*, *67*(2), 225-249.

Stokes, M. A., & Smiley, T. L. (1968). An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, Illinois.

van der Maaten-Theunissen, M., van der Maaten, E., & Bouriaud, O. (2015). pointRes: an R package to analyze pointer years and components of resilience. *Dendrochronologia*, *35*, 34-38.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate*, *23*(7), 1696-1718.

Wang, T., Hamann, A., Spittlehouse, D.L. & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One* 11: e0156720.

Zang, C., & Biondi, F. (2015). treeclim: an R package for the numerical calibration of proxy‐climate relationships. *Ecography*, *38*(+4), 431-436.

Chapter 4: Results

The results from the research are presented in the following order: (1) mortality rates; (2) growth rates of mature whitebark pine reserve trees in low retention harvest sites; and, (3) the growth-climate relationships of this high elevation tree species.

4.1. Mortality

4.1.1 Rate of Mortality

Death dates based on dendrochronological data showed pronounced mortality within 5 years post-harvest (Figure 4.1). The overall mortality trend of reserve trees in four of the five sites indicated a negative exponential curve. The exception was FW which exhibited the highest levels of survivorship of reserve trees at 80% (Figure 4.1). The steepest decline in reserve trees was at LV, with less than 20% of the selected reserve trees surviving after 2 years post-harvest. FE was the second most pronounced loss of reserve trees among the five sites selected. In addition, standing dead trees were the least representative out of all dead trees surveyed, snags accounted for 22% of dead trees, whereas uprooted trees accounted for 78%.

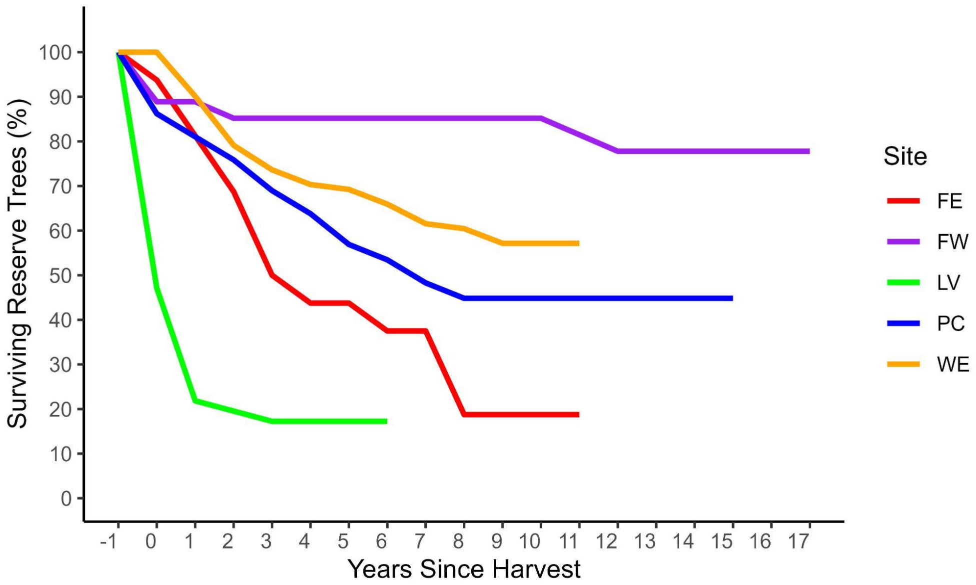


Figure 4.1 Post-harvest mortality rate of reserve whitebark pine at five harvest sites in southeastern British Columbia (FE = Findlay East, FW=Findlay West, LV= Lavington, PC= Paturages Creek, WE=West Elk).

4.1.2 Direction of Windthrow

The Rayleigh test for uniform circularity revealed that windthrow was not uniformly distributed at each site. PC, FE, LV and WE all had significant p-values < 0.001 for the Rayleights test. The mean azimuth of windthrow orientation at each site is shown in Figure 4.2. Across all sites, the predominant direction of windthrow trended towards a northeasterly direction which suggests that fetch at these sites is predominantly from the southwest. The mean azimuth of windthrow for PC was more easterly compared to the other three sites. Due to the low sample numbers of windthrown trees at FW (n = 3), a Rayleighs test for uniform circularity could not be conducted.

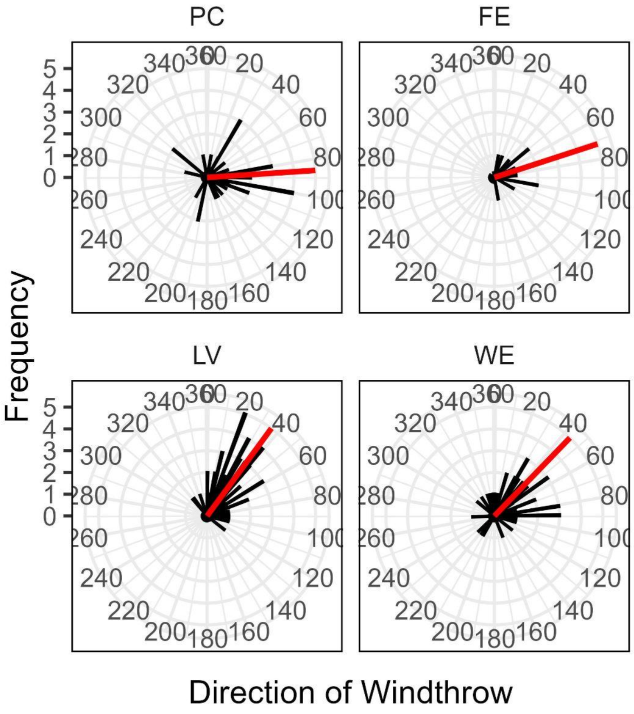


Figure 4.2. Circular histograms of windthrown trees at four harvest sites. Black bars: azimuth frequency of windthrown trees. Red bars: mean azimuth of windthrow. (PC= Paturages Creek, FE=Findlay East;LV= Lavington;WE= West Elk).

4.2 Growth Rates

4.2.1 Radial Growth Chronologies

Standardized master chronologies for reserve trees were completed for four of the five harvest sites. Due to an insufficient number of surviving reserve trees at FE, a reserve tree site chronology for this cutblock could not be constructed. For the remainder of the thesis chronology development and growth rate analysis pertains only to FW and will be referred to as FN. The tree-ring chronologies indicate that across all stands the chronologies were representative of old-growth trees >140 years in age (Feller, 2003). Chronology lengths ranged from 170 to 310 years after a ten-tree minimum was applied. Inter-series correlation for the master chronologies constructed ranged from 0.359 - 0.546 (Table 4.1). The reserve tree chronology for FN was composed of 20 trees. PC reserve tree chronology was the longest chronology with the ten tree minimum threshold, with 21 reserve trees. LV had the fewest trees in the reserve tree chronology with 14 trees. WE chronology had the most robust sample depth with 35 trees. Summary statistics for reserve and control tree chronologies are found in Table 4.1.

Table 4.1. Summary statistics of control and reserve tree chronologies by site (PC= Paturages Creek, FN= Findlay, LV= Lavington, WE= West Elk)

Site	Treatment	Chronology 10 Tree Minimum Starts	Chronology 10 Tree Minimum Ends	No. of Years	Interseries Correlation	Mean Sensitivity	No. Trees
PC	Control	1788	2018	230	0.485	0.218	19
PC	Reserve	1775	2018	243	0.359	0.212	21
FN	Control	1716	2017	301	0.489	0.187	18
FN	Reserve	1848	2018	170	0.441	0.173	20
LV	Control	1784	2018	234	0.546	0.162	18
LV	Reserve	1828	2018	190	0.469	0.169	14
WE	Control	1811	2018	207	0.444	0.172	19
WE	Reserve	1797	2018	221	0.412	0.181	21

Note FN has only one reserve tree chronology (FW) due to the lack of reserve trees at FE

Reserve and control tree chronologies for the four sites were visually well synchronized for the majority of the time series. Pearson correlation coefficients between reserve and control tree chronologies were generally well-matched across all sites for common time periods between the paired chronologies (Figure 4.2). PC reserve and control master chronologies were highly synchronous and had the highest Pearson correlation coefficient ($r = 0.78$). Both PC chronologies illustrated similar multi-decadal trends: (1) a positive growth trend from ~ 1890 to 1930; and, (2) a waning growth trend from ~1930 to 1980. Both chronologies also exhibited a synchronization in two growth suppression periods at ~ 1830 and ~1890. The control tree chronology for PC, however, had lower tree-ring index values compared to the reserve tree chronology for these suppression periods. FN had the lowest Pearson correlation coefficient of the four sites (r = 0.38), however, the degree of synchronization is still visible between the reserve and control tree chronologies (Figure 4.2). FN reserve tree chronology demonstrated lower tree-ring index values compared to the control tree chronology for two multi-decadal time periods ~1870 to 1885 and ~ 1943 to 1966. LV had the second highest correlation coefficient (r = 0.56) for the common time period shared between reserve and control tree chronologies. Tree-ring index values remained very similar throughout the time-series, with slightly higher growth index values for the reserve tree chronology for the common multi-decadal growth trend from ~1920 to 1948. Both chronologies illustrate a steady growth decline from about ~1950 to 2000. The Pearson correlation coefficient for WE (r = 0.50) indicated that the reserve and control tree chronologies exhibited similar growth trends for most of the common time series. The visual comparison indicates two non-synchronous periods; (1) The control tree chronology has lower tree-ring values from ~1917 to 1930 compared to the reserve tree chronology; and, (2) The reserve tree chronology departs from the control chronology with a negative growth trend from approximately ~1998 to 2010.

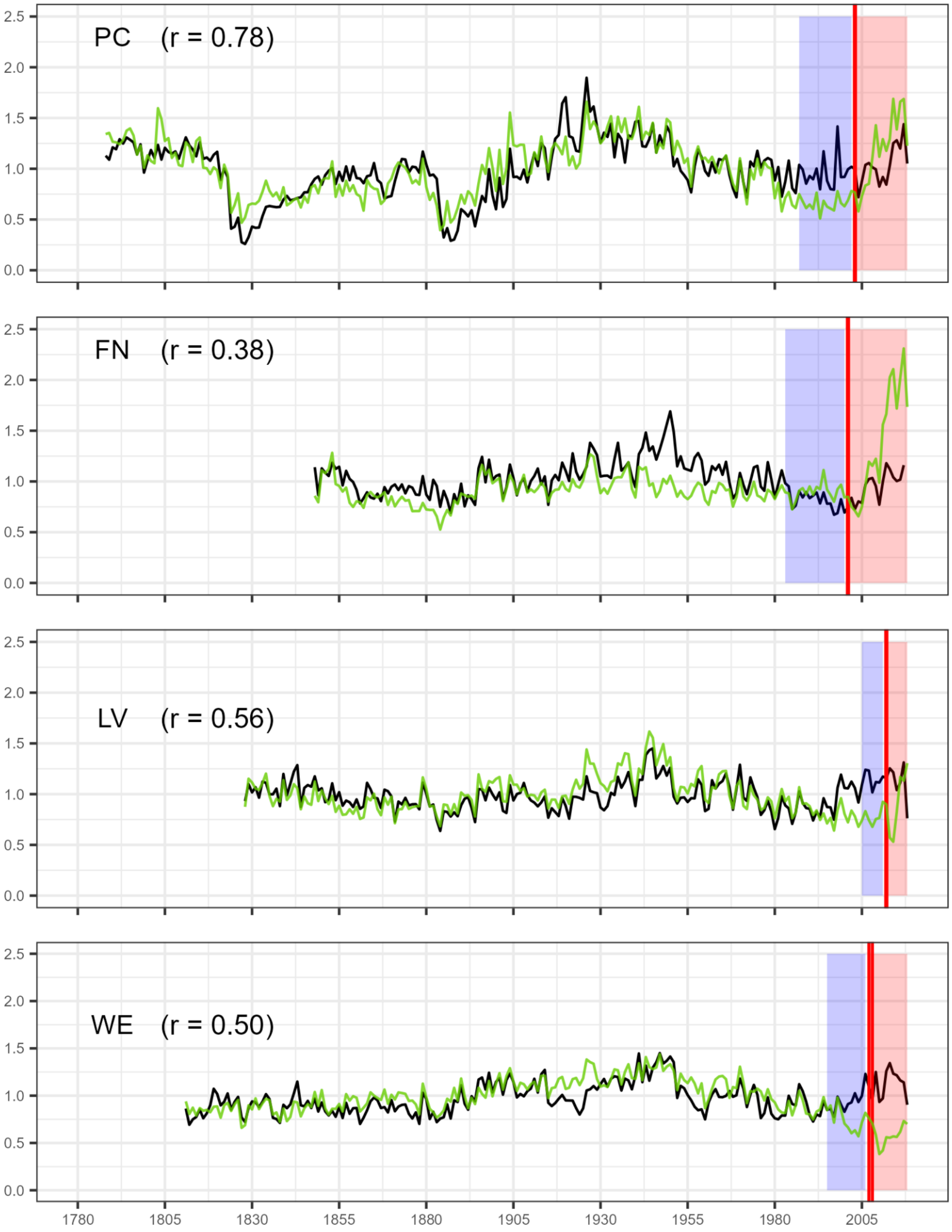


Figure 4.3 Standardized control tree master chronology (solid black line). Standardized reserve tree master chronology (solid green line). Date of harvest (red line). Pre-harvest interval (shaded blue rectangle). Post-harvest interval (shaded red rectangle). (PC= Paturages Creek, FN= Findlay, LV= Lavington, WE= West Elk)

The results from the pointer year analysis indicated that two of the four sites (PC and FN) had positive event years in the post-harvest interval for reserve trees that were not shared by the control trees (Table 4.2): (1) Reserve trees at PC indicated a growth release event in 2014 which corresponds to 11 years after harvest; and, (2) FN had two growth release events (2007 and 2017) which are respectively, 6 and 16 years post-harvest (Table 4.2).

Positive pointer years for reserve trees that are non-synchronous with the control tree-ring data suggest a significant growth release due to the removal of tree-to-tree competition. However, other non-synchronous pointer years were detected for the post-harvest interval. This included the inverse relationship, whereby control trees showed a significant growth release that was not shared by reserve trees during the same time interval. A total of three growth release events of this nature were observed, one at FN for 2002 (1-year post-harvest) and two release events 2009 (1-year post-harvest) and 2013 (5 years post-harvest) at WE (Table 4.2). LV was the only site of the four that had no growth releases detected for the post-harvest interval for neither the control nor reserve trees (Table 4.2). The complete pointer year analysis for all chronologies from 1901-2018 are included in Appendix A and B, for the negative and positive event years, respectively. Negative pointer years utilized for the resistance index and recovery period analysis are reported in section 4.2.3 (Growth Response to Event Years).

Table 4.2 Positive growth release events for post-harvest intervals at four harvest sites (PC= Paturages Creek, FN= Findlay, LV= Lavington, WE= West Elk)

Site	Treatment	Harvest Year	Positive Event Year After Harvest
PC	Control	--	2017
PC	Reserve	2003	2014, 2017
FN	Control	--	2002
FN	Reserve	2001	2007, 2017
LV	Control	--	
LV	Reserve	2012	
WE	Control	--	2009, 2013
WE	Reserve	2007, 2008	

4.2.2 Pre- and post-harvest Radial Growth Chronologies

The visual comparison between radial growth trends for the pre-and post-harvest time intervals revealed that three of the four sites demonstrated greater positive radial growth for reserve tree chronologies within the post-harvest time interval. PC and FN had the most distinctive positive growth trends. PC and FN had the longest post-harvest intervals, 15 and 17 years, respectively; both reveal a short 2-3 year lag prior to the substantial increase in radial growth (Figures 4.4a and 4.4b). Although LV had one of the shortest time intervals post-harvest (6 years) it also demonstrated a positive increase in radial growth 2 years post-harvest (Figure 4.3c). Furthermore, the reserve tree chronology for LV had lower annual tree-ring index values during the pre-harvest period but surpassed the control chronology four years following the lag response (2014 to 2018) (Figure 4.4c). However, the higher annual tree-ring index values for the reserve trees by 2018 are also in conjunction with a negative growth trend for LV control trees recorded for 2018. WE reserve trees indicate a gradual positive growth trend two years after the final harvest year. WE was the only site to have two consecutive years of harvest activity. In addition, WE was the only site of the four to show asynchronous radial growth for the pre-harvest interval. The reserve tree chronology departs from the control chronology before harvest around 1998. The general growth trend between 1998 and 2010 was negative, however, after 2011 the reserve tree chronology recovered with a gradual positive growth trend (Figure 4.4d).

In addition to the visual comparison between control and reserve tree master chronologies, the radial growth differences between pre-and post-intervals for these four harvest sites was quantified. PC and FN exhibited the largest difference between the control and reserve tree chronologies. While the radial percent growth change for the PC control chronology was 7%, the reserve tree chronology was 77%. FN also indicated a substantial difference between the percent growth change between the control chronology (16%) vs. the reserve tree chronology (51%). LV indicated a less substantial growth gain, the control chronology had a radial percent growth change of -1.7% whereas, the reserve tree chronology was 18%. WE was the only site that resulted in a negative percent growth change in the reserve tree chronology -17.5% while the control chronology indicated a 24% growth change after harvest.

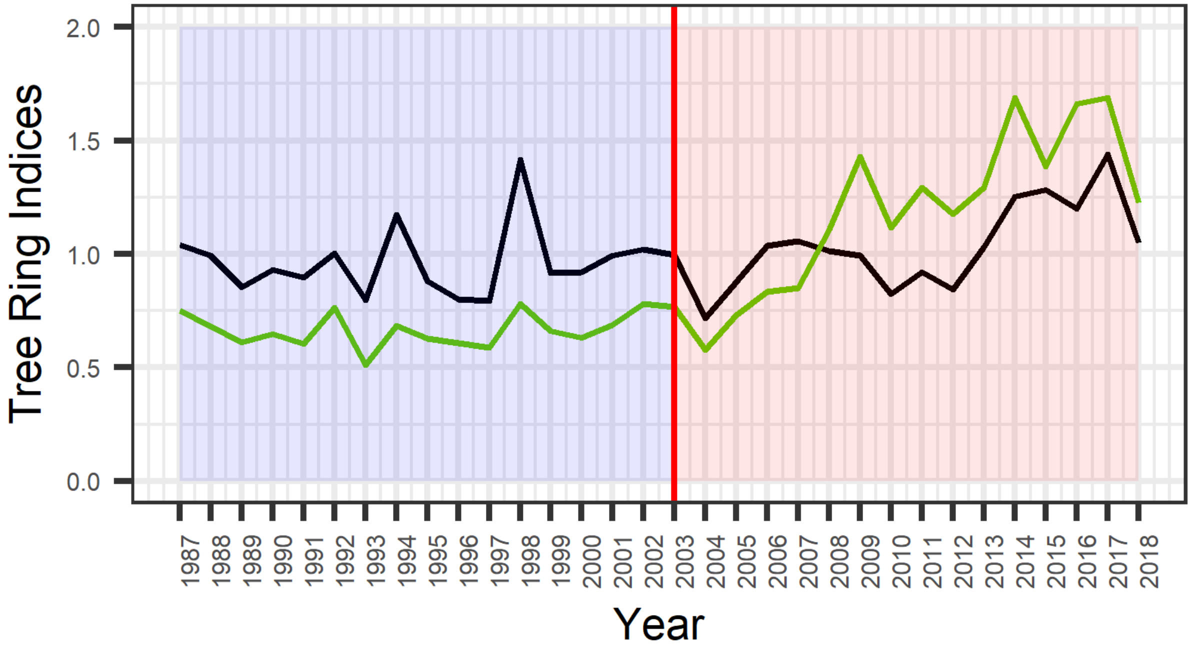


Figure 4.4a Comparison of Paturages Creek standardized control chronology (black solid line) with standardized reserve tree chronology (solid green line) for the time period (1987 - 2018). The red vertical lines represent harvest years.

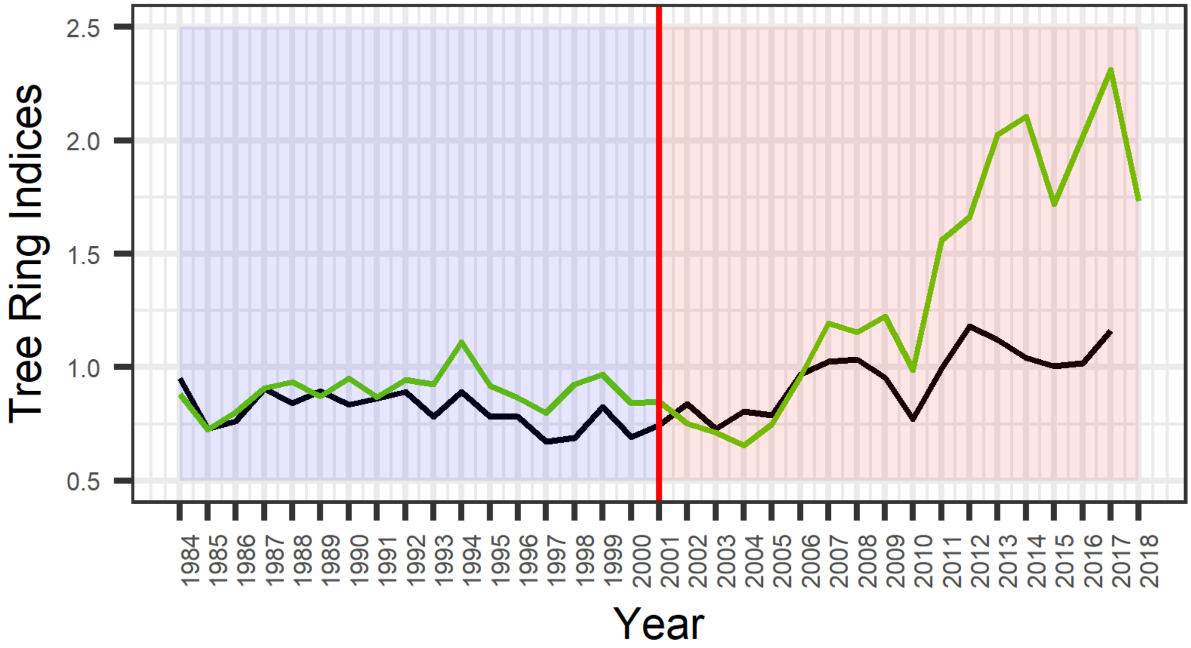


Figure 4.4b Comparison of Findlay standardized control chronology (black solid line) (1984 - 2018) with standardized reserve tree chronology (solid green line) for the time period (1984 - 2017). The red vertical lines represent harvest years.

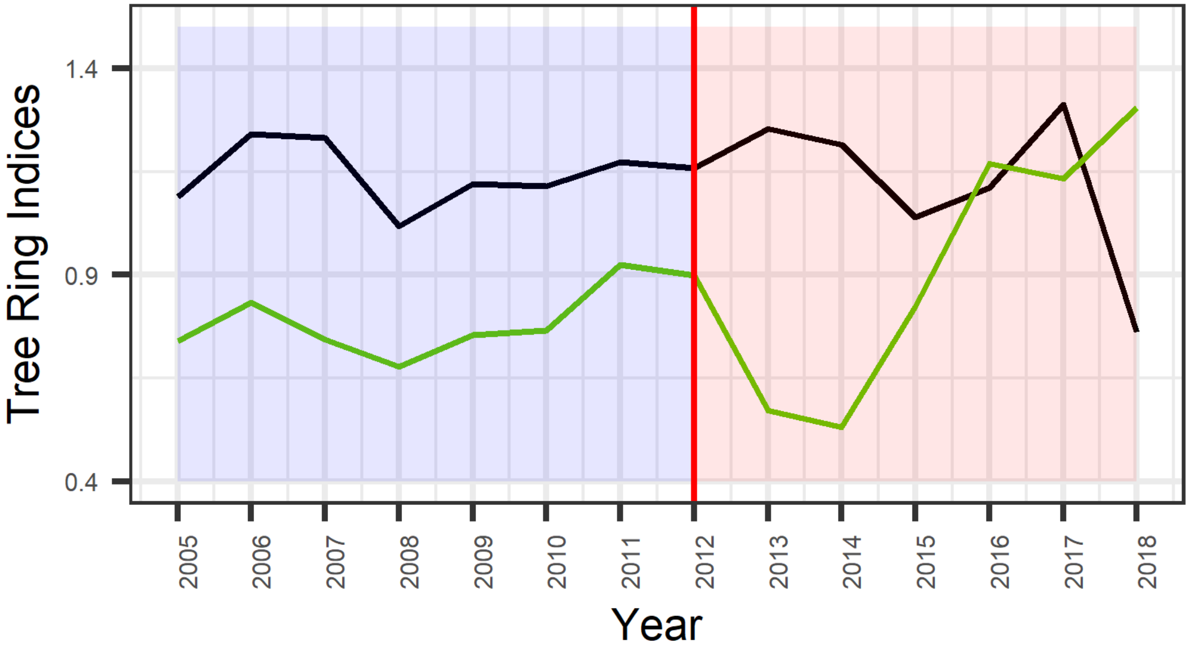


Figure 4.4c Comparison of Lavington standardized control chronology (black solid line) with standardized reserve tree chronology (solid green line) for the time period (2005 - 2018). The red vertical lines represent harvest years.

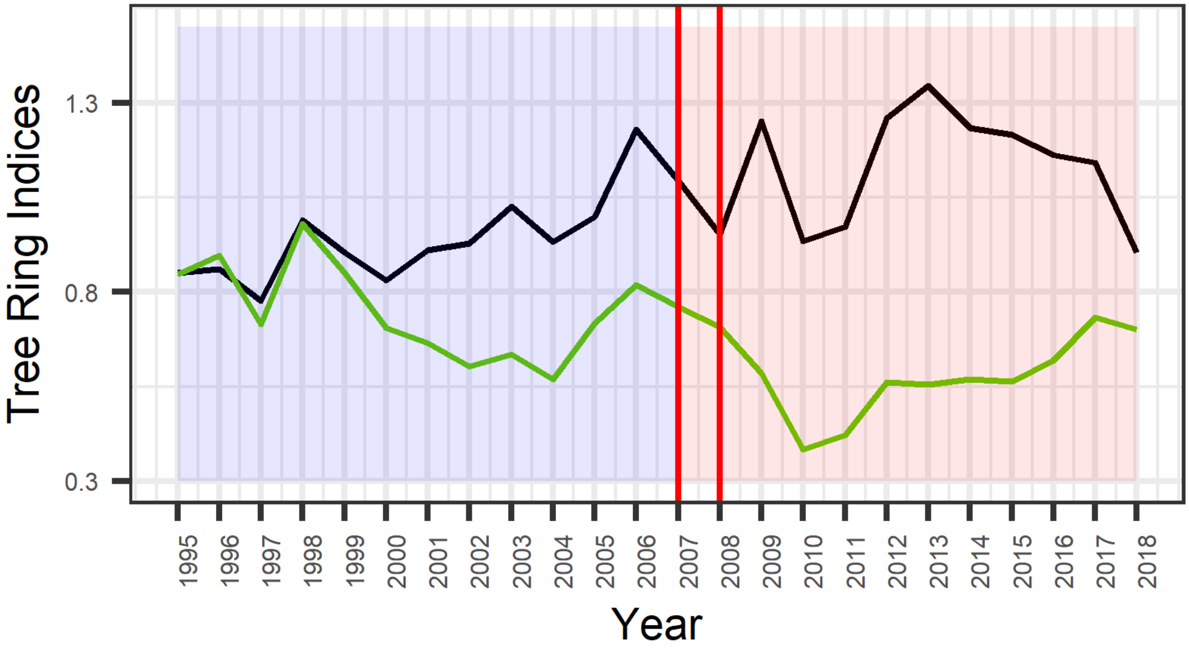


Figure 4.4d Comparison of West Elk standardized control chronology (black solid line) with standardized reserve tree chronology (solid green line) for the time period (1995 - 2018). The red vertical lines represent harvest years.

4.2.3 Growth Response to Event Years

The two sample Welch t-tests revealed that only one of the four sites tested contained a significant difference between the mean resistance index of reserve and control trees for the associated harvest event year. WE indicated a significant difference in resistance index means for the associated harvest event year of 2009 (t = 2.50, t = 50.72, p-value = 0.02). WE reserve trees indicated greater radial growth reduction with a mean resistance index of 0.94, whereas the control trees had a mean resistance index of 1.19 (Figure 4.5d and Appendix C). The remaining three sites (PC, FN, and LV) showed no significant difference between control and reserve trees for the resistance index with associated harvest event year. Furthermore, despite no significant difference between resistance means for the reserve and control trees, the median resistance index was substantially lower in reserve trees at Lavington (0.61) compared to control trees (1.06) for the harvest event (Figure 4.5c). Both PC and LV also had large variability in growth reduction according to the resistance index values (Figures 4.5a and 4.5c). Results for the three negative event years for each site indicated that there was a significant difference between reserve and control trees for two negative event years; LV's negative event year 2001 (t = 2.47, t = 28.92, p-value = 0.02) and WE's negative event year 2010 (t = 3.40, t = 39.92, p-value > 0.001).

The two sample Welch t-test indicated that two of the four harvest events showed a significant difference in mean recovery periods between reserve and control trees. FN reserve trees indicated that recovery periods were significantly different between reserve and control trees for the associated harvest year event (t = -2.14, t = 33.88, p-value = 0.04). The mean recovery period for FN reserve trees for 2002 was 3.41 years, whereas the control trees had a mean recovery period of 1.52 years (Figure 4.5b and Appendix D). WE also indicated a longer mean recovery period for reserve trees (1.85 yrs) compared to the control trees (0.56 yrs) (Figure 4.5d and Appendix D), which resulted in a significant difference (t = -2.16, df = 33.54, p-value = 0.04). WE was the only site to indicate a significant difference in mean recovery periods between reserve and control trees for a negative event year; WE indicated a significant difference in mean recovery period for the negative event year 2010 (t= -2.62, t=25.33, p-value = 0.01).

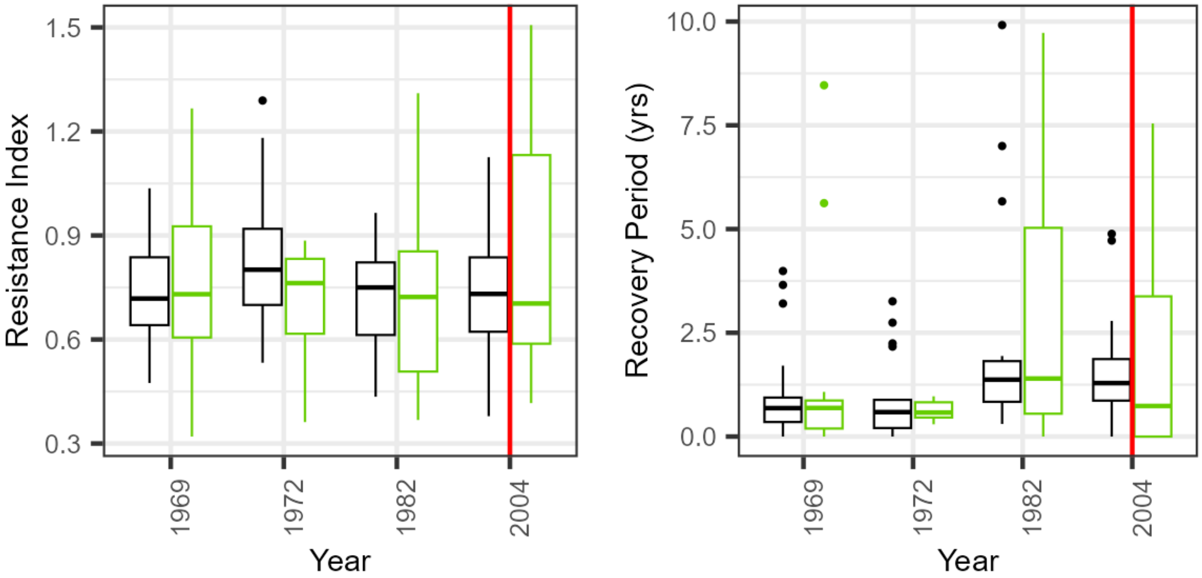


Figure 4.5a Paturages Creek Resistance Index (left) and Recovery Period (yrs) (right) comparison of 3 negative event years and 1-year lag post-harvest (red vertical line). Boxplots illustrate the control trees (black) and reserve trees (green).

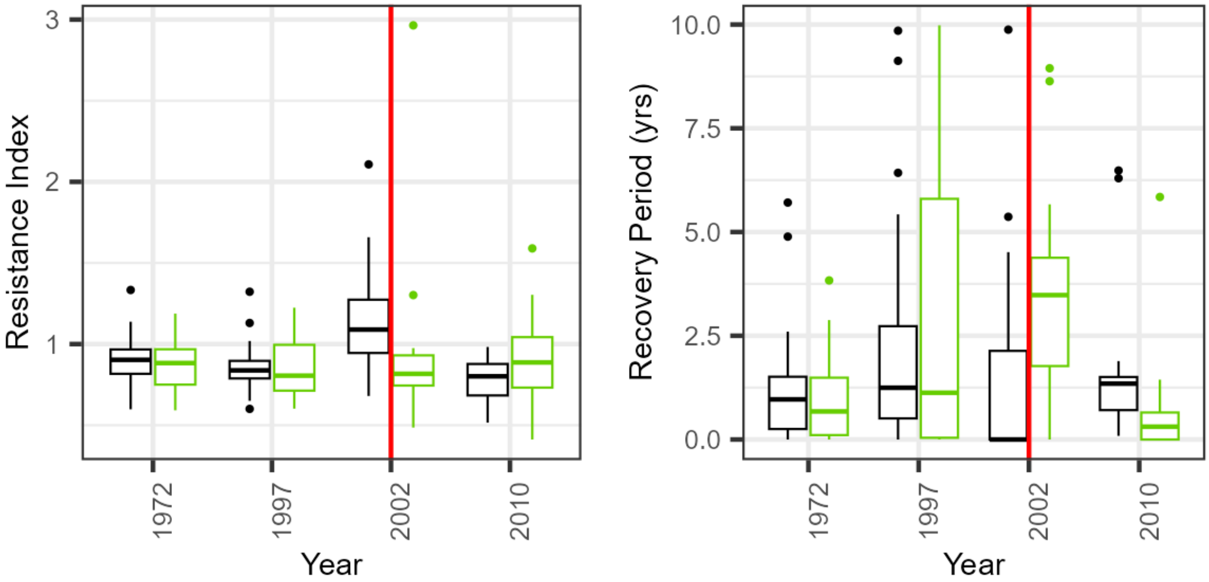


Figure 4.5b Findlay Resistance Index (left) and Recovery Period (yrs) (right) comparison of 3 negative event years with 1-year lag post-harvest (red vertical line). Boxplots illustrate the control trees (black) and reserve trees (green).

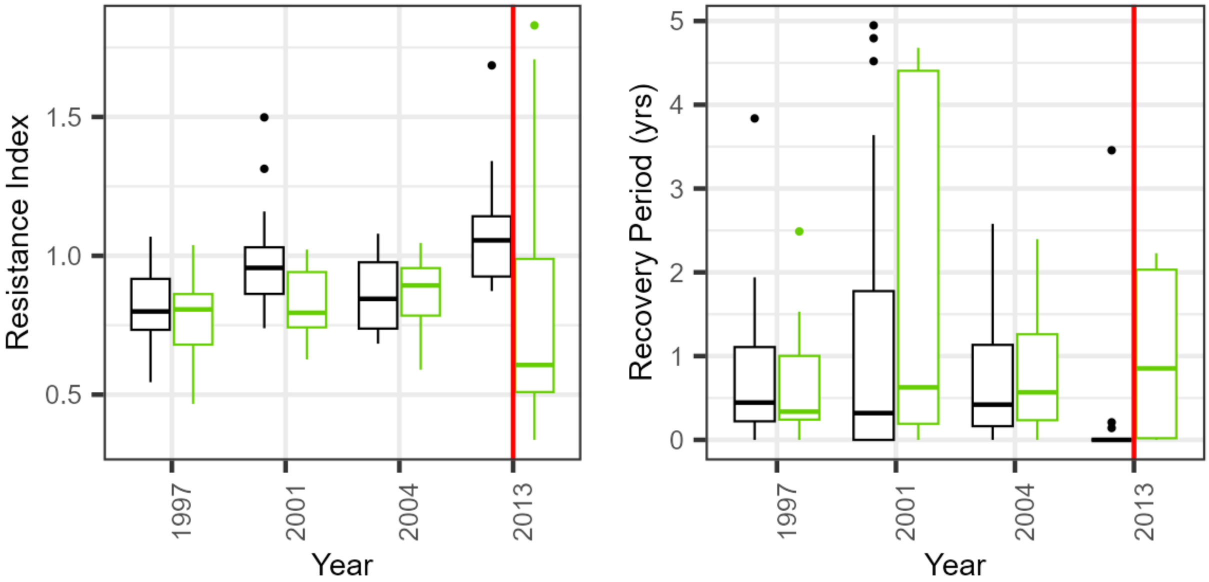


Figure 4.5c Lavington Resistance Index (left) and Recovery Period (yrs) (right) comparison of 3 negative event years and 1-year lag post-harvest (red vertical line). Boxplots illustrate the control trees (black) and reserve trees (green).

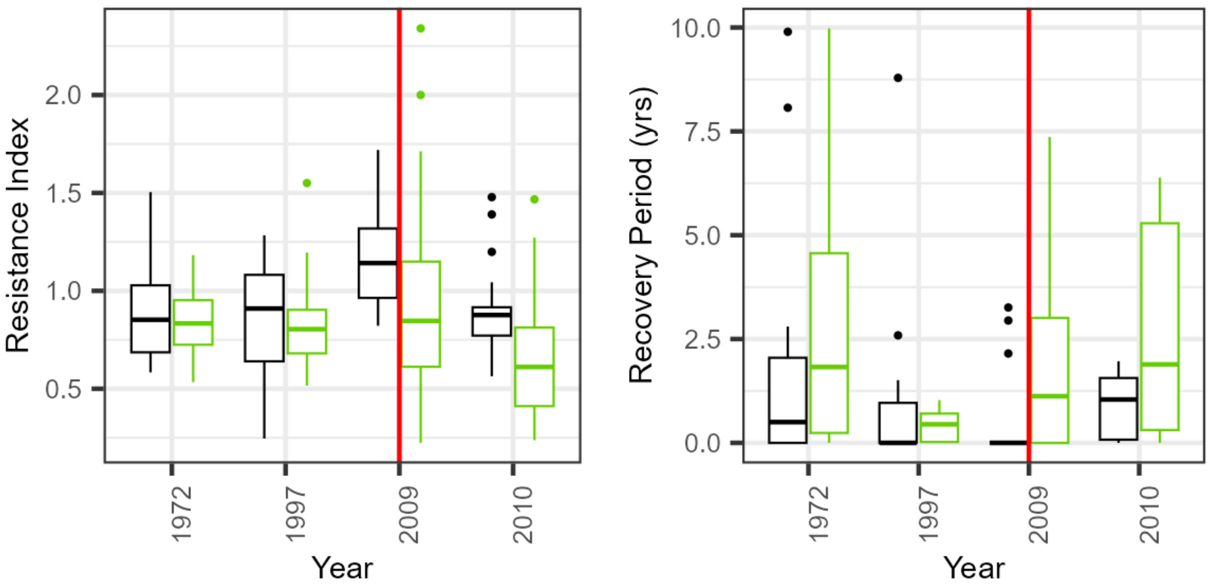


Figure 4.5d West Elk Resistance Index (left) and Recovery Period (yrs) (right) comparison of 3 negative event years and 1-year lag post-harvest (red vertical line). Boxplots illustrate the control trees (black) and reserve trees (green).

4.3 Growth-Climate Response

The residual master control tree chronologies for the four sites (PC, FN, LV, and PC) indicated an expressed population signal (EPS) above the 0.80 threshold from 1901 to 2018 (with the exception of FN 1901 to 2017). The EPS indicates how well each site chronology given the sample depth is representative of the hypothetical population (Wigley et al., 1984). Mean sensitivity for the control chronologies used in the growth-climate analysis ranged from 0.162 to 0.218 (Table 4.1). Mean sensitivity is a metric commonly used in dendroclimatology to assess the year-to-year variability of the tree-ring time series (Fritts, 1971). Comparison of annual climate variables and mean summer SPEI, with the residual control chronologies showed no significant correlation between all three variables (Table 4.3).

Table 4.3 Pearson Correlation Coefficients with residual control tree chronology and mean annual temperature (MAT), mean annual precipitation (MAP) and Summer Mean SPEI (PC= Paturages Creek, FN= Findlay, LV= Lavington, WE= West Elk)

Site	MAP	MAT	Summer mean SPEI
PC	-0.05	0.16	-0.18
FN	-0.04	-0.11	-0.10
LV	-0.08	0.12	-0.11
WE	0.01	0.08	-0.10

Significant correlations were shown between all four WBP control chronologies and current July SPEI (with a 6 month time scale) (Table 4.4). The correlation values for current July precipitation indicated to be negatively correlated to radial growth at three of the four control sites (Table 4.4). The remaining significant correlations were variable between chronologies and monthly climatic variables. Temperature was not consistently correlated to WBP tree-ring series across sites for the same monthly climate variable. For example, FN was the only chronology to have negative correlations to tree-ring widths for numerous monthly mean temperature (current January, February, March and August) (Table 4.4). LV was positively correlated to current September temperature and PC was positively correlated with previous July temperature. However, PC and LV chronologies did indicate a common positive correlation to current July temperatures. WE was the only site that did not record any correlations with temperature.

Aside from the three shared correlations to current July precipitation, the growth-climate analysis also contained four additional asynchronous monthly correlations to precipitation: (1) PC indicated a negative correlation with current May precipitation; (2) FN indicated a negative correlation with current September precipitation; (3) LV indicated a positive correlation with previous June precipitation; and, (4) WE indicated a positive correlation with current March precipitation (Table 4.4). Additionally, the SPEI correlations include additional monthly asynchronous correlations: (1) PC indicated a negative correlation with current June SPEI; (2) FW indicated a negative correlation with current September SPEI; and, (3) WE indicated a positive correlation with current March SPEI.

Table 4.4 Correlation coefficients (r) between radial growth and monthly climate variables from 1901-2018 for four harvest control sites in southeastern British Columbia (PC= Paturages Creek, FN= Findlay, LV= Lavington, WE= West Elk)

	PPT		Temp		SPEI	
PC	current	MAY -0.255	previous	JUL 0.291	current	MAY -0.273
	current	JUL -0.338	current	JUL 0.379	current	JUN -0.179
					current	JUL -0.385
FN	current	JUL -0.189	current	JAN -0.256	current	MAY -0.181
	current	SEP -0.147	current	FEB -0.244	current	JUL -0.184
			current	MAR -0.348	current	SEP -0.200
			current	AUG -0.172		
LV	previous	Jun 0.234	current	JUL 0.290	current	JUL -0.237
	current	JUL -0.235	current	SEP 0.202		
WE	current	MAR 0.162			current	MAR 0.168
					current	JUL -0.174

4.4 Works Cited

Feller, M. C. (2003). Coarse woody debris in the old-growth forests of British Columbia. *Environmental Reviews*, *11*(S1), S135-S157.

Wigley, T. M., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Applied Meteorology and Climatology*, *23*(2), 201-213.

Fritts, H. C. (1971). Dendroclimatology and dendroecology. *Quaternary Research*, *1*(4), 419-449.

Chapter 5: Discussion

In this thesis I chronicle the post-harvest mortality and growth rates of reserve trees in variable retention (VR) cutblocks at five ESSF stands in southeastern B.C. In addition, I examined the growth-climate relationship of four control sites. I demonstrated how forest demography measurements and dendrochronology can be paired to assess the success of VR silviculture strategies, namely, for conservation and restoration efforts related to endangered whitebark pine (WPB). In the following sections, the key finding related to thesis objectives are highlighted.

5.1 Mortality

The survivorship of WBP retained on low variable retention cutblocks in southeastern B.C. showed an increased windthrow vulnerability within the first 5 years post-harvest with subsequent attrition of mortality for several years post-harvest. These findings are similar to those reported by Huggard et al. (1999) in an experimental ESSF variable retention study. They found that variable retention at high-elevation sites led to increased windthrow mortality 2.7 years post-harvest. The results emphasize the need to monitor stands over longer time frames, as the impacts of harvest were still observable on the landscape for several years after harvesting activity was completed. This finding was consistent with previous work demonstrating mortality rates remain active on the landscape for up to 10 years post-harvest in boreal forests (Thorpe et al., 2007; Solarik et al., 2012).

The overall rates of mortality varied considerably between sites, with annual mortality rates ranging from 3% to 80% in the initial post-harvest years. The trend of increased mortality in the initial years after harvest due to windthrow was strongly suggestive of 'thinning shock', where the removal of surrounding trees exposed the reserve trees to heavier wind stress (Kozlowski et al., 2012). The assumption that the observed windthrow mortality rates are directly related to harvesting practices is highly feasible given that Temesgen and Mitchell (2005) found that individual mortality rate models for complex stands in southeastern B.C. ranged between 0.3 to 2.6%. In contrast, the mortality rates for FW suggest that the retained density and refugia patch in this clear cut offered greater protection to windthrow. These findings support previous reports that spatial distribution increases vulnerability as dispersed trees have the least protection as isolated stems (Maguire et al., 2006).

Across the four harvest sites, windthrown trees exhibited significant directionality, indicating that the majority of reserve trees were uprooted from prevailing winds. The common windthrow direction tended to be northeasterly, indicating that fetch at these sites was primarily from the southwest. During the winter, storm events that move eastward across southern B.C. are commonly characterized by high winds from the southwest or west (Mitchell, 2013). These findings are in agreement with earlier data for the southern interior of B.C., where southwesterly winds were the primary influence for windthrown trees with a northeast azimuth (Huggard et al., 1999).

The azimuths of windthrown trees that don't reflect the prevailing wind direction suggest an alternative mechanism, most likely associated with storm cells, during the summer months. For example, thunderstorm activity during the summer months can produce strong downward air flows called downbursts (Peterson, 2000). These strong vertical down drafts don't necessarily lend to a prevailing wind direction and could explain the occurrence of atypical windthrow directions observed at the harvest sites.

As a result of observing a commonality in the relative directionality of windthrow, it is suspected that the topographic features of the four harvest sites influenced these outcomes. Ruel (1995) indicates that landscape, site and stand characteristics are contributing factors to windthrow. However, topography has a more pronounced effect when it comes to stand replacing disturbances in contrast to small gap openings (Ruel et al., 1998). Topographic features such as mountain valleys that influence local variation in wind behaviour (Dorner and Wong, 2003) could explain similarities across all sites, as the major valleys associated with these sites share a common North to South orientation.

5.2 Growth Rates

Similar long-term radial growth trends were observed across all site chronologies. All control and reserve tree chronologies were representative of old-growth WBP in closed canopy forests until harvest. Pearson correlation coefficients indicated that the control tree chronologies were a good long-term reference for all harvest sites with reserve tree chronologies. Site chronologies with the closest proximity, in the southeastern corner of the study area, indicated similar long-term growth trends. This finding is suggestive of long lasting climate influences like the Pacific Decadal Oscillation (PDO) which impacts the surface climate and hydrology of western North America (Whitefield et al., 2010). Several synchronous pointer years suggested that these stands responded similarly to climatic influences for the common pre-harvest time interval. However, the only stand to suggest that growth trends between the harvest site and control had incongruences prior to harvest was the WE site. Forest agents have been shown to impact radial growth chronologies of whitebark pine stands across the distribution of this species (Alfaro et al., 2003; Wong and Daniels, 2017). Therefore, the six-year radial growth reduction period that began ten years before harvest for WE reserve trees suggests that biotic factors were at play, since short-term climatic influences tend to display high-frequency variability.

The WE site continually showed that pre-harvest growth rates had a significant impact on post-harvest growth responses. Although an upward growth trend was observed six years after the initial decline in 1998, the reserve tree chronology was already in decline one year before harvest (2006). WE was the only site that showed reserve trees that had a significantly lower mean resistance index compared to control trees for the harvest event year plus a one year lag. In addition, the recovery period comparison between reserve and control trees also indicated a significant difference for reserve trees for both the harvest year plus one year lag (2009) and the subsequent (2010) negative event year. These results suggest that tree vigor before harvest had the greatest effect at the WE site and that the response to abiotic or climatic stressors post-harvest had similar growth impeding effects.

Aside from the WE pre-harvest condition anomaly, the remaining harvest sites indicated that there was no significant reduction in radial growth one year after harvest for reserve trees. While post-harvest conditions have been shown to increase water stress (Bose et al., 2014) and lead to greater irradiance levels (Harrington and Reukema, 1983), the results of this research suggest that this was not the case for the majority of the reserve WBP sites that were closed canopy forests prior to harvest. WBP have low shade tolerance and often cannot endure being ‘crowded’ out by Engelmann spruce. This trait compromises their survivorship in maturing stands (Murray et al., 2000). Halpern and Urgenson (2021) describe how species-specific growth responses are shaped by establishment traits defined by physiological tolerances and requirements. The removal of neighbouring competitors for light appears to be favourable for WBP given that it succeeds well as an early successional species. The adaptation to new canopy openings is suggestive of a physiological response in WBP to light acclimation (Lovelock et al., 1994).

Although clearcutting practices with reserve trees created an immediate structural change to the WBP of this study, the radial growth responses of reserve trees demonstrated a distinctive one to three year lag. The lagged response was not associated with significant growth reduction as highlighted by the results of two sample Welch t-test that showed no significant difference in the mean resistance index between control and reserve trees one year after harvest in three of the four sites examined. Growth response lags have been shown in other structural retention studies, including a four year lag reported by Bebber et al. (2004) in mature white pine *(Pinus strobus)*. Trees can make other investments in response to newly acquired resources such as crown and root development (Mitchell, 2013).

5.3 Growth-Climate Relationship

Overall my results show that the strongest response of tree-ring growth was negatively correlated to July SPEI, indicating that the radial growth of mature whitebark pine in closed canopy forests were more sensitive to excess moisture or pluvial events in July. Furthermore, the negative correlation to July precipitation in three of the four tree-ring chronologies corroborates this trend.

The importance of the soil moisture balance has been highlighted in previous WBP studies. Dendroclimatic investigations of WBP in the northern Rockies indicated a positive correlation to winter precipitation, coupled with cooler spring to early summer temperatures, led to enhanced radial growth most likely as a result of a slow melting snowpack which regulated soil moisture into current growing season (Perkins and Swetnam, 1996). It is worth noting, however, that Perkins and Swetnam (1996) sampled open stand trees at higher elevations on steeper slopes. Therefore, the soil moisture regimes they reported on are not directly comparable to those included in this study, as open stands are more reliant on the timing of melting snowpack due to exposure compared to closed canopies that are heavily shaded.

The negative correlation to July precipitation may seem counterintuitive but other subalpine studies have suggested that a negative correlation to precipitation suggests that tree growth is inhibited when cooler temperatures and precipitation as snow shorten the growing season (Villalba et al., 1994). Furthermore, the negative correlation between the tree-ring records at PC and FN with current May SPEI indicates that WBP is less likely to support radial growth if the growing season is delayed in early spring. My results do show a positive correlation shared between PC and LV chronologies with current July temperatures suggesting that these sites are more energy limited than moisture limited. Tree-rings in subalpine environments are more likely to be sensitive to temperature in mesic conditions (Villalba et al., 1994). Since there is evidence that some of my sites are responding positively to July temperatures it is unlikely these are moisture limited systems. According to Fritts (1971) moisture limited tree-ring networks respond poorly to increased rates of evapotranspiration. WBP, however, has been shown to be more energy limited at higher elevations in the western Canadian Cordillera (Youngblut and Luckman, 2013). Similar findings were reported by Maher et al. (2018) who found that WBP sampled between 2100-2560 m in Montana, Idaho, and Oregon were less sensitive to moisture availability but were more sensitive to growing season temperatures. In contrast, Van de Gevel et al. (2017) found previous summer, current spring and current summer precipitation promoted radial growth of whitebark pine in the northern Rocky Mountains, USA. Likewise, Millar et al. (2012) found the whitebark pine responded poorly to moisture deficits in the Sierra Nevadas, USA. Malanson (2017) points out that spatial heterogeneity in precipitation across regional scales could be influencing mixed climatic signals for high-elevation trees.

5.4 Limitations

5.4.1 Mortality

A high degree of accuracy for tree-ring reconstruction is required to make inferences about the stand dynamics. The analysis for mortality rate of reserve trees only used windthrown trees that could be crossdated. The exclusion of non-dated cores results a partial omission of the mortality time series at each study site. Although three of the five sites have negligible differences in total windthrow vs total windthrow crossdated, the number of windthrown trees excluded at PC and LV could alter the slope of the mortality time-course of these two sites. However, the sample depth at these two sites is quite robust and the interpretation of the percent of surviving reserve trees would not affect the overall trend of attrition substantially.

5.4.2 Growth Rates

The dendrochronological sampling methodology for reserve trees consisted of collecting one core per tree. This methodology was prioritized to ensure no unintentional consequences impacted reserve trees as a result of sampling and to increase sampling over the population. Dendrochronological methodologies typically employ two cores per tree to improve the accuracy of cross-dating, as well as to compensate for differences in radial growth due to irregularities in concentric growth patterns (e.g., compression wood) (Speer, 2010). Although reserve trees in this research were sampled perpendicular to the fall line to specifically negate the impact of compression wood, there still remains some degree of uncertainty as to whether ring widths were partially biased due to the one core per tree sampling strategy. In addition, the low number of reserve trees at the LV site (n =14) also introduces some questions as to how robust the results are for all aspects of the radial growth analysis section. Most chronology development methodologies employ a 20 tree minimum (Speer, 2010); however, various researchers have undertaken dendroecological investigations with as few as ten trees (e.g., Baker et al., 2008, Alfaro et al., 2018). The interseries correlation for the LV reserve tree-ring chronology, however, was comparable with the other reserve chronologies which had greater sample depths, which is an important diagnostic on the common signal among sampled individuals.

The pre- and post-harvest percent change in growth were based on equal time intervals before and after the known disturbance date. Typically this approach is used to detect change based on a moving average in order to identify abrupt changes attributable to the removal of competition in disturbance ecology (e.g., Lorimer and Frelich, 1989; Fraver and White, 2005). Nowacki and Abrams (1997) consider a 10-year interval as a robust time interval that would sufficiently capture canopy release events while mediating the effects of short-term climate responses. LV was the only site that had less than ten years and is somewhat limited to an inference as to the extent of change endured by reserve trees given its shorter (6-year) interval. Furthermore, the use of a standardized master chronology for both reserve and control trees limits the scope of elucidating the growth response variability at the individual tree-level, which is why the pointer year analysis was applied to supplement this shortcoming. Cropper values were calculated to quantify how many trees demonstrated a significant growth release at set thresholds. However, Cropper values were set to detect notable differences for the normalized mean growth within a 3-year moving window (Bijak, 2008), which means that if substantial growth was occurring within a consecutive 3-year window the analysis would be less equipped to detect these cumulative growth responses. Growth release detection works best with abrupt changes (Schweingruber et al., 1990).

The two sample Welch t-test found no significant difference between the resistance index of control and reserve trees one year after harvest in three of the four sites examined, suggesting that radial growth reduction was negligible in these stands. However, the radial growth of windthrown trees was not included in the analysis. Therefore, it is possible that windthrown reserve trees had windfirm deficits due to significant radial reduction (Holgén et al., 2003)

5.4.3 Growth-Climate Relationship

Sampling for dendroclimatology requires careful consideration for both site and tree selection in order to optimize climate signals within tree-ring records (Fritts, 1971). Consequently, most dendroclimatic sampling focuses on trees located close to the edge of their ecological range in order to acquire a sensitive climate signal (Speer, 2010). For example, trees that are growing in moisture-rich environments tend to display complacent ring structures which reduces the interannual variability making climate signal detection difficult. Furthermore, sampling for trees that reduce the effects of tree-to-tree competition can improve the climate signals within the tree-ring record (Teets et al., 2018). Since the design of this study prioritized for an evaluation of the outcome of specific silviculture practices, the control tree chronologies that were developed from trees found growing in closed canopy mesic sites, were not ideal candidates for a robust dendroclimatological analysis.

5.5 Works cited

Alfaro, R. I., Campbell, R., Vera, P., Hawkes, B., & Shore, T. (2003, October). Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. In *Mountain Pine Beetle Symposium: Challenges and Solutions,* 245-256.

Alfaro, R. I., vanAkker, L., Berg, J., Van Hezewijk, B., Zhang, Q.B., Hebda, R., Smith, D., & Axelson, J. (2018). Change in the periodicity of a cyclical forest defoliator: An indicator of ecosystem alteration in Western Canada. *Forest Ecology and Management*, *430*, 117–125.

Baker, P. J., Palmer, J. G., & D'Arrigo, R. (2008). The dendrochronology of Callitris intratropica in northern Australia: annual ring structure, chronology development and climate correlations. *Australian Journal of Botany*, *56*(4), 311-320.

Bose, A. K., Harvey, B. D., & Brais, S. (2014). Sapling recruitment and mortality dynamics following partial harvesting in aspen-dominated mixedwoods in eastern Canada. *Forest Ecology and Management*, *329*, 37-48.

Bijak, S. (2008). Various factors influencing the pointer year analysis. *Tree Rings Archaeology. Climatology. Ecology*, *6*, 77-82.

Bladon, K. D., Lieffers, V. J., Silins, U., Landhäusser, S. M., & Blenis, P. V. (2008). Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. *The Forestry Chronicle*, *84*(1), 70-75.

Dorner, B., and Wong, C. (2003). Natural disturbance dynamics in the CIT area. Report for the CIT. Available at : http://www.citbc.org/pubback.html

Fraver, S., & White, A. S. (2005). Disturbance dynamics of old‐growth Picea rubens forests of northern Maine. *Journal of Vegetation Science*, *16*(5), 597-610.

Fritts, H. C. (1971). Dendroclimatology and dendroecology. *Quaternary Research*, *1*(4), 419-449.

Kozlowski, T. T., Kramer, P. J., & Pallardy, S. G. (2012). *The physiological ecology of woody plants*. Academic press.

Lovelock, C. E., Osmond, C. B., & Jebb, M. (1994). Photoinhibition and recovery in tropical plant species: response to disturbance. *Oecologia*, *97*(3), 297-307.

Maguire, D. A., Mainwaring, D. B., & Halpern, C. B. (2006). Stand dynamics after variable-retention harvesting in mature Douglas-fir forests of Western North America. *Allgemeine Forst und Jagdzeitung, 177 (6/7): 120-131*.

Maher, C. T., Nelson, C. R., Larson, A. J., & Sala, A. (2018). Ecological effects and effectiveness of silvicultural restoration treatments in whitebark pine forests. *Forest Ecology and Management*, *429*, 534-548.

Malanson, G. P. (2017). Mixed signals in trends of variance in high-elevation tree ring chronologies. *Journal of Mountain Science*, *14*(10), 1961-1968.

Millar, C. I., Westfall, R. D., Delany, D. L., Bokach, M. J., Flint, A. L., & Flint, L. E. (2012). Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research*, *42*(4), 749-765.

Mitchell, S. J. (2013). Wind as a natural disturbance agent in forests: a synthesis. *Forestry: An International Journal of Forest Research*, *86*(2), 147-157.

Murray, M. P., Bunting, S. C., & Morgan, P. (2000). Landscape trends (1753–1993) of whitebark pine (Pinus albicaulis) forests in the West Big Hole Range of Idaho/Montana, USA. *Arctic, Antarctic, and Alpine Research*, *32*(4), 412-418.

Nowacki, G. J., & Abrams, M. D. (1997). Radial‐growth averaging criteria for reconstructing disturbance histories from presettlement‐origin oaks. *Ecological Monographs*, *67*(2), 225-249.

Peterson, C. J. (2000). Catastrophic wind damage to North American forests and the potential impact of climate change. *The Science of the Total Environment*, *262*(3), 287–311.

Perkins, D. L., & Swetnam, T. W. (1996). A dendroecological assessment of whitebark pine in the Sawtooth–Salmon River region, Idaho. *Canadian Journal of Forest Research*, *26*(12), 2123-2133.

Holgén, P., Söderberg, U., & Hånell, B. (2003). Diameter increment in Picea abies shelterwood stands in northern Sweden. *Scandinavian Journal of Forest Research*, *18*(2), 163-167.

Halpern, C. B., & Urgenson, L. S. (2021). Level and spatial pattern of overstory retention impose trade‐offs for regenerating and retained trees. *Ecological Applications*, *31*(4), e02296.

Harrington, C. A., & Reukema, D. L. (1983). Initial shock and long-term stand development following thinning in a Douglas-fir plantation. *Forest Science*, *29*(1), 33-46.

Heithecker, T. D., & Halpern, C. B. (2007). Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *Forest Ecology and Management, 248*(3), 163-173.

Huggard, D. J., Klenner, W., & Vyse, A. (1999). Windthrow following four harvest treatments in an Engelmann spruce-subalpine fir forest in southern interior British Columbia, Canada. *Canadian Journal of Forest Research*, *29*(10), 1547-1556.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgard, M., & Esseen, P.A. (2007). Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management, 242*(2-3), 306-313.

Mitchell, S. J. (2013). Wind as a natural disturbance agent in forests: a synthesis. *Forestry: An International Journal of Forest Research*, *86*(2), 147-157.

Martin, A. R., Caspersen, J. P., Fuller, M. M., Jones, T. A., & Thomas, S. C. (2014). Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest. *Forest Ecology and Management*, *314*, 183-192.

Olson, M. G., Gwaze, D., & Elliott, A. G. (2015). Fate of live trees retained in mixed bottomland hardwood stands during the first decade after harvest. *Forest Science*, *61*(1), 190-196.

Perkins, D. L., & Swetnam, T. W. (1996). A dendroecological assessment of whitebark pine in the Sawtooth–Salmon River region, Idaho. *Canadian Journal of Forest Research, 26*(12), 2123-2133.

Ruel, J. C. (1995). Understanding windthrow: silvicultural implications. *The Forestry Chronicle*, *71*(4), 434-445.

Ruel, J. C., Pin, D., & Cooper, K. (1998). Effect of topography on wind behaviour in a complex terrain. *Forestry: An International Journal of Forest Research*, *71*(3), 261-265.

Schweingruber, F. H., Eckstein, D., Serre-Bachet, F., & Bräker, O. U. (1990). Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia*, *8*, 9-38.

Solarik, K. A., Volney, W. J. A., Lieffers, V. J., Spence, J. R., & Hamann, A. (2012). Factors affecting white spruce and aspen survival after partial harvest. *Journal of Applied Ecology*, *49*(1), 145-154.

Speer, J. H. (2010). *Fundamentals of Tree-Ring Research*. University of Arizona Press.

Teets, A., Fraver, S., Weiskittel, A. R., & Hollinger, D. Y. (2018). Quantifying climate–growth relationships at the stand level in a mature mixed‐species conifer forest. *Global Change Biology*, *24*(8), 3587-3602.

Temesgen, H., & Mitchell, S. J. (2005). An individual-tree mortality model for complex stands of southeastern British Columbia. *Western Journal of Applied Forestry*, *20*(2), 101-109.

Thorpe, H. C., & Thomas, S. C. (2007). Partial harvesting in the Canadian boreal: success will depend on stand dynamic responses. *The Forestry Chronicle*, *83*(3), 319-325.

Van de Gevel, S. L., Larson, E. R., & Grissino-Mayer, H. D. (2017). Separating trends in whitebark pine radial growth related to climate and mountain pine beetle outbreaks in the Northern Rocky Mountains, USA. *Forests, 8*(6), 195.

Villalba, R., Veblen, T. T., & Ogden, J. (1994). Climatic influences on the growth of subalpine trees in the Colorado Front Range. *Ecology*, *75*(5), 1450-1462.

Whitfield, P. H., Moore, R. D., Fleming, S. W., & Zawadzki, A. (2010). Pacific decadal oscillation and the hydroclimatology of western Canada—Review and prospects. C*anadian Water Resources Journa*l, *35*(1), 1-28.

Wong, C. M., & Daniels, L. D. (2017). Novel forest decline triggered by multiple interactions among climate, and introduced pathogen and bark beetles. *Global Change Biology*, *23*(5), 1926-1941.

Youngblut, D. K., & Luckman, B. H. (2013). Evaluating the temperature sensitivity of radial growth patterns from whitebark pine in the western Canadian Cordillera. *Dendrochronologia*, *31*(1), 16-28.

Chapter 6: Conclusions

6.1 Summary

The rapid decline of WPB throughout its range is a pressing conservation issue. The adoption of silviculture practices that focus on retaining cone-bearing trees has great potential to meet land manager objectives of increasing the survivorship of this species and thus protecting these endangered subalpine ecosystems. The research conducted in this study focused on: (1) mortality rate; (2) growth rates of mature WBP reserve trees in low retention harvest sites; and, (3) the growth-climate relationships of this high-elevation tree species. These objectives are important components for evaluating the success of VR practices as a means to conserve this endangered keystone species in high-elevation ecosystems.

My research indicated that VR in high-elevation ESSF stands in southeastern B.C. intended to support endangered WBP had elevated mortality rates within the initial five-year post-harvest period. Although no mortality rates were calculated in the adjacent control stands the assumption that windthrow rates are a result of harvest disturbance has long been acknowledged in VR literature (i.e. Coates, 1997). In addition, windthrow direction was not randomly distributed which suggested that prevailing winds from Pacific storms had a significant influence on windthrow mortality.

Overall, the tree-ring record for control and reserve WBP indicated similar long-term radial growth patterns. The discrepancy in pre-harvest radial growth trends at WE, however, highlighted that despite the close proximity of reference stands to harvest sites forest health dynamics show fine-scale spatial variability. Pre- and post-harvest growth rate comparisons, as well as the pointer year analysis, demonstrate that large-scale removal of competing trees can increase tree vigor for mature old-growth WBP but only when the pre-harvest conditions were not impacted by reduced radial growth due to insect or pathogen infestations. Furthermore, pointer year analysis indicated that significant growth releases at the stand level were not detectable until at least six years following harvest. This result was mainly characterized by post-harvest intervals greater than ten years at two of the four sites. The absence of positive pointer years for reserve trees in the remaining two sites for the post-harvest interval was most likely attributed to a limited post-harvest interval at LV (6 years) and the negative pre-harvest growth trend at WE. No significant difference was detected between the mean resistance index of control and reserve trees one year after harvest in three of the four sites examined. However, examination of reserve tree chronologies indicate a common growth lag one to three years from the harvest event year. Reserve trees indicated a significant difference in the recovery period for the harvest event year with a one-year lag in two of the four sites. However, this result was confounded by the following two occurrences: (1) one of the sites showed a negative radial growth trend pre-harvest; and, (2) the pointer year analysis identified an inflated growth response in the control trees for the same year for the second site.

WBP in closed canopy forests with mesic site conditions demonstrated to be energy-limited systems and had a significant negative correlation to current July SPEI on a 6-month timescale. The WBP tree-ring network also showed to a lesser extent a significant negative correlation to current July precipitation.

6.2 Implications and Recommendations

In order to respond to the rapid decline of WBP, forest managers need to understand the ecological and climatic elements that affect WBP tree mortality and growth in VR stands in southeastern B.C. Adaptive management strategies for endangered high-elevation five-needle pine species include silviculture as a stand-level intervention (Keane et al., 2022). My research indicated that elevated windthrow post-harvest mortality and significant growth releases have intersecting timelines at approximately 5 years post-harvest. These findings suggest an increased probability of uncertainty as to the success of conserving cone-bearing WPB trees in VR stands.

On the one hand, my findings suggest that the levels and length of attrition of reserve trees could potentially compromise the natural seed dispersal mechanism of WBP from the mutualistic relationship of the Clark's Nutcracker *(Nucifraga columbia)* by creating a deficit in cone-bearing trees. High-elevation five-needle pine ecosystems that have dramatically fewer cone-bearing trees can cause seed shortage for this obligate bird species because pine squirrels (*Tamiasciurus spp.*) are able to outcompete for this food source (McKinney and Tomback, 2007; Keane et al., 2022). Furthermore, the Clark's Nutcracker will leave an area with low cone production because they are energy-sensitive foragers (Tomback et al., 2022) and, although they have the ability to travel great distances to store seeds, they frequently behave locally (Lorenz et al., 2011).

Significant post-harvest radial growth increases for reserve trees provided evidence of increased tree vigor (Dobbertin 2005). Trees with increased vigor can expend greater resources towards cone production, especially when tree-to-tree competition has been removed (Gonzalez-Ochoa et al., 2004). Consequently, the reserve trees from this study show promising opportunities to contribute to cone production since they were also representative of the optimal age cohort (200 yrs old) for cone-bearing capacity (Keane et al., 2017).

These conflicting seed source dynamics have some long-term implications for the success of WBP conservation/restoration strategies. Although this study didn't examine the pre-harvest tree vigor for windthrown reserve trees, it was postulated that these trees were less resilient than those that did survive to the time of sampling. This seems a reasonable conclusion as there was no significant difference for resistance index means between the control and surviving reserve trees one year after harvest for the majority of the sampled stands. Therefore, VR treatments have the potential to effectively alter the dominance of more resistance trees.

Morris et al. (2022) suggest that thinning practices that remove low-vigor trees have the capacity to enhance the survivorship of legacy trees when faced with subsequent disturbances. For example, increased tree vigor for reserve trees can mean enhanced tree defenses against disease and insect attacks (Hansen et al., 2016). Specifically, the long-term survivorship of more resilient trees can impact community dynamics that may fare better in the face of future disturbances (Young et al., 2020; Morris et al., 2022). It is recommended that forest managers return to these VR treatment stands in the future to identify and quantify how many of the remaining reserve trees have WBP rust resistance genetic attributes. Trees infected with WBP rust can potentially survive on the landscape for decades but cone production is quickly compromised (McKinny and Tomback, 2007). Given the low success of WBP survivorship among these VR sites, it is imperative that forest managers review and validate the fecundity of WBP survivorship following silviculture practices. This information could have adaptive management implications insofar as land managers could then implement effective tree-level restoration strategies such as supplementing ingress trees with WBP rust resistant seed plantings.

Given the limitations of this research and the possible implication of these preliminary findings, this work can serve as a building block for future research. Employing an experimental study design would ultimately be the best strategy to elucidate the finer processes and phenomena that affect the survivorship of WBP in VR stands (Maher et al., 2018). Keane et al. (2022) suggest that statistically, reliable sample designs are vitally important to tailor restoration strategies to local environments and specific treatments designed to increase efficacy.

6.3 Future Research

My research was intended to evaluate the success of variable retention as a tool for conserving and restoring WBP within the ESSF of southeastern B.C. The findings of this research suggest multiple avenues of future research:

1) The census methodology employed in my research serves as a strong foundation for long-term programs. Key components include tagged trees with spatial referencing, as well as, a comprehensive inventory of forest health agents, crown lengths and percent of crown foliage at the time of sampling. Keane et al. (2022) indicate that long-term programs that include comprehensive inventory and mapping offer valuable information that can be incorporated into finer-scale restoration and conservation measures.
2) The tree-ring network archived in this study includes additional opportunities in the field of dendrochronological investigations. An analysis of pre-harvest radial growth from cross dated windthrown trees could illuminate the relationship between pre-harvest growth and post-harvest mortality. Examining the radial growth of windthrown trees

could quantify the magnitude of radial growth reduction as a result of harvesting practices.

3) The growth-climate analysis was only done on control trees, leaving knowledge gaps to how VR treatment might potentially shape growth-climate relationships post-harvest. PC and FW are the best candidates for a more in-depth growth-climate analysis as these sites have the longest post-harvest time-series and, provide adequate sample depths. In addition, growth-climate stability should be taken into consideration in future work.
4) Silviculture treatments are studied for both short-term and long-term consequences. One long-term influence of clearcutting practices is the impact it has on altering species composition (Harplen and Urgenson, 2021). Bose et al. (2013) define recruitment as a top consideration for evaluating silviculture practices. Therefore, there is an important opportunity to examine regeneration on these cutblocks, especially since the nature of this anthropogenic disturbance could foster early successional trees species (Clark and Covey, 2012), such as WBP.

6.4 Works Cited

Bose, A. K., Harvey, B. D., Brais, S., Beaudet, M., & Leduc, A. (2014). Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry*, *87*(1), 11-28.

Coates, K.D. (1997) Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia. *Canadian Journal of Forest Research, 27(*10*)*, 1695-1701.

Clark, J. A., & Covey, K. R. (2012). Tree species richness and the logging of natural forests: A meta-analysis. *Forest Ecology and Management*, *276*, 146-153.

Dobbertin, M. (2005). Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *European Journal of Forest Research*, *124*(4), 319-333.

González-Ochoa, A. I., López-Serrano, F. R., & de las Heras, J. (2004). Does post-fire forest management increase tree growth and cone production in Pinus halepensis?. *Forest Ecology and Management*, *188*(1-3), 235-247.

Hansen, A., Ireland, K., Legg, K., Keane, R., Barge, E., Jenkins, M., & Pillet, M. (2016). Complex challenges of maintaining whitebark pine in Greater Yellowstone under climate change: A call for innovative research, management, and policy approaches. *Forests*, *7*(3), 54.

Halpern, C. B., & Urgenson, L. S. (2021). Level and spatial pattern of overstory retention impose trade‐offs for regenerating and retained trees. *Ecological Applications*, *31*(4), e02296.

Keane, R. E., Holsinger, L. M., Mahalovich, M. F., & Tomback, D. F. (2017). Restoring whitebark pine ecosystems in the face of climate change. *General Technical Report RMRS-GTR-361. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 123*.p. *361*.

Keane, R. E., Schoettle, A. W., & Tomback, D. F. (2022). Effective actions for managing resilient high elevation five-needle white pine forests in western North America at multiple scales under changing climates. *Forest Ecology and Management*, *505*, 119939.

Lorenz, T. J., Sullivan, K. A., Bakian, A. V., & Aubry, C. A. (2011). Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). *The Auk*, *128*(2), 237-247.

Maher, C. T., Nelson, C. R., Larson, A. J., & Sala, A. (2018). Ecological effects and effectiveness of silvicultural restoration treatments in whitebark pine forests. *Forest Ecology and Management*, *429*, 534-548.

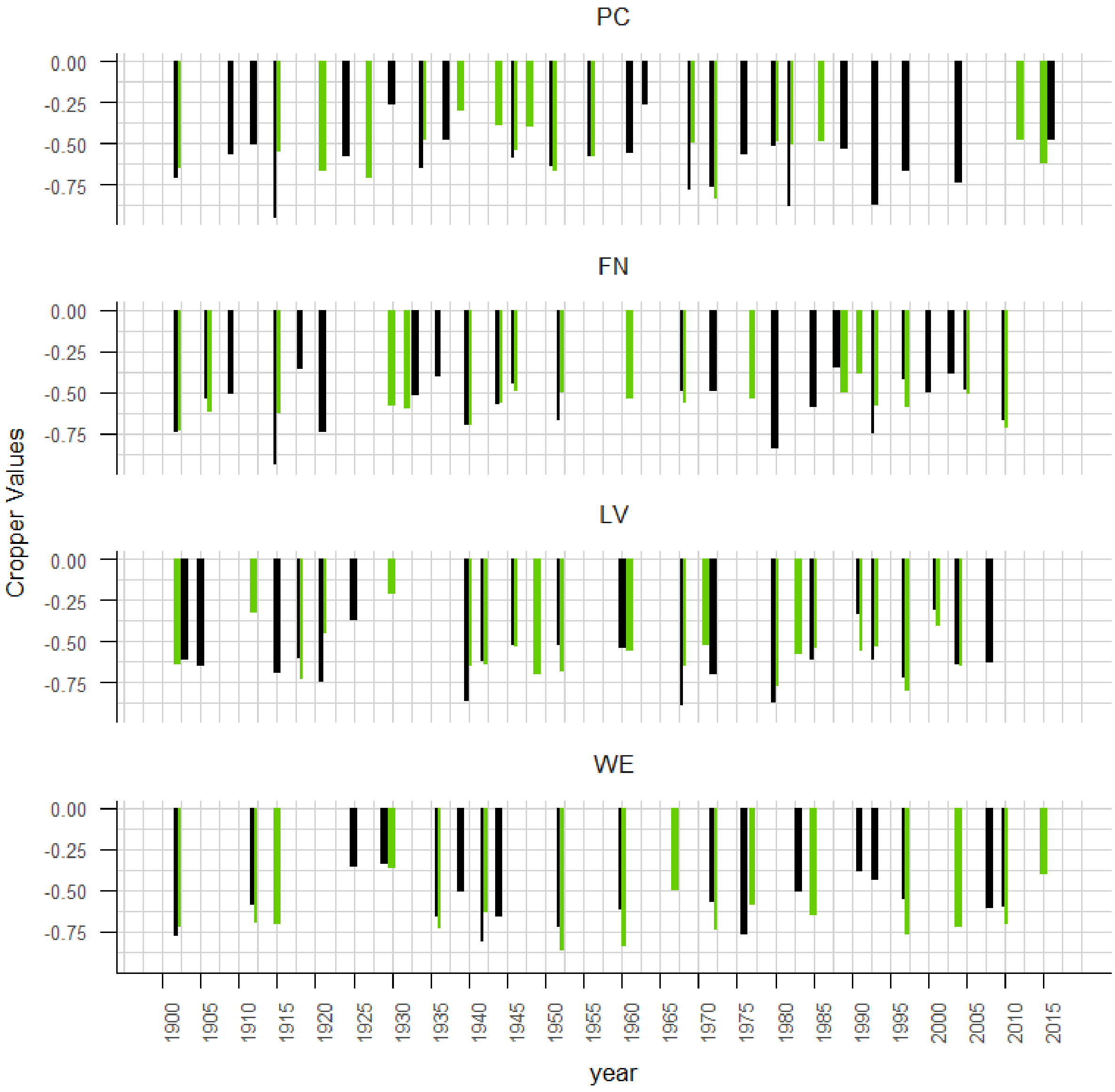
McKinney, S. T., & Tomback, D. F. (2007). The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research*, *37*(6), 1044-1057.

Morris, J. E., Buonanduci, M. S., Agne, M. C., Battaglia, M. A., & Harvey, B. J. (2022). Does the legacy of historical thinning treatments foster resilience to bark beetle outbreaks in subalpine forests?. *Ecological Applications*, *32*(1), e02474.

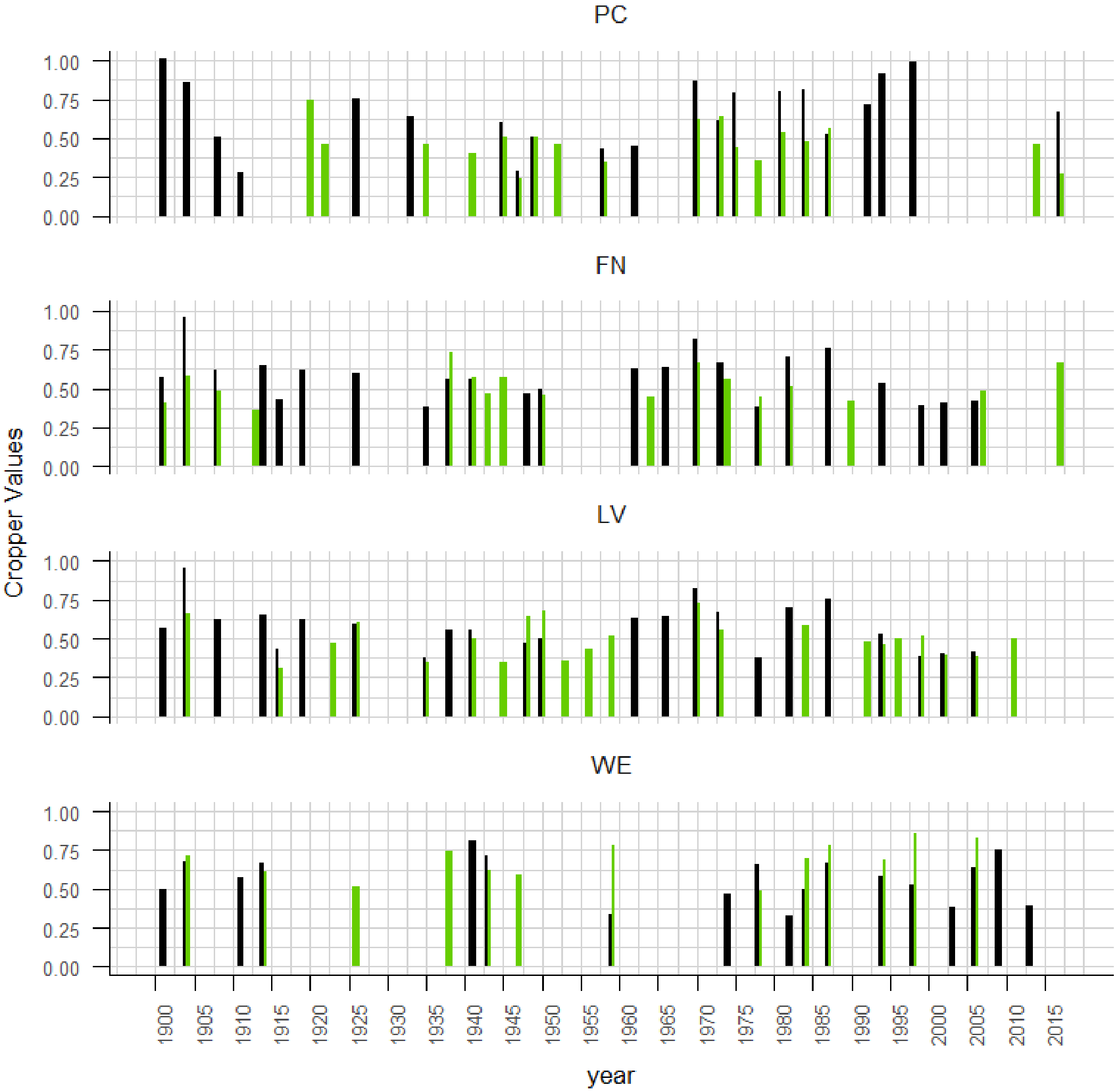
Tomback, D. F., & Sprague, E. (2022). The National Whitebark Pine Restoration Plan: Restoration model for the high elevation five-needle white pines. *Forest Ecology and Management*, *521*, 120204.

Young, D. J., Meyer, M., Estes, B., Gross, S., Wuenschel, A., Restaino, C., & Safford, H. D. (2020). Forest recovery following extreme drought in California, USA: natural patterns and effects of pre‐drought management. *Ecological Applications*, *30*(1), e02002.

APPENDIX A: Identification of Negative Pointer Years for Control and Reserve Trees for the common time period of 1901-2018 (FN:1901-2017)



APPENDIX B: Identification of Positive Pointer Years for Control and Reserve Trees for the Common Time Period of 1901-2018 (FN:1901-2017)



APPENDIX C: Two sample Welch T-test on Resistance Index Means

		Tree Sample Depth		Resistance Index Means				
Site	Event Year	Reserve	Control	Reserve	Control	t	df	p-value
PC	1969	17	19	0.75	0.74	-0.19	24.54	0.85
PC	1972	17	19	0.71	0.82	1.94	32.88	0.06
PC	1982	17	19	0.72	0.71	-0.13	24.96	0.90
PC	**2004**	17	19	0.89	0.74	-1.52	22.36	0.14
FN	1972	20	18	0.88	0.89	0.32	32.92	0.75
FN	1997	20	18	0.86	0.86	0.03	36.00	0.98
FN	**2002**	20	18	0.92	1.16	1.67	33.13	0.10
FN	2010	20	18	0.88	0.78	-1.46	28.50	0.16
LV	1997	13	18	0.79	0.82	0.49	25.08	0.63
LV	2001	13	18	0.83	0.98	2.47	28.92	0.02*
LV	2004	13	18	0.86	0.86	-0.07	24.14	0.94
LV	**2013**	13	18	0.87	1.09	1.42	14.81	0.18
WE	1972	36	18	0.84	0.88	0.66	25.70	0.51
WE	1997	36	18	0.83	0.87	0.46	25.83	0.65
WE	**2009**	36	18	0.94	1.19	2.50	50.72	0.02*
WE	2010	36	18	0.65	0.90	3.40	39.92	0.00*

Event Year's in bold represent harvest event year with a one year lag
* indicates significant difference between mean resistance index

APPENDIX D: Two sample Welch T-test on Recovery Period Means

		Sample Depth		Mean Recovery Period				
Site	Event Year	Reserve	Control	Reserve	Control	t	df	p-value
PC	1969	13	18	1.49	1.10	-0.51	16.01	0.62
PC	1972	14	19	0.62	0.88	1.10	20.45	0.29
PC	1982	12	18	3.11	2.23	-0.72	18.28	0.48
PC	**2004**	17	17	1.78	1.64	-0.21	24.36	0.84
FN	1972	15	18	1.02	1.36	0.70	30.26	0.49
FN	1997	18	16	3.13	2.97	-0.11	31.22	0.91
FN	**2002**	18	18	3.41	1.52	-2.14	33.88	0.04*
FN	2010	20	18	0.61	1.63	1.98	30.36	0.06
LV	1997	10	18	0.69	0.83	0.42	21.65	0.68
LV	2001	8	17	1.88	1.31	-0.64	12.04	0.54
LV	2004	12	16	0.80	0.71	-0.30	23.29	0.77
LV	**2013**	10	13	1.01	0.29	-1.75	19.19	0.10
WE	1972	30	15	2.70	1.86	-0.88	26.83	0.38
WE	1997	26	14	0.43	1.10	1.06	13.33	0.31
WE	**2009**	23	15	1.85	0.56	-2.16	33.54	0.04*
WE	2010	21	14	2.42	0.92	-2.62	25.33	0.01*

Event Year’s in bold represent harvest event year with a one year lag
*indicates significant difference between mean recovery period