

Utilizing Dendrochronology to Investigate Multiscale Drivers of Conifer Growth in the Pacific Northwest

A Dissertation
Presented in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
with a
Major in Water Resources Science and Management
in the
College of Graduate Studies
University of Idaho
by
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May 2020

Authorization to Submit Dissertation

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Abstract

Conifers dominate temperate and boreal forests around the world and many species are economically important for structural timber production. They are also adapted to extreme climatic conditions, such as drought and cold temperatures. Numerous conifer species occur within the Pacific Northwest United States (PNW) including firs, hemlocks, cedars, larches, and pines. The diversity of hydrologic and geographic variables across the PNW creates distinctive localized climates with differing limiting factors on conifer growth, such as temperature, moisture, and nutrient availability. Dendrochronology, or tree-ring dating, is a multidisciplinary methodology that utilizes annual tree ring widths to investigate environmental conditions influencing trees or stands throughout their life. A substantial amount of information is known about tree-growth responses to climate and stand dynamics. However, investigations into interacting silvicultural and climatological influences, as well as spatial variability of growth relationships, may inform future management and dendrochronological techniques. The first three chapters of this dissertation utilize dendrochronology to investigate multiple drivers of species-specific tree growth.

The first chapter investigates the impacts of density reductions, via different thinning intensities, on tree growth in moist mixed coniferous forests in northern Idaho, USA. Species that respond rapidly to available sunlight and/or nutrients, like western larch and western redcedar, show the greatest growth increases following thinning. The less consistent responses to thinning by western hemlock and grand fir were likely due to their autecological characteristics and inherent lack of responses to greater growing space. Findings from Chapter 1 align with past thinning experiments and found that thinning is an effective tool for increasing growth in most species. However, if the objectives are to favor injury-prone and less competitive species like western hemlock and grand fir, precautions must be taken during and after treatment to limit tree damage that could produce undesired responses.

Chapter 2 presents the temporal variability of growth-drought relationships for the same species from Chapter 1, and how that relationship is influenced by thinning. The four species in this study, western larch, grand fir, western redcedar, and western hemlock, show a wide range of responses to drought depending on timing of drought, length of drought, intensity of drought, and forest stand density. Findings indicate that length and season of drought, species-specific drought tolerance, and stage of stand development, influence

growth-drought responses. Drought sensitivity often involves trade-offs among other limiting factors like direct competition for resources. Moreover, trees growing in moist forests may not be as highly susceptible to droughts as those in dry forests. Therefore, it is suggested that stands be managed as complex adaptive systems by prioritizing species, age, and structural diversity. Results from Chapter 1 and Chapter 2 demonstrate that strip clearcutting in moist forest results in diverse conifer species composition and structure that can be further managed to create complexity through mid-rotation thinning.

Chapter 3 focused at a larger spatial scale (e.g., greater PNW) to examine the effects of geographical factors on flow-growth relationships of four different conifer species. Streamflow correlated negatively with subalpine fir and mountain hemlock growth, species commonly found at cool, moist, high elevation sites, indicating that they are likely more sensitive to severe environmental variation like those experienced with climate change. Drier-site species, Douglas-fir and ponderosa pine were mostly positively correlated with flow, though a few had significant negative correlations, indicating that they are species with high adaptive capacity. Results help simplify planning for field collections and strengthen methodologies for future streamflow reconstructions by supplying knowledge about which streams, species, elevations, and directions will yield the most robust models in the spatially diverse terrain of the PNW.

Chapter 4 is a collaborative synthesis of climate change research in the Columbia River Basin (CRB). Results show that spatial distribution and thematic content of research varies across an international border, with greater concentrations of research in the United States than Canada. A general scarcity of social science research and limited interaction between social and biophysical content reinforce the need for increased collaboration between disparate disciplines. Future research focus areas should include research related to climate change adaptation and mitigation, increased integration between social and biophysical sciences, and collaborations that bridge the international border for a more unified basin-wide focus. Focusing on these new directions for research will increase the potential for science and management communities to co-produce actionable science and effective responses to climate change.

With the utilization of dendrochronological techniques, many of the interacting drivers of species-specific tree growth in the PNW were discovered. Shade tolerance,

disturbance dynamics, and hydroclimate all influence conifer growth in the region. The relationships between streamflow and growth are heightened for trees growing in extreme climates, and these relationships are driven by geographical features. Overall, this dissertation provides insight into dendrochronological techniques as well as silvicultural management in moist mixed conifer forests; it also lends support that forest management can assist tree growth and alter growth-drought relationships depending on species. Finally, the dissertation offers additional evidence to the decades-long theory that trees growing at the edges of their ranges show higher sensitivity to limiting factors.

Acknowledgements

I would like to thank the National Science Foundation (NSF) Integrative Graduate Education and Research Traineeship (IGERT) program for providing me with funding, collaborators, internships, workshops, and office space. I also thank Paul Kimmell and the AVISTA Waters of the West Scholarship for additional research funding. I especially thank the Director of the Water Resources Program at the University of Idaho, Dr. Tim Link, for supporting me as a mentor, for challenging me to think critically, participating on my committee, and for leading the IGERT program with stewardship, tact, and generosity. He has also helped with fundamental navigations of graduate school, and for that I'm forever grateful. I would like to thank my committee for their insight, guidance, support, and wisdom. My advisor, Dr. Andrew Nelson has been pivotal in helping me complete my dissertation – thanks are extended to him for encouraging me to research mixed coniferous forests using dendrochronology, for believing in me as a scientist, and for supplying me with critical feedback and advice. I thank Dr. Randy Brooks who was instrumental in helping me continue working toward my PhD when early roadblocks appeared. I thank Dr. Grant Harley for encouraging me to use dendrochronology in new and creative ways and for the many helpful edits he supplied. I also appreciate the critical feedback and edits from Dr. Teresa Jain – she always makes me think critically about natural phenomena and I sincerely thank her for that. I thank Dr. Brant Miller for believing in me as a science educator, for giving me professional guidance and opportunities, and for always being available when I needed him. Special thanks are extended to Dr. Penny Morgan of The University of Idaho and Dr. Dorian Burnette of the University of Memphis for their continued friendship and mentorship throughout this academic venture. I would also like to thank the students and mentors of the IGERT program; there are too many names to mention here, but each person I interacted with in the program has forever made an impression on my spirit and I will never forget them. I specifically thank my IGERT collaborators on Chapter 4 who helped significantly in bringing that research to fruition, Dr. Andrienne Marshall, Courtney Cooper, Dr. Paris Edwards, Dr. Shana Hirsch, and Dr. Micah Russell. I extend a special thanks to my brother, Dr. Eric Foard, who enthusiastically helped me with my field collections for a hefty paycheck of “thank you, thank you, thank you!” – I'm sincerely appreciative for your willingness to work long days under the supervision of a mildly OCD sister. I thank my close friends whose emotional

support and humor was pivotal to my mental health (first names are: Sonja, Anne, Ashleigh, Becky, Carrie, Jessie, Julia, Katie, Maggie, Ruby, and Sarah). Last, but not least I thank my husband, Nick Fuller, who volunteered to help me collect field data but more importantly helped me brave the storm of academic life.

Dedication

I would like to dedicate this dissertation to my family and especially my husband; words cannot truly express how much you all did to help me finish this PhD. Additionally, I dedicate this to the spruces, mooses, and geoses, of the Palouses; the largest larches; and bears!

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Statement of Contribution

I am the sole author of the Prologue, Chapter 1, Chapter 2, and Epilogue. All concepts were originated by me, and statistical analyses sole-conducted. The other authors listed in Chapter 3 played editorial and advisory roles. Chapter 4 is a collaborative manuscript that is co-authored by five other fellows of the National Science Foundation (NSF) Integrative Graduate Education and Research Traineeship (IGERT) program members, as well as Tim Link, who played an advisory and editorial role. I co-led the production of the manuscript with Adrienne Marshall.

Prologue

There are two distinct classifications of trees – gymnosperms and angiosperms. The word “gymnosperm” directly translates from Latin to English as “naked seed,” which refers to seeds that do not form in an ovary, like the fruit of angiosperms. In angiosperms, which translates to “covered seed,” seeds come from flowers that make fruit, and these include all the many “hardwood” and “broadleaved” tree species. On the other hand, gymnosperms do not produce flowers, and their seeds form on cones; this is where the term *conifer* comes from (Singh, 2006). Conifers are the most abundant and economically important phylum of gymnosperms and include all tree species that produce cones. Conifers have unique adaptations in their water-conducting tissue, xylem, that allows them to withstand water stress and freeze-thaw cycles better than their angiosperm cousins. The xylem of conifers consists of tracheid cells that require water to pass through pit membranes as it moves upward. These pit membranes function like a door and can close the compartment off when air bubbles form in a cell (in response to drought or freezing). The ability of conifers to isolate and decommission cavitated cells gives them advantages in extreme climates over broadleaved trees (Choat & Pittermann, 2009; Pittermann, Sperry, Hacke, Wheeler, & Sikkema, 2005; Singh, 2006). Angiosperm trees often grow in warm and wet climates while conifers live in places with low precipitation and/or extreme temperatures.

Well-adapted conifer species dominate the Pacific Northwest United States (PNW) including firs, hemlocks, cedars, and pines. The climate, which generally involves hot-dry summers and cool-wet winters, is highly variable and can be extreme in some locations as a result of complex terrain, maritime and continental weather patterns, and the jet stream (Waring & Franklin, 1979). The Cascade Mountains line the western coast while the Rocky Mountains draw the eastern boundary. In between these vast mountain ranges arises the dry intermountain steppe grasslands. The geographical heterogeneity results in stark variation in local climates based on slope, aspect, longitude, latitude, and elevation (Fagre, Peterson, & Hessler, 2003; Mock, 1996). Longitudinally, the climate is more hydric in the west and drier in the east. Most precipitation falls in the winter from large maritime fronts. These westerly fronts deposit mass amounts of precipitation west of the Cascade crest – leading to a rainforest on the Olympic Peninsula that receives at least 6000 mm of annual water

equivalent on the top of Mount Olympus (Halofsky, Peterson, O'Halloran, & Hoffman, 2012). The coastal weather systems move east, where most of the remaining moisture descends in the highest elevations of the Cascade Mountains (Mock 1996). The intermountain west receives little precipitation, continental climate (dry with highly variable temperature fluctuations), and consists of deserts, steppes, and grasslands. East of the intermountain region is the western foothills of the Rocky Mountains in central and northern Idaho, where total precipitation increases once again as elevation rises to the crest of the Rocky Mountains. Latitudinally, temperatures are generally colder in the north. Moisture also increases slightly from south to north, except for the intermountain zone in central Washington. Like all mountainous landscapes, precipitation increases and temperature decreases with ascending elevation. The PNW is also along the path of the jet stream, which separates polar air masses from temperate mid-latitude air masses. Thus, climates may vary significantly from year to year and within years. As the climate continues to change, the position and strength of the jet stream will also likely change, resulting in highly variable climate models for this region (Barnes & Screen, 2015; Francis & Vavrus, 2012). The diversity of hydrologic and geographic variables across the region creates distinctive localized climates with differing limiting factors on conifer growth.

Dendrochronology is a multidisciplinary method that utilizes annual tree ring widths to investigate environmental conditions present throughout the life of trees or stands (James Hardy Speer, 2010; Stokes & Smiley, 1968). Trees produce annual growth rings made of layers of xylem cells. The thickness of these rings indicates the favorability of environmental conditions throughout the seasons. Trees grow fastest in favorable conditions, which is reflected by wider than average annual rings. Under unfavorable growing conditions, tree growth will be slower and annual rings thinner. Variations in yearly ring width growth of trees depend on several intrinsic and environmental factors. Annual width is a simple linear model with five major predictor variables: (1) age; trees often decline in radial growth as they age – usually recognizable around 100 years old, (2) climate; including drought, precipitation, and temperature, (3) neighborhood disturbances; such as species competition and canopy gaps, (4) stand-level disturbances; such as bark beetle outbreaks, heavy frosts, or silvicultural thinning, and (5) random variability in annual growth not explained by the other variables, which is often insignificant (Edward R. Cook & Kairiukstis, 1990). Only a fraction

of total growth for each annual ring is attributable to each of these predictor variables (i.e., there is a trade-off among these growth predictor variables). For example, when trees experience intense stand competition, they may become less drought-sensitive (i.e., they are less correlated with drought) and the variability in annual ring widths becomes mostly influenced by competition rather than drought (Pérez-de-lis, García-gonzález, & Arévalo, 2011). Within each significant predictor variable, there may also be multiple interacting players that alter growth-predictor relationships. For example, when considering growth-climate relationships, trees may respond to precipitation when rain is scarce, but when precipitation is abundant trees may become more sensitive to temperature (Edward R. Cook & Kairiukstis, 1990). These growth predictors may be significant at different times throughout the lifespan of trees and often are dependent upon species-specific stresses, level of stand development, and stand density (Niinemets, 2010). The strength of the growth-predictor relationship also varies with geographical location. While trees well within the bounds of their productive habitats would show greater growth sensitivity to stand dynamics, such as competition, trees growing in their outer range limits are often more sensitive to climatic growth-limiting factors (Edward R. Cook & Kairiukstis, 1990; King, Gugerli, Fonti, & Frank, 2013; James Hardy Speer, 2010).

There is a lot of information known about tree-growth responses to climate and stand dynamics. However, investigations into interacting silvicultural and climatological influences, as well as spatial variability of growth relationships, may inform future management and dendrochronological techniques. The first three chapters of my dissertation utilize dendrochronology to investigate multiple drivers of species-specific tree growth, including: stand density reductions, growth-drought relationships and growth-drought responses to density reductions, and spatial variability of flow-growth relationships. The final chapter is a collaborative interdisciplinary synthesis of the spatial and topical distributions of climate change research. Chapter 4 also places many disciplines that depend on dendrochronology into a regional climate change context. This dissertation improves understanding of conifer growth relationships across the broader northwestern United States and informs future decision-making processes for management and research.

Chapter 1: Short- and long-term growth responses to varying thinning intensities for multiple coniferous species in the Northern Rocky Mountains

Abstract

Pre-commercial thinning increases forest growth and yield; however, growth response may depend on inter- and intra-specific competition and species-specific characteristics. Moreover, immediate, short-term, and long-term responses to treatment are not well investigated, especially in mixed-species stands. This study utilizes dendrochronology to investigate the temporal variability of growth responses of three shade-tolerant and one shade-intolerant species to thinning treatments in a moist mixed-species coniferous forest in northern Idaho, USA. I identified immediate growth releases using radial growth averaging criteria. Short- and long-term radial growth responses to thinning, corrected for diameter, were investigated using a before-after/control-impact experimental design. All species showed immediate growth releases. However, grand fir and western hemlock releases were weaker and shorter-term than western redcedar and western larch. Two-factor mixed-effects ANCOVA found significant interaction effects for all species; however, only two species' growth increased compared to unthinned references. Western larch and western redcedar showed significantly higher growth in treatments than in reference plots – both in the short- and long-term. However, no increases in growth for grand fir and western hemlock were present. Sunlight can be a limiting factor for shade-intolerant species, such as western larch, in dense stands, so it is not surprising I observed short- and long-term growth increases in Moderate and High thinning treatments. Western redcedar exhibited a similar response even though the species is shade tolerant. The less consistent responses to thinning by western hemlock and grand fir were likely due to their autecological characteristics and innate responses to more growing space. I conclude that thinning is an effective tool for increasing growth in moist mixed-species forests, but not for all species. Species that respond rapidly to available sunlight and/or nutrients, like western larch and western redcedar respectively, show the most significant growth increases. Moreover, extra precautions should be taken

during and after treatment to get growth increases in more injury-prone and determinant species that show delayed responses to limiting factors, like western hemlock and grand fir.

Introduction

Forest thinning is the process of reducing stand density to minimize competition in residual trees and often results in increased forest growth and yield (Oliver, Larson, & Oliver, 1996). Thinning has been utilized to accomplish various forest management objectives including increasing overland flow (Lesch & Scott, 1997), improving fire and pest resilience (Knapp et al. 2012; Ashton and Kelty 2018), increasing above-ground carbon stores, improving wildlife habitat (Horner et al., 2010), changing forest composition (Shen, Nelson, Jain, Foard, & Graham, 2019), and improvement cutting (Ashton & Kelty, 2018). Often, however, the goal of forest thinning is to increase growth and yield of forests (Hamilton, 1981). Thinning is typically done during the stem exclusion phase of stand development when trees still are relatively small (< 30 cm DBH) and have the capacity to respond to changes in resource availability. Many studies note increased growth with decreasing residual stand densities (Cochran, 1999; Seidel, 1982). Post-thinning growth rates often increase because limiting factors like sunlight, nutrients, and water are redistributed and utilized by fewer individuals (Ashton & Kelty, 2018).

Growth increases in response to stand density are widely recognized, although recent short- and long-term comparisons of responses among species in mixed-species stands are uncommon (Aldea, Bravo, Rodríguez, & Río, 2017). Mixed forests experience higher levels of interspecific competition and resource partitioning than monocultures. In other words, individual species from mixed forests are sensitive to different limiting factors of sunlight, nutrients, and water and may respond differently to reductions in density than other species (Forrester, 2014). Forrester (2013) discovered that increases in growth in response to thinning is much higher in light-limited sites than nutrient-limited sites, except in dry years. Thus, I posit that tree species limited by light might show a more robust response to thinning than species limited by nutrients or water, especially if there is a productive understory utilizing the soil resource availability but not the light. Conversely, if thinning results in greater growth releases for nutrient- or water-limited species then it stands to reason that thinning freed up essential nutrients for residual trees of that species. Resource partitioning of mixed forests leads to variable responses to increases in resource availability resulting from

density reductions. Therefore, investigations of species-specific responses to thinning will provide insight into the future management of mixed-species stands (Forrester, 2013, 2014).

Even though thinning is promoted for enhancing forest growth for commercial wood production, in addition to a variety of other management objectives, very few studies have examined long-term (more than 20-years) trends in forest growth responses to thinning (Pitt & Lanteigne, 2008). It is generally understood that reductions in stand density will result in short-term increases in growth in residual trees for most species (Oliver et al., 1996). However, immediate increases in growth may not hold in the longer term. Long-term studies of thinning responses could negate or corroborate results from short-term studies that support thinning increases overall stand growth. For example, stands of Norway spruce (*Picea abies*) showed growth increases in drought years immediately after thinning but not in the long-term. However, residual trees showed greater resilience to drought in the long-term when compared to unthinned plots (Sohn et al., 2013). In another example, Pitt and Lanteigne (2008) validate that reduced density results in long-term increases in stand volume and decreased time to merchantability. These long-term investigations of thinning growth responses may aid in estimates of total merchantable wood at a rotation-length many years after thinning.

Dendrochronology, or tree-ring dating, is a common method for investigating releases and growth responses to silvicultural treatments (Guillemot, Klein, Davi, & Courbet, 2015; Misson, Vincke, & Devillez, 2003; James Hardy Speer, 2010; Vitali, Brang, Cherubini, Zingg, & Nikolova, 2016). Trees produce annual rings that indicate the favorability of conditions during the growing season. When rings are wider than average, the factors that limit tree growth (e.g., nutrients, sunlight, and water) are often abundant, leading to rapid radial growth. When these limiting factors are in short supply, or there are high levels of competition, trees grow slower, and rings are narrower. Measurements of radial growth are frequently used to quantify growth post-thinning in various coniferous species including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Megraw, 1972), slash pine (*Pinus elliottii* Engelm.), loblolly pine (*Pinus taeda* L.) (Moschler, Dougal, & McRae, 2007), black pine (*Pinus nigra* Arnold) and Scots pine (*Pinus sylvestris* L.) (Baldwin Jr, Feduccia, & Haywood, 1989; Silvestru-Grigore et al., 2018), white spruce (*Picea glauca* (Moench) Voss) (Juodvalkis, Kairiukstis, & Vasiliauskas, 2005), black spruce (*Picea mariana* (Mill.) Britton,

Sterns & Poggenb.) (Tong, Tanguay, & Zhang, 2011), and Norway spruce (*Picea abies* (L.) Karst.) (Mäkinen & Isomäki, 2004).

In addition to measuring and quantifying radial growth, the dendrochronological technique of radial growth averaging (RGA) identifies years of immediate growth “releases” (and suppressions) for tree series (Nowacki & Abrams, 1997). This method calculates a percent growth change for each year for each series based on growth in surrounding years. This technique has proven effective at identifying years of stand disturbances by comparing disturbance years among series within stands or landscapes (Nowacki & Abrams, 1997), including thinning responses (Pérez-de-lis et al., 2011). This method is specifically applied to identify immediate responses to stand disturbances such as thinning treatments.

The objectives of this study are to evaluate the short- and long-term growth response of density reduction via thinning in common conifer tree species in the moist mixed-species forests of the Northern Rocky Mountains of Idaho, USA. I specifically (1) investigate and compare species-specific RGA thinning releases for four conifer species (western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), and western larch (*Larix occidentalis* Nutt.)) – the initial, short-term, thinning response. (2) and compare post-thinning growth responses between treatment plots and reference plots for the same species. I hypothesized that shade tolerance would drive thinning responses because the research site is known for having abundant moisture and nutrients; thus, photosynthetically active radiation (PAR; i.e. sunlight) would be the most limiting factor. Results from this study can help predict short- and long-term responses to thinning in mixed forests and may inform thinning responses given different climate stressors. Furthermore, investigations of species-specific responses to reduced density will provide insight into future management of mixed-species stands by identifying species with positive thinning responses and potentially informing managers of proper thinning methodologies.

Methods

Site Description.

The research site is a coniferous forest within the Central Rocky Mountain Interior Western Redcedar - Western Hemlock Forest classification (Minore, 1979) on the north aspect of the Benton Creek watershed in the Priest River Experimental Forest (PREF) in the

Rocky Mountains of northern Idaho, USA. Soils are Andisols with more than 200 cm to a restrictive layer and parent material volcanic ash over residuum weathered from metasedimentary rock (USDA-NRCS, 2012). The ash-cap leads to highly productive forests that retain more water for extended periods (Kimsey, Gardner, & Busacca, 2007; Page-Dumroese, Miller, Mital, McDaniel, & Miller, 2007). The climate is continental and maritime; thus, both dry-continental and moist-marine air masses from the Pacific Ocean influence the site (Tinkham, Denner, & Graham, 2015). The continental climate results in extreme seasonal variability with hot, dry summers and cold, wet winters. Maritime characteristics include substantial winter precipitation and low-frequency climate variability that coincides with oceanic teleconnections. The mean annual precipitation is 950 mm, half of which falls as snow. Temperatures range from -4.2°C in January to 18.1°C in July, on average (Tinkham et al., 2015). The PREF is also along the path of the jet stream, which separates polar air masses from temperate mid-latitude air masses. Thus, climates may vary significantly from year to year and within years. As the global climate continues to change, the position and strength of the jet stream will also likely change, resulting in highly variable climate models for this region (Barnes & Screen, 2015; Francis & Vavrus, 2012). The PREF climate is also significantly influenced by topography – north aspects are much cooler and moister than south aspects. Higher elevations are also cooler and receive much more precipitation than lower elevations. The forests are a complex mixture of conifers, shrubs, grasses, and forbs adapted to various environmental disturbances, including root disease, disease and mortality of western white pine, and ice storms. Common overstory species found in the PREF are mixed conifers, including western redcedar, hemlock, grand fir, western larch, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and western white pine (*Pinus monticola* Douglas ex D. Don). The forest understory often consists of deciduous trees like hawthorn and rocky mountain maple, plus shrubs like currant, ninebark and huckleberry.

Study Area

In 1942 the US Forest Service created a strip clearcut through a commercial harvest (900 m long x 91 m wide) along a north aspect perpendicular to Benton Creek, a first-order stream (Figure 1.1). The strip clearcut elevations range from approximately 1020 m next to Benton Creek to 1240 m on top of the ridge. The harvested area naturally regenerated to a

crowded density of $10,022 \pm 2,421$ trees ha^{-1} (1 m mean spacing) dominated by western hemlock and western redcedar (72% of all trees) (Shen et al. 2019). In 1967 an experimental thinning study was conducted, which favored shade-tolerant tree species. The research design was a systematic block design of seven blocks. The seven replicated thinning blocks increased in numeric assignment as the elevation decreased (Figure 1.1). Each block contained treatment plots, while blocks one, seven, and four contained unthinned, reference plots. In 1972 the reference plot from block one was fertilized, which resulted in significantly higher growth compared to the other control plots according to a t-test ($p < 0.01$); therefore, this location was excluded from the analyses. In summer 1967, trees were thinned from below with two thinning intensities. The lowest intensity thinning treatment (Low) resulted in a residual density of 1,976 trees ha^{-1} (2.1–2.4 m mean spacing), while the Moderate thinning (Moderate) had 988 trees ha^{-1} (3.0–3.4 m mean spacing). Initial thinning treatments were in rectangular plots of approximately 0.66-ha, and the control plots were 0.42-ha rectangles, on average. In the summer of 1970, additional thinning occurred in all treatment plots to improve spacing accuracy. At the same time, the Low plots were split, and half were thinned at a high intensity (High), resulting in 494 trees ha^{-1} (4.3–4.6 m mean spacing). The final size of the High and Low plots was approximately 0.033-ha, on average

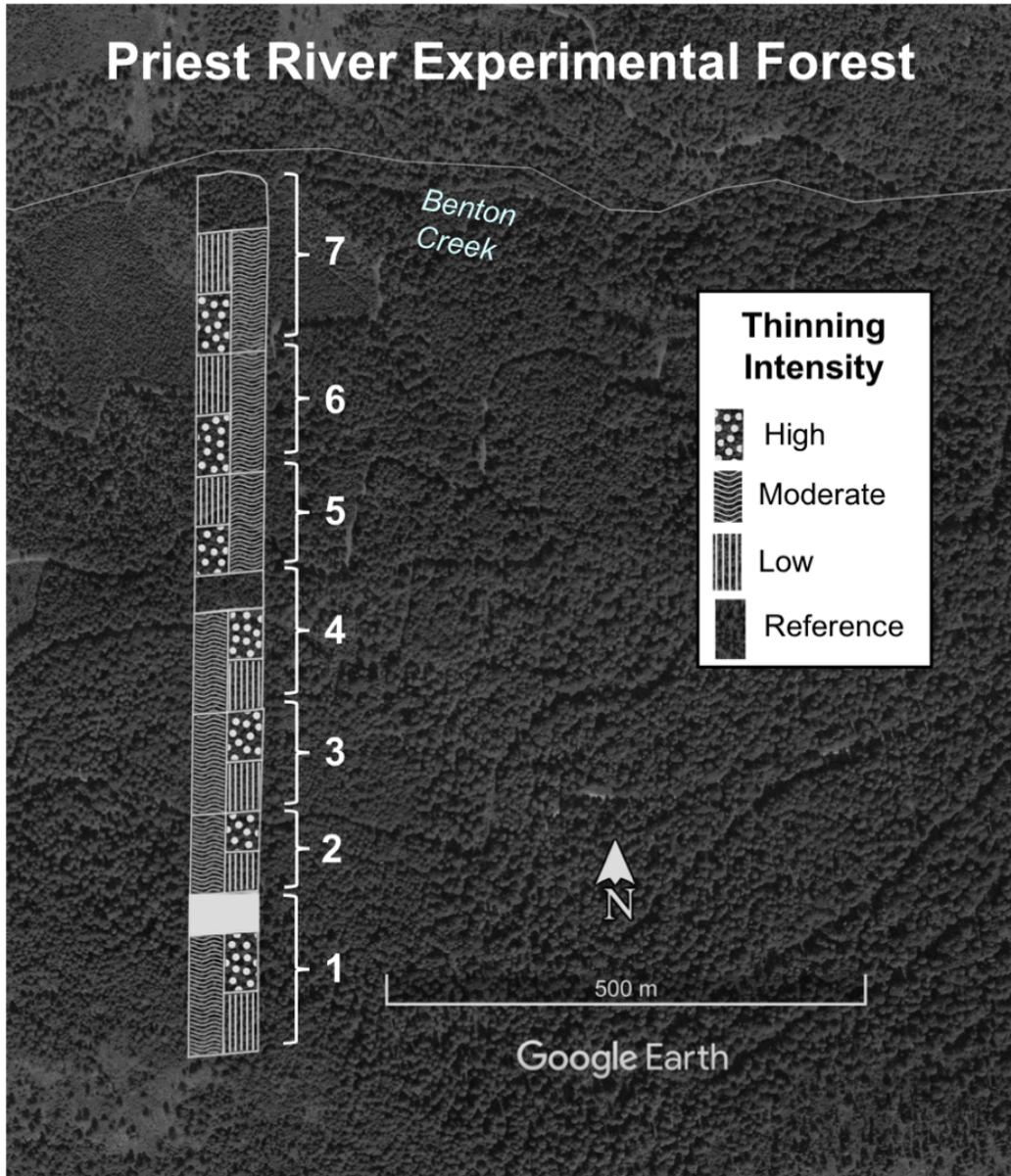


Figure 1. 1. Map of thinning intensities and blocks along the transect of Priest River Experimental Forest. Block numbers are along the right axis of the transect. Thinning intensities are in the legend (Low = 1,976 trees ha⁻¹, Moderate = 988 trees ha⁻¹, and High = 494 trees ha⁻¹). Reference plots are locations with no thinning (note that in block 1 there is a solid white reference plot excluded from the analyses due to an additional fertilization treatment)

Tree Species Characteristics

I sampled the most abundant residual species in the study plots – western larch, grand fir western redcedar, and western hemlock. All of these species favor moist sites, though there are few other similarities. Western larch is the most shade-intolerant species in the region (Fiedler & Lloyd, 1995), grand fir exhibits moderate shade tolerance, while cedar and hemlock, are very shade tolerant (Burns & Honkala, 1990). Western larch, a deciduous conifer, is known for its role as a pioneer species due to its shade intolerance and rapid early growth ability to proliferate and survive in drought conditions (Minore, 1979). The most shade-tolerant species in my study is western hemlock, which thrives in humid climates. Roots of western hemlock are relatively shallow and are just beneath the organic horizon (Minore, 1979). Western hemlock is vulnerable to damage from thinning because of its thin bark, disease susceptibility, and high decomposition rates (Wallis & Morrison, 1975). Western hemlock and western redcedar are sensitive to frost and drought; however, western redcedar can endure more arid and nutrient-poor sites than western hemlock (Burns & Honkala, 1990). Grand fir is less sensitive to late spring frosts than western redcedar and hemlock. It is known for its high productivity and ability to store vast amounts of nutrients in its foliage, especially in moist and nutrient-rich sites (Parent & Coleman, 2016). Grand fir can also survive in climates with lower annual precipitation than western redcedar, though precipitation only becomes the most limiting factor in dry years (Joseph Avery Antos, 1977). The variable limiting factors of each species lends evidence that thinning responses in mixed forests will vary among species and may result in a trade-off of limiting factors of growth from one variable to another.

Field Sampling

Besides an 11-year post-thinning inventory (Chen et al. 2019), plots were not remeasured again until 2016/17. In the summers of 2016 and 2017, I located the original thinning treatment replicates then I sampled within 0.04-ha circular plots (11.28 m radius) in each plot center (Figure 1.1). Within each treatment–block combination, I collected increment core samples from trees within four diameter classes for each target species, if present. Four diameter classes were selected to get the best representation of thinning response for trees of all sizes (Class 1, 13–21 cm; Class 2, 21.1–34 cm; Class 3, 34.1–45 cm; and Class 4 > 45 cm.; Table 1.1). Many cores were ultimately deemed unusable for analysis

due to wood defects, heartwood rot, or short temporal coverage. Results from the complete plot inventory documenting short and long-term stand developmental responses to the thinning intensities were previously reported (Chen et al. 2019).

Table 1. 1. Number of sampled trees sorted by thinning intensities vs. blocks and diameter classes.

Note: Ref, reference site; Low, low thinning intensity; Mod, moderate thinning intensity; High, high thinning intensity.

Block	Western Larch				Grand Fir				Western Redcedar				Western Hemlock			
	Ref	Low	Mod	High	Ref	Low	Mod	High	Ref	Low	Mod	High	Ref	Low	Mod	High
1	3	-	-	-	6	-	7	6	9	-	4	2	6	1	-	3
2	-	1	-	-	-	1	2	3	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	3	1	-	-	1	1	-	2	5	1
4	2	2	1	5	4	1	-	-	3	2	1	4	2	-	-	2
5	-	1	1	-	-	1	-	3	-	1	1	3	-	1	1	2
6	-	3	1	4	-	1	1	-	-	5	3	2	-	6	6	4
7	5	-	2	-	1	-	2	1	4	1	4	2	3	-	2	1
DBH Class	Western Larch				Grand Fir				Western Redcedar				Western Hemlock			
	Ref	Low	Mod	High	Ref	Low	Mod	High	Ref	Low	Mod	High	Ref	Low	Mod	High
1	2	-	-	1	2	-	2	1	4	1	-	4	1	2	2	3
2	5	4	2	3	5	2	4	4	6	4	7	4	6	4	4	4
3	2	3	3	4	1	2	4	2	4	2	5	3	4	3	6	2
4	1	-	-	1	3	-	5	7	2	2	2	3	-	1	2	4
Total	10	7	5	9	11	4	15	14	16	9	14	14	11	10	14	13

Tree Ring Analysis

I visually cross-dated the core samples using the list method (James Hardy Speer, 2010). Cores were scanned on an Epson Expression XL 12,000 scanner at 1200 dpi. Then annual tree ring widths were measured to an accuracy of 0.01 mm using Coo Recorder (Larson, 2013). The measurements were checked for quality in the computer program COFECHA, which outputs important mean sensitivity and series intercorrelation values (Holmes, 1983). Preferred mean sensitivity values are around 0.2 for a chronology, and intercorrelation values must be greater than 0.4 to be used for data analysis (James Hardy Speer, 2010). Results show that all species were within acceptable ranges (Table 1.2). Because I wanted to examine the intrinsic response of trees to thinning, I analyzed raw radial ring width rather than detrended growth because detrending removes low-frequency variability that would be observed in growth releases (Edward R. Cook & Kairiukstis, 1990).

Table 1. 2. Relevant output from quality control software, COFECHA, for each species.

	Number Dated	Mean age	Mean Sensitivity	Inter-series correlation
Western Larch	31	62	0.286	0.510
Grand Fir	42	54	0.206	0.487
Western Redcedar	51	52	0.177	0.507
Western Hemlock	48	55	0.223	0.503

Statistical Models

I used two different statistical methods to accomplish my objectives. (1) Radial growth averaging (RGA) criteria were used to calculate immediate growth releases for each series so I could quantify growth releases (immediate responses) from thinning for each series and species/treatment combination. (2) Annual radial growth, corrected for diameter and autocorrelation, was investigated using a before-after/control-impact (BACI) model for each species at various short- and long-term time intervals (E. P. Smith, El-shaarawi, & Piegorsch, 2002). The BACI models were used to (i) determine if there was a significant thinning effect, and (ii) identify post-thinning radial growth responses between treatment plots versus the reference plots in the short- and long-terms. All statistics were conducted in R 3.4.3 unless otherwise stated (R Core Team 2017). BACI models were calculated using the “lme” function in the nlme package (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2007), and

Tukey's HSD pairwise comparisons were calculated using the emmeans package in R (Lenth, 2019).

Radial Growth Averaging

To identify immediate releases following thinning, and to inform time intervals for the BACI models, I investigated the growth release signals of each series using radial growth averaging (RGA) criteria (Nowacki & Abrams, 1997). This method calculates releases at various thresholds by applying a percent change to the current year's growth for each series based on growth in surrounding years.

The formula used to calculate growth releases follows:

$$\Delta G_t = \frac{\mu G_a - \mu G_b}{\mu G_b}$$

where ΔG_t = fractional change in growth rate at time = t, μG_a = mean radial growth for the selected two-year window after time = t, μG_b = mean radial growth in a five-year window before time = t. Percent change in growth is then calculated by multiplying ΔG_t by 100. All series that did not have a temporal coverage of at least five years before thinning (1967) were removed from this analysis. Annual mean percent growth increases (releases) and decreases (suppressions) were calculated for all years and species/thinning combinations to determine the strength of yearly release and intervals of sustained releases/suppressions for all years within ten years prior- or post- thinning. Release years (and suppression years) were defined as years with a mean annual release or suppression rate of at least 30% for each species/thinning-treatment combination (Table 1.3). For each series, years with a percent increase in growth greater than 40% were displayed using Fire History Analysis and Exploration Systems (FHAES) software in Figure 1.2 (Brewer et al. 2016). The results from the RGA can be thought of as initial thinning responses – i.e., the short-term or immediate response to thinning.

Table 1. 3. Shows release and suppression years for all species within ten years before to ten years after thinning (1957–1976). Note: Release (Relc.) and suppression (Supr.) years are years with a mean annual suppression or release of at-least 30%

	Western Larch				Grand Fir				Western Redcedar				Western Hemlock			
	<i>Supr.</i> <i>Years</i>	<i>Supr.</i> <i>%</i>	<i>Relc.</i> <i>Years</i>	<i>Relc.</i> <i>%</i>												
Reference	'66-'68	55%	'71-'74	57%	'59-'60	35%	-	-	'59-'60	34%	-	-	-	-	-	-
Low	'65-'67	56%	'70-'74	82%	'62-'63	34%	'67-'70	49%	-	-	'67-'71	94%	'66	32%	'69-'73	53%
Moderate	'66-'67	60%	'69-'74	79%	-	-	'67-'69	41%	-	-	'67-'69	96%	-	-	-	-
High	'65-'67	58%	'69-'72	91%	-	-	'68-'70	49%	'59-'60	33%	'67-'70	113%	-	-	-	-

BACI analysis

The BACI model is a mixed-effects analysis of covariance (ANCOVA) with random effects to control for tree size and autocorrelation. The response variable was radial growth (mm), the fixed independent variables were before/after thinning and thinning intensity (Ref, Low, Moderate, High), the random independent variable was block. The final diameter at breast height (DBH; 1.37 m from the ground) was a covariate to control for tree size. The year was included as a continuous random variable to account for autocorrelation in the dependent variable. The BACI model design is an appropriate tool to infer causation in this study because the “control” (reference) and impacted (thinned) plots were selected for treatment prior to experimental thinning (E. P. Smith et al., 2002). The output from the interaction term between before/after and thinning treatments reveals whether there is a significant BACI effect – if the interaction term is significant then there was a significant impact as a result of thinning (E. P. Smith et al., 2002). The interaction term will be referred to as the “BACI effect” henceforth. In a full BACI analysis of all data, with species as a fixed independent variable, the interaction among species, thinning intensity, and before/after thinning was significant for all post-thinning time intervals ($p < 0.001$), indicating that the thinning response by species was significantly different. All possible combinations of species were re-analyzed in the BACI model for each time-interval, and species was a significant predictor of growth in each model. Moreover, species significantly interacted with before/after, and thinning intensity ($p < 0.05$), therefore BACI models were analyzed for each species separately. Not all populations met the assumptions for parametric testing; however, ANCOVA is robust to violations of the assumption, and non-parametric testing prevents analysis into interaction terms (Tomarken & Serlin, 1986).

The ten year period before thinning (1957–1966) was compared to five, ten, 15, 20, 30, and 40-year intervals after thinning in the species-specific BACI models. I compared ten years before thinning to ensure a sampling depth of at least ten series per species. I referred to the results from the RGA to determine post-thinning intervals for each species based on years of overlap for growth releases in each thinning intensity. For example, western redcedar and grand fir had an overlap of growth releases for each thinning intensity from 1967–1970 (Table 1.3); thus, the post-thinning intervals began in 1967 for those species. Western hemlock and western larch showed the majority of series with growth releases

starting in the year 1969. Thus, intervals post-thinning began in 1969 for western larch and hemlock. Intervals of five, ten, 15, 20, 30, and 40-years were analyzed for all species post-thinning.

Results

Immediate Growth Release Signal Response from RGA

Western larch, grand fir, and western redcedar all show years with significant growth release signals for all thinning intensities. However, western hemlock had significant releases in Low only (Figure 1.2; Table 1.3). Western redcedar shows the strongest releases from thinning followed by western larch, then grand fir, and finally, western hemlock shows the weakest thinning release. For western hemlock, the average growth release increases for all thinning treatments was 35.8% compared to western redcedar with an average of 95.0%, over a five-year period from 1969 to 1972. Western redcedar and grand fir trees showed releases beginning the year of thinning in 1967. Western larch and western hemlock had the strongest releases beginning two years post-thinning.

Western larch showed the second strongest sustained release of 72.7% over a six-year period beginning two years post-thinning. Western larch also showed releases in the reference plot, with smaller magnitudes and amplitudes than treatment plots. The mean release of 72.0% in the reference plot started four-years post-thinning and lasted only two years, from 1971–1972. Growth suppressions in western larch, measured by at least 30% reductions in growth, occurred the year of thinning (1967) and two consecutive years before thinning (1965–1966) in reference plots by an average of 47.6%. The difference in RGA releases in treatment plots compared to Reference was 25%, 22%, and 34% higher in Low, Moderate, and High treatments, respectively. The release was most substantial in High and was an average of 91% over four years, beginning one year after thinning. Low showed the second-highest percent release of 82%. Moderate showed the longest sustained release at 74%, which sustained over a six-year period beginning two years after thinning. Trees in all treatments, including the reference, also displayed suppressions in the years before thinning. The pre-thinning suppressions range from 55% in reference plots to 60% in Moderate. Durations of sustained suppression before thinning ranged from two years (Moderate) to three years (Reference, Low, High).

Contrary to western larch, grand fir showed a relatively weak thinning response, with an average growth increase of 38.3% over a four-year period. The greatest release for grand fir averaged 49% in Low and High and was sustained over four- and three-year periods, respectively. Moderate thinning treatments had a release of 41% sustained over three years, beginning the year of thinning. High, which was thinned twice to two different densities, did not show a release until the year after the second thinning. There were no releases in reference plots within a ten-year interval pre- and post-thinning. Western redcedar showed the greatest overall RGA release percentages, which decreased with increased stand density. The greatest release, of 113%, occurred in High and was sustained over four years. Moderate had a release of 96% sustained over a three-year period. Low showed the longest sustained release of five-years at a lower percentage of 94%. There were no releases in reference plots within a ten-year interval pre- and post-thinning. Hemlock trees only showed significant growth releases in Low. The release was most substantial in Low and was an average of 53% over five years after thinning. Individual series in Moderate and High did show years with releases post thinning; however, they were quite variable in the timing of their releases (Figure 1.2). Different series from each thinning treatment showed releases beginning in 1967 and ending in 1975, although no years fit the criteria of a release year (from methods) for Moderate and High. There were no releases in reference plots, nor did any treatments show suppressions, within a ten-year interval pre- and post-thinning.

Short- and long-term BACI effects

Although pairwise comparisons between species are not meaningful due to interactions, there are still many inferences that can be made since the same BACI models were applied uniformly across species. First, all BACI models showed a significant BACI effect ($p < 0.05$), confirming that reductions in stand density caused significant changes in growth for all species. Western larch and western redcedar showed significant increases in growth compared to reference sites after thinning (Table 1.5). Western hemlock showed no significant differences between growth in reference plots vs. thinning treatments at any post-thinning time intervals. Grand fir also showed no increases in post-thinning growth compared to the reference. In fact, grand fir actually showed a significant reduction in growth in Low by an average of 0.86 and 0.70 mm at 20- and 30-years post thinning, respectively.

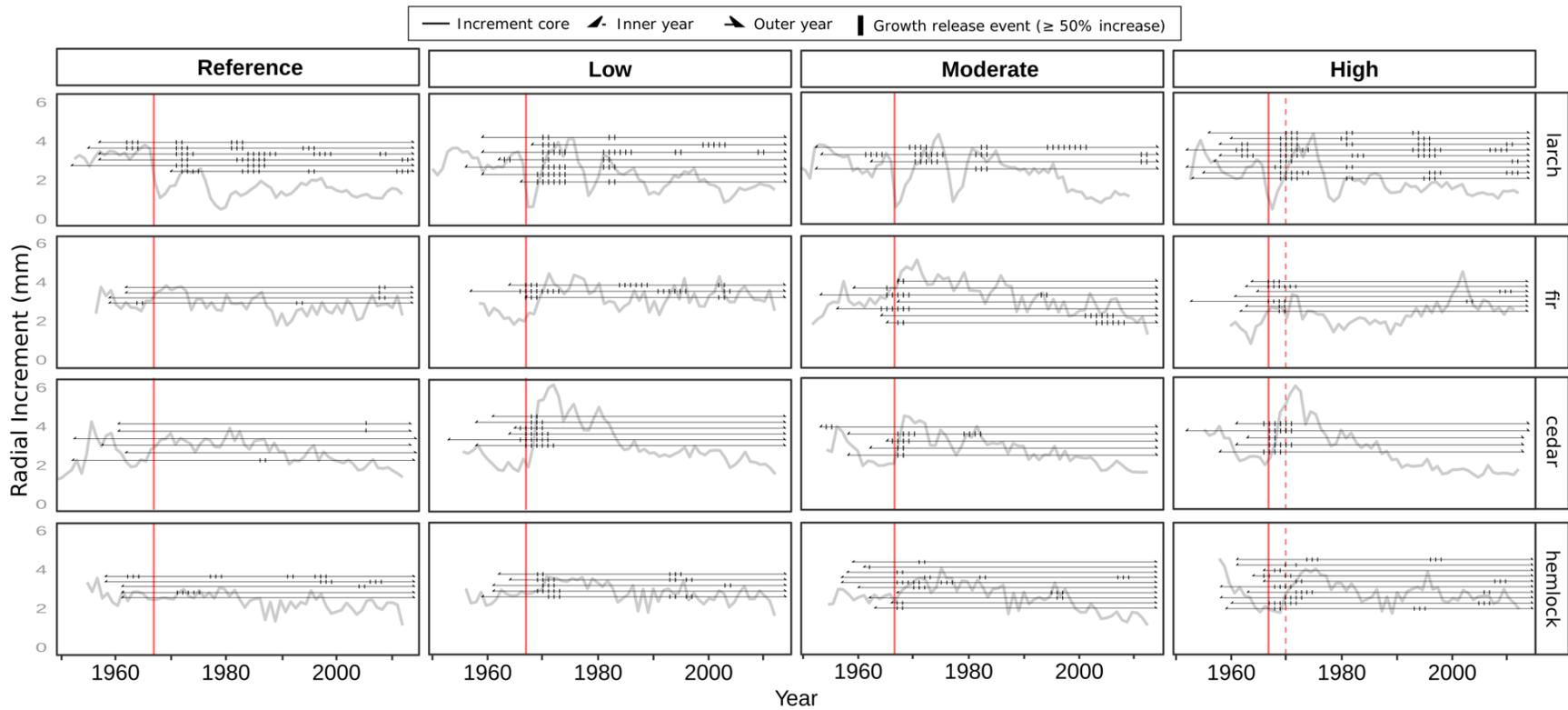


Figure 1. 2. Visual of release years where there was at least 40% increase in growth sustained over at least a two year period. Data are displayed using Fire History Analysis and Exploration Systems (FHAES) software. The red solid vertical line shows the year of initial thinning (1967), while the dotted red vertical line in High shows the year of secondary thinning (1970). The grey time-series shows the master chronology of the series in each cell.

Table 1. 4. Mean growth and confidence interval estimates from the BACI model for each thinning intensity before and after thinning (columns) by time interval after thinning (rows). Note: Shaded cells represent significant difference ($p < 0.05$) between growth in the thinning treatment and reference after thinning. Bolded numbers represent a significant change ($p < 0.05$) in growth after thinning compared to before within thinning treatments. Asterisks next to bold or highlighted numbers represent significant reductions in growth, while those without asterisks are significant increases. A single quotation next to highlighted or bold numbers represent increases in growth compared to reference and decreases in growth compared to before thinning. Common abbreviated names used in place of full species common names

Interval	Reference		Low		Moderate		High	
	<i>Before</i>	<i>After</i>	<i>Before</i>	<i>After</i>	<i>Before</i>	<i>After</i>	<i>Before</i>	<i>After</i>
Western larch								
5	2.84 ± 0.90	1.17 ± 0.98*	2.66 ± 0.84	2.58 ± 0.90	1.80 ± 0.85	2.05 ± 0.93	2.44 ± 0.87	2.66 ± 0.94
10	2.93 ± 0.78	1.52 ± 0.77*	2.67 ± 0.70	2.92 ± 0.70	1.82 ± 0.73	2.40 ± 0.72	2.50 ± 0.74	2.94 ± 0.73
15	2.95 ± 0.75	1.23 ± 0.68*	2.69 ± 0.67	2.46 ± 0.62	1.83 ± 0.69	2.10 ± 0.64	2.50 ± 0.71	2.59 ± 0.65
20	3.01 ± 0.64	1.29 ± 0.53*	2.68 ± 0.55	2.34 ± 0.47	1.84 ± 0.58	2.11 ± 0.49	2.53 ± 0.59	2.54 ± 0.50
30	3.17 ± 0.52	1.57 ± 0.31*	2.67 ± 0.42	2.02 ± 0.26"	1.89 ± 0.46	2.10 ± 0.28	2.60 ± 0.45	2.32 ± 0.28
40	3.17 ± 0.51	1.59 ± 0.26*	2.69 ± 0.41	1.87 ± 0.22*	1.90 ± 0.45	1.94 ± 0.24	2.62 ± 0.44	2.16 ± 0.24
Grand fir								
5	2.68 ± 1.47	3.22 ± 0.86	2.53 ± 1.51	3.41 ± 1.68	2.79 ± 0.45	3.98 ± 0.46	2.35 ± 0.44	3.32 ± 0.45
10	2.97 ± 1.38	3.29 ± 0.68	2.73 ± 1.42	3.51 ± 0.87	2.77 ± 0.44	3.97 ± 0.38	2.37 ± 0.44	3.61 ± 0.37
15	3.37 ± 1.32	3.49 ± 0.63	3.00 ± 1.31	3.10 ± 0.70	2.71 ± 0.46	3.84 ± 0.38	2.34 ± 0.46	3.68 ± 0.38
20	3.62 ± 1.30	3.66 ± 0.60	3.16 ± 1.27	2.80 ± 0.64*	2.67 ± 0.49	3.62 ± 0.40	2.30 ± 0.49	3.45 ± 0.40
30	3.32 ± 1.27	3.19 ± 0.49	2.83 ± 1.22	2.49 ± 0.52*	2.79 ± 0.47	3.51 ± 0.34	2.35 ± 0.46	3.42 ± 0.34
40	3.77 ± 1.41	3.44 ± 0.53	3.05 ± 1.34	2.92 ± 0.55	2.81 ± 0.54	3.24 ± 0.39	2.31 ± 0.53	3.32 ± 0.39
Western redcedar								
5	1.84 ± 1.11	1.78 ± 1.05	1.91 ± 0.84	3.83 ± 0.89	1.91 ± 0.85	3.29 ± 0.90	2.38 ± 0.87	4.07 ± 0.92
10	2.32 ± 0.95	2.35 ± 0.68	2.00 ± 0.59	4.31 ± 0.54	2.00 ± 0.61	3.47 ± 0.50	2.16 ± 0.63	4.16 ± 0.54
15	2.43 ± 0.89	2.48 ± 0.55	2.00 ± 0.56	3.95 ± 0.44	1.97 ± 0.58	3.24 ± 0.42	2.15 ± 0.59	4.10 ± 0.42
20	2.50 ± 0.86	2.52 ± 0.48	2.00 ± 0.54	3.74 ± 0.38	1.94 ± 0.56	3.20 ± 0.36	2.11 ± 0.57	3.87 ± 0.36
30	2.53 ± 0.86	2.37 ± 0.38	1.96 ± 0.53	3.18 ± 0.29	1.99 ± 0.55	2.98 ± 0.27	2.16 ± 0.56	3.44 ± 0.26
40	2.60 ± 0.88	2.31 ± 0.36	1.96 ± 0.54	2.79 ± 0.29	1.99 ± 0.57	2.75 ± 0.27	2.18 ± 0.58	3.26 ± 0.27
Western hemlock								
5	2.91 ± 1.23	3.20 ± 1.63	3.02 ± 0.57	3.12 ± 0.58	2.82 ± 0.49	3.36 ± 0.5	2.72 ± 0.43	3.29 ± 0.47
10	2.91 ± 1.21	3.31 ± 1.21	2.91 ± 0.53	3.41 ± 0.44	2.77 ± 0.43	3.43 ± 0.39	2.67 ± 0.39	3.30 ± 0.37
15	2.85 ± 1.21	3.71 ± 1.03	2.91 ± 0.56	3.39 ± 0.44	2.79 ± 0.47	3.43 ± 0.41	2.64 ± 0.44	3.25 ± 0.40
20	2.88 ± 1.16	3.45 ± 0.89	2.87 ± 0.54	3.21 ± 0.40	2.75 ± 0.46	3.33 ± 0.38	2.63 ± 0.42	3.09 ± 0.37
30	2.99 ± 1.19	3.08 ± 0.75	2.73 ± 0.52	2.96 ± 0.30	2.58 ± 0.41	2.99 ± 0.29	2.63 ± 0.37	2.90 ± 0.28
40	2.97 ± 1.19	2.87 ± 0.67	2.73 ± 0.54	2.85 ± 0.32	2.58 ± 0.44	2.76 ± 0.31	2.61 ± 0.40	2.75 ± 0.31

Western larch showed a significant BACI effect in response to thinning for all thinning intensities ($p < 0.001$; Table 1.5; Figure 1.3). The strongest BACI effect, measured by the lowest P -value, was 30 years after thinning ($F_{(3, 1068)} = 22.31, p < 0.001$). In High and Moderate, growth after thinning was significantly greater than reference plots for all time intervals ($p < 0.05$). Low showed significantly higher growth vs. reference in the five, ten, 15, and 20-year time intervals post-thinning ($p < 0.001$), by 1.40, 1.40, 1.23, 1.04 mm, respectively. The only time interval that did not show a significant increase in growth compared to the reference was Low at 40-years post thinning.

Grand fir showed a significant BACI effect in response to thinning for all post-thinning intervals ($p < 0.01$; Table 1.5; Figure 1.4). The most substantial BACI effect, measured by the lowest P -value, was 15 years after thinning ($F_{(3, 680)} = 14.61, p < 0.001$). Unlike western hemlock and western redcedar, Low grew significantly less after thinning than reference plots at 20- and 30-years post thinning by 0.86 and 0.71mm, respectively ($p < 0.001$). Thus, low-intensity thinning appears to have long term negative impacts on tree growth of grand fir in mixed forests.

Western redcedar showed a significant BACI effect in response to thinning for all post-thinning intervals ($p < 0.001$; Table 1.5; Figure 1.5). The strongest BACI effect was 15 years after thinning ($F_{(3, 684)} = 22.49, p < 0.001$). All thinning treatments showed significant increases in growth compared to reference plots at all time intervals after thinning ($p < 0.05$). The greatest mean difference in growth between reference plots and thinned plots occurred at the five-year interval after thinning, where there was a 129% increase in mean annual growth. At five years post-thinning, Low, Moderate, and High grew significantly more than reference plots by an average of 2.05, 1.52, and 2.29 mm, respectively. At 15-years post thinning, Low, Moderate, and High grew more than reference plots by an average of 1.47, 0.76, and 1.63 mm, respectively. By 30-years post-thinning, Low, Moderate, and High grew more than reference plots by an average of 0.81, 0.61, and 1.07mm, respectively.

Hemlock showed a significant BACI effect in response to thinning compared to the reference for the 5–30-year post-thinning intervals ($p < 0.05$; Table 1.5; Figure 1.6). The strongest BACI effect was ten years after thinning ($F_{(3, 646)} = 8.40, p < 0.001$). There was no significant effect 40 years after thinning ($F_{(3, 1901)} = 1.48, p = 0.22$). Although there was a

significant BACI effect, there were no significant differences between the reference plot and thinning plots at any time interval after thinning ($p > 0.99$).

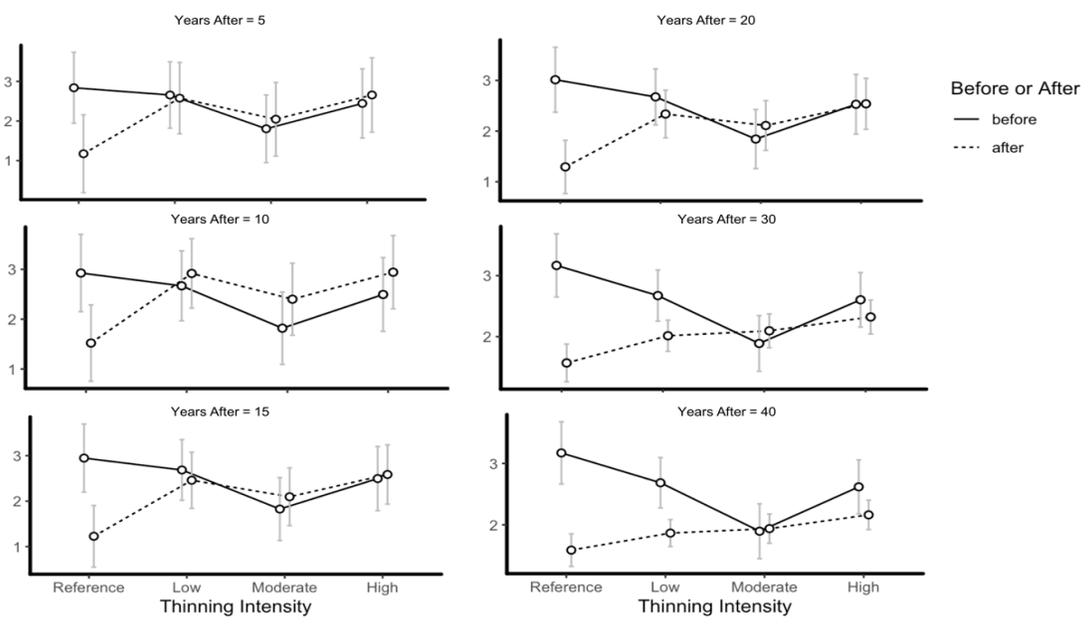


Figure 1. 3. Western larch interval plot with radial growth in mm (y-axis) and thinning intensity (x-axis). Note: The solid line shows growth ten years before thinning and the dotted line shows mean growth at five-year intervals after thinning. The error bars are 95% confidence intervals from the BACI models.

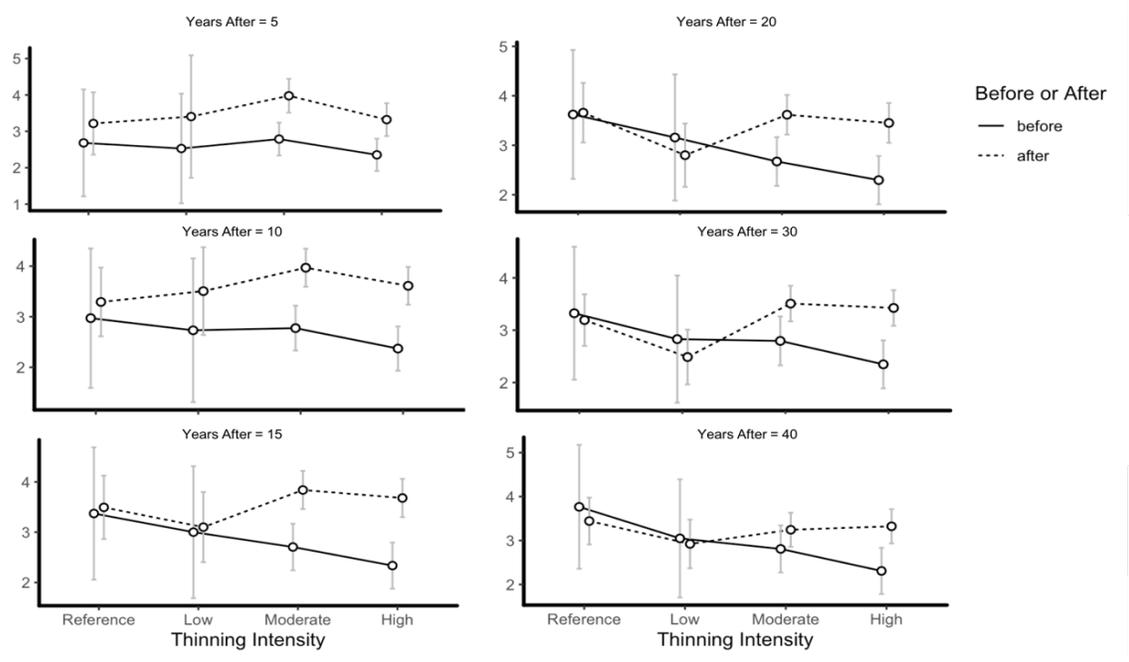


Figure 1. 4. Grand fir interval plot with radial growth in mm (y-axis) and thinning intensity (x-axis). Note: The solid line shows growth ten years before thinning and the dotted line shows mean growth at five-year intervals after thinning. The error bars are 95% confidence intervals from the BACI models.

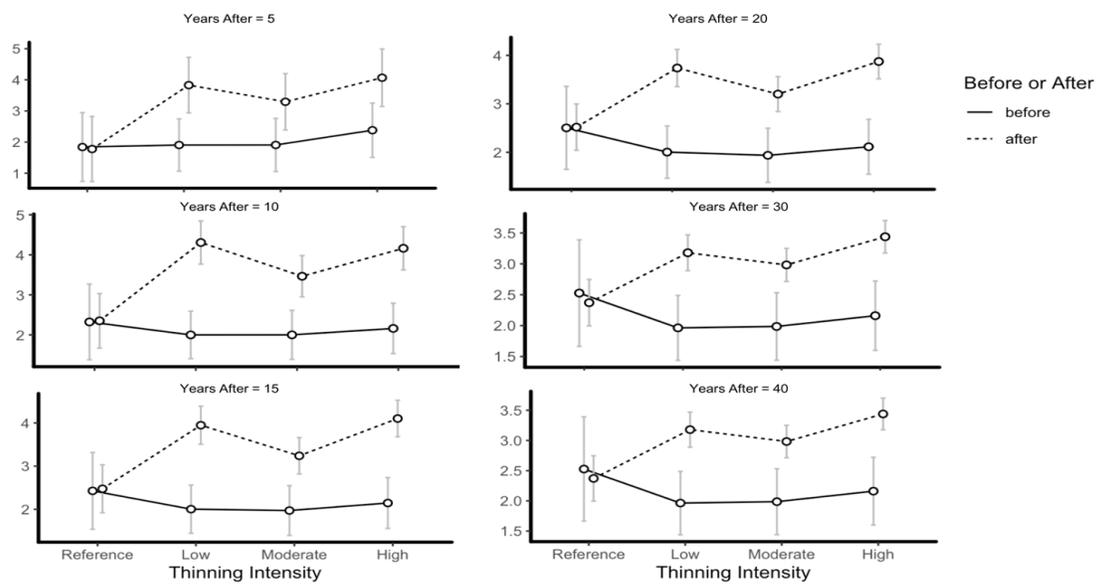


Figure 1. 5. Western redcedar interval plot with radial growth in mm (y-axis) and thinning intensity (x-axis). Note: The solid line shows growth ten years before thinning and the dotted line shows mean growth at five-year intervals after thinning. The error bars are 95% confidence intervals from the BACI models.

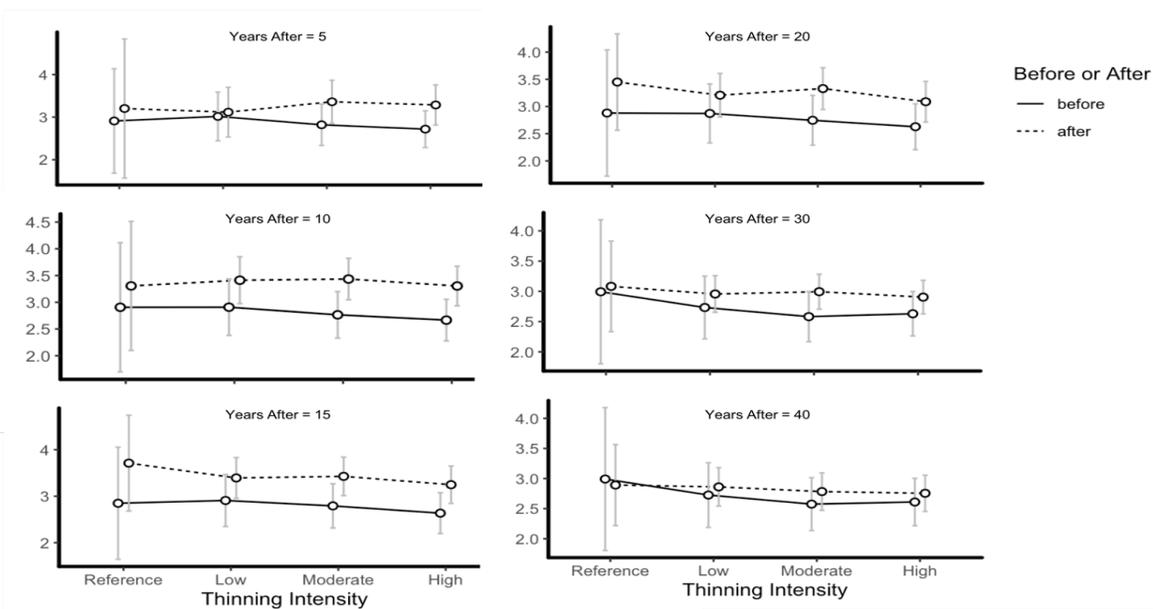


Figure 1. 6. Western hemlock interval plot with radial growth in mm (y-axis) and thinning intensity (x-axis). Note: The solid line shows growth ten years before thinning and the dotted line shows mean growth at five-year intervals after thinning. The error bars are 95% confidence intervals from the BACI models.

Discussion

Nearly all series of each species showed an immediate RGA release for all thinning treatments within six-years post thinning. However, these releases were different strengths, occurred at different years, and lasted different durations of time for each species and thinning intensity. Grand fir and western hemlock releases were weak and short-term in comparison to western redcedar and western larch, the two species with the strongest, and longest-lasting, responses. There appears to be a trade-off between western redcedar and western larch in the timing of release with western redcedar responding more rapidly. Western redcedar releases began the year of thinning and stopped approximately 2-4 years later – the approximate year western larch began showing significant releases (Table 1.3). Western redcedar is in the *Cupressaceae* family, a family known for rapid growth responses to changing site conditions (Harry, 1987). In addition to releases, western larch and western redcedar trees in the thinned plots showed significantly higher growth than Reference after thinning, which is likely due to increases in light availability. However, thinning does not increase the growth of grand fir and may even inhibit growth in hemlock.

Western larch

The longer response time for western larch may be due to high levels of interspecific competition during the stem exclusion stage of stand development (Oliver and Larson 1996). High competition at the time of thinning likely required western larch time to increase crown size before enough photosynthates could be produced to allocate toward cambial growth. At the time of thinning, the stand was quite dense, and crowns were overcrowded (Shen et al., 2019). Based on the results of the RGA suppressions, growth was significantly suppressed around two years before thinning (Table 1.3). The suppression may be because the shade-intolerant, deciduous, crowns were losing foliage in the lower canopy as other species grew tall and dense enough to compete for sunlight. Western larch is disadvantaged compared to evergreen species in lower canopy competition because it has to completely produce a new crown each year. Therefore, when evergreen species like western redcedar surpass the height of the lower crown, little to no sunlight reaches the lower canopy, and western larch is unable to regrow foliage in the lower limbs leading to reductions in photosynthesis (Fiedler & Lloyd, 1995). Schaedel et al. (2017) found that even-aged western larch trees growth decreases around 25–30 years post-regeneration; stands were 25-years old at the time of

thinning (Cochran, 1999; Seidel, 1982). When western larch did release 2–4- years after thinning, western redcedar lost its competitive advantage. This delayed thinning response is consistent among other thinning studies of western larch (Seidel, 1982). Interesting to note, however, is that the reference plots for western larch also showed a slight release five-years post thinning. This release may have occurred due to natural thinning, but clearly, reductions in stand density still resulted in greater releases. Growth increases following thinning were expected for western larch because it is the most shade-intolerant species (Minore, 1979), and thus likely most responsive to increases in light at the canopy level. Given the sensitivity of this species to light, increases in growth lasted longer in plots thinned to lower densities. Other studies confirm that higher intensity-thinning results in increased western larch growth (Cochran 1999) with maximum responses 10–15 years post-thinning (Seidel, 1987). Post-thinning western larch response to initial increases in light availability decreased over time, but by 30- and 40- years after thinning growth was similar to the Reference. In order to sustain higher growth, another thinning could have been applied near the time when tree growth subsided to maintain vigor and accelerate wood production and resilience to additional stress.

Grand fir

Grand fir showed a release in all thinning treatments vs. western hemlock, which only released in Low. However, grand fir releases only lasted 2–3years, and increases in growth were only around 40%, the same percentage observed by Seidel (1987). These releases, however, do not result in significantly greater growth compared to Reference, indicating that grand fir is not competitive in release situations in mixed-species forests with western redcedar and western larch.

Grand fir growth in thinning treatments was similar to the reference (Table 6). The lack of before/after response might be because grand fir was already growing faster than all the other species at the time of thinning; therefore, the growth rate difference compared to before thinning may not be as substantial (Parent & Coleman, 2016). Grand fir growth responses to thinning also may depend on tree vigor pre-thinning – where taller, dominant, trees do not respond as well as suppressed trees (Ferguson & Adams, 1980). Grand fir is among the most productive species, and it is more shade-intolerant than western redcedar and western hemlock; thus, it is likely that grand fir trees were taller and therefore less able to

release at the time of thinning. In comparison to western larch, the other early seral species in this mixed forest, grand fir has drastically different crown characteristics of multiple cohorts of foliage retention and deeper crowns due to an ability to withstand greater self-shading (Minore, 1979). Thinning would, therefore, have less of an effect on trees in this canopy position since they may already have been capturing the light needed to maintain productivity. Moreover, grand fir has higher foliar nutrient concentrations than other associated species; therefore, it is likely that grand fir also had enough nutrients before thinning to remain productive (Parent & Coleman, 2016). Another possible reason for lack of treatment response includes damage during thinning (Ferguson & Adams, 1980), though greater responses in the higher intensity sites may negate that hypothesis.

Western redcedar

Western redcedar showed a very strong and immediate release from thinning indicating that limiting factors became more available after thinning and western redcedar was able to take advantage of released nutrients. Other studies support the findings from this study, that western redcedar growth increases in response to thinning treatments and nutrient availability (Devine & Harrington, 2009; Negrave, Prescott, & Barker, 2007). Western redcedar had the greatest response to thinning in the short-term, and the responses were sustained up to 40 years after thinning. This suggests western redcedar was able to take advantage of previously limiting factors made available by thinning. Although western redcedar can tolerate low nutrients it also has been shown to increase significantly in growth when nutrients are freed up, plus it is able to store nutrients in its foliage (Minore, 1983). Therefore, it is likely that nutrients were limiting growth of western redcedar on this site and that stand density reductions increased nutrient availability and allowed western redcedar to increase growth (Korol, 2001), which may also lead to greater nutrient-use-efficiency (Binkley, Luiz, & Ryan, 2004).

Western hemlock

Western hemlock showed the weakest immediate response to thinning with a mild release in Low and no significant release years in Mid or High, indicating it was unable to take advantage of newly available resources in thinned sites, or that thinning was, in fact, harmful. Western hemlock showed a similar lack of response to thinning as grand fir, but is more shade tolerant and likely occupied a lower canopy class similar to western redcedar at

the time of thinning. This suggests an intermediate response among the four species investigated based on likely canopy position and inherent inability to respond to new resource availability. The lack of Moderate and High thinning growth increases in western hemlock may be attributed to intraspecific competition, decay wounds, windthrow, and/or shade-tolerance. In a study investigating growth responses of mixed western redcedar-western hemlock forests to fertilizer, western hemlock was more responsive to fertilization than western redcedar (Blevins, Prescott, & Niejenhuis, 2006). They concluded that western redcedar outcompeted western hemlock for nutrients because western redcedar has deeper roots and can alter pH to improve nutrient uptake. Other studies also confirm that western redcedar has deeper roots than western hemlock. Thus, western hemlock may be non-competitive in mixed-stands with western redcedar (Blevins et al., 2006). However, other studies have shown that western hemlock outcompetes western redcedar, especially on rich sites like PREF (Canham, LePage, & Coates, 2004), thus thinning may have impacted this competition and resulted in a competitive advantage for western redcedar. Thinning may have created decay wounds on residual trees (i.e., scars that become diseased), leading to rapid decomposition at the site of damage and overall tree stress. Western hemlock is vulnerable to thinning because of its thin bark, disease susceptibility, and high decomposition rates (Wallis & Morrison, 1975). Field studies confirm that western hemlock shows 53–90% decay in wounds resulting from falling (Chavez Jr, Edmonds, & Driver, 1980; Englerth, 1942; Hunt & Krueger, 1962; Wright & Isaac, 1956), and similar damage to residual trees can occur from post-thinning windthrow. Western hemlock is the most shade-tolerant species in this region (Minore, 1979). Therefore, it is possible that the increased exposure to sun and frost in treatments led to thinning shock, which countered any possible releases. Indeed, slower growth in western hemlock immediately following thinning is proportional to the intensity of thinning (Ruth & Harris, 1979). Despite my findings, increased growth due to thinning is still possible for western hemlock if extra precautions are taken during felling (Wallis & Morrison, 1975), or fertilization is accompanied (Blevins et al., 2006).

Management Implications

Thinning is an effective tool for increasing growth in moist mixed-species forests of the northern Rocky Mountains for some species. My results show drastically different species responses to treatment that provide guidance for thinning to achieve a diversity of

management objectives depending on the species favored. Species that can rapidly respond to available sunlight and/or nutrients, like western larch and western redcedar, show the greatest growth increases. Grand fir showed intermediate responses likely because trees were vigorous in the upper canopy at the time of thinning and therefore showed minimal responses to increased growing space. This may be a situation unique to this study, especially as the site was strip clearcut providing some shade from the sides of the clearcut that allowed for initial regeneration of moderately tolerant species such as grand fir. Western redcedar and western hemlock also regenerated well within the clearcut and were favored in the thinning treatments. The immediate and sustained growth responses of western redcedar are promising, suggesting early intervention can maintain productivity of western redcedar, one of the most economically important species in the region that also provides important wildlife habitat and browse (Meiselman & Doyle, 1996; N. J. Smith & McLeod, 1992). Hemlock, in comparison with all other species likely occurred as mid- to lower strata trees at the time of thinning and exhibited no growth response to increased resource availability. The lower wood value and prolific post-disturbance regeneration suggest managing for this species in this region with thinning provides minimal long-term value, with the possible exception of wintering areas for ungulates due to lower below-canopy snow retention.

Conclusion

My results agree with general findings in the literature – that density reductions increase individual-tree wood production post-thinning with greater increases associated with higher removal intensities (Figure 1.2 and 1.3 and 3; Oliver et al. 1996). However, this did not hold for all species – specifically western hemlock – the most shade-tolerant species, and grand fir – a species with shallow roots and low competitiveness. Shade tolerance appears to drive growth responses to density reductions for this mixed stand; however, pre-thinning tree height, crown size and structure, interspecific competition, and root depth may all impact treatment responses (Blevins et al., 2006; Fiedler & Lloyd, 1995; Seidel, 1987; Wallis & Morrison, 1975). Moreover, thinning damage may lead to unpredictable intensities and durations of growth responses, especially in thin-barked species like western hemlock and grand fir (Chavez Jr et al., 1980; Englerth, 1942; Ferguson & Adams, 1980; Hunt & Krueger, 1962; Wright & Isaac, 1956). For shade-intolerant species such as western larch, sunlight can be a limiting factor in dense stands, so it is not surprising to observe short- and long-term

growth increases in Moderate and High thinning treatments. Western redcedar exhibited a similar response even though the species is classified as shade tolerant, which may be because western redcedar is responding to nutrient releases.

Chapter 2: Growth-drought sensitivity in mixed conifer forests in Northern Idaho: Influences of seasonality, drought, and density

Abstract

Increased drought occurrences and durations may have adverse consequences in the mixed coniferous forests of the Pacific Northwest. Growth-drought responses in these forests vary and depend on numerous interacting factors, such as species specific factors, species competition and thinning intensity. Therefore, forest management objectives should consider how these variables impact growth when suggesting or implementing silvicultural treatments. This study utilizes dendrochronology to investigate species-specific growth-drought relationships and the role thinning has on changing drought sensitivity of moist mixed-conifer forests. Specifically, I identify seasonality, strengths, and directions of growth-drought responses. Next, I compare growth-drought responses among thinning treatments to identify potential impacts of thinning on growth-drought sensitivity. Finally, I investigate changes in growth-drought relationships over time to determine whether relationships are stationary or dynamic. Particularly, I focus on the growth-drought sensitivity during a ten year drought from 1986–1995 – a drought I termed the Millennial Drought. The four species in this study show a wide range of responses to drought depending on forest stand density plus seasonality, length, and intensity of droughts. Moreover, drought sensitivity often involves trade-offs among other limiting factors like direct competition or nutrients. Western larch, the most drought-tolerant deciduous species in this study, was the most sensitive to drought, followed by western hemlock, western redcedar, and finally grand fir – which shows weak correlations overall and significant negative relationships at times. Western larch was most sensitive to long-term winter drought, while western redcedar responded most to short-term growing-season drought. Grand fir and western hemlock react equally to short- and long- term drought, though seasonality differs from winter to summer, respectively. The high thinning intensity treatment showed greater positive drought relationships compared to low and reference for western larch and grand fir, the drought avoiders, at the long- and short-timescales, respectively; this suggests that these species demonstrate trade-offs between neighborhood competition and moisture-limitations – avoiding drought in times of

competition and responding to it when there are fewer neighbors. Western redcedar did not show any notable changes in drought-sensitivity based on thinning intensity, indicating that variables other than drought are more strongly affecting the radial growth of western redcedar. Western hemlock is more sensitive to short-term drought stress where there are fewer neighbors, but limited resources in high-density plots cause greater sensitivity to long-term drought. Western larch and grand fir show significant inverse relationships with drought during the Millennial Drought. Contrary to western larch and grand fir, western redcedar and western hemlock both showed mostly positive growth-drought relationships during the Millennial Drought. Western redcedar also had greater sensitivity and slower growth in high-density sites during the Millennial Drought, indicating that low moisture and high competition results in more sensitivity to drought. Findings indicate that length and season of drought, species-specific drought tolerance, and stand density, influence growth-drought responses. Drought sensitivity often involves trade-offs among other limiting factors like direct competition. Therefore, conclusions suggest that future management goals should encourage complex adaptive systems by prioritizing site diversity (species, age, density) Moreover, results from this chapter (and Chapter 1) demonstrate thinning at various densities to favor shade-tolerant species is sustainable in future climate change scenarios.

Introduction

Climate change projections suggest increasing temperatures in the Northern Rocky Mountains with many consequences, including increased drought frequency, duration, and intensity (Dai, Zhao, & Chen, 2018; Halofsky et al., 2018). Predictions of increased drought occurrences and durations may have adverse consequences in the forests of the Pacific Northwest (PNW) such as greater risk for wildfire (Williams et al., 2019) increased insect outbreaks (Mattson & Haack, 1987), and increased tree mortality (C. D. Allen et al., 2010). Diverse mountain systems, like those found at the Priest River Experimental Forest (PREF), are among the many ecosystems vulnerable to climate change (Muccione, Salzman, & Huggel, 2016; Tinkham et al., 2015). Much of the vulnerability in the region results from the dependency on snowpack to supply water to forests and streams, with 40-70% of total annual precipitation in the region falling in the form of snow (Serreze, Clark, Armstrong, McGinnis, & Pulwarty, 1999). Many trees in this region depend on snowpack to insulate roots from freezing winter temperatures and to recharge soil moisture for the growing season (Maurer &

Rowling, 2014). Early snowmelt, reduced snowpack, and increased years of consecutive snow droughts are already happening in the region and are projected to intensify (Bates, Kundzewicz, Wu, & Palutikof, 2008; Marshall, Abatzoglou, Link, & Tennant, 2019). Despite that some studies expect impacts from climate change to increase forest productivity (Sohngen & Sedjo, 2005), many other studies confirm that higher temperatures associated with climate change will increase drought stress and tree mortality (C. D. Allen et al., 2010). These increases in drought frequencies lead to soil water deficits that cause trees to close stomata, reduce photosynthesis, and assimilate less carbon – possibly leading to mortality.

Potential effects of climate change and drought should be incorporated into management actions, however, studies that incorporate climate change and forest management in the region are limited (Dalton, Snover, & Mote, 2013; Kemp et al., 2015). The demand of forest managers to adapt their silvicultural treatments to climate change is increasing (Nagel et al., 2017), and thinning has been proposed to enhance adaptive capacity and drought resistance (D'Amato, Bradford, Fraver, & Palik, 2013; Sohn, Saha, & Bauhus, 2016). Reductions in stand density may lead to reduced stand competition for limiting factors and increased growing space and resource availability for individual trees (Ashton & Kelty, 2018). Specifically, thinning may reduce drought-induced tree stress and increase growth because of reduced competition for available water (Martin-Benito, Del Rio, Heinrich, Helle, & Canellas, 2010; Pérez-de-lis et al., 2011). Mechanistically, individual tree transpiration increases after thinning despite that overall stand transpiration decreases in response to reduced density (Bréda, Granier, & Aussenac, 1995). In other words, after thinning, stands utilize less water overall, leaving a net increase in plant accessible water and allowing residual trees to utilize more water (García, Fernandes, & Herrera, 2014). Therefore, management plans across the world are promoting thinning to reduce forest loss to drought now and into the future (Sohn et al., 2016). Reductions in stand density may not always lead to reduced drought stress of residual trees, however (Korol, 2001). Increased solar radiation and turbulence within thinned forests vs. unthinned forests can promote greater evapotranspirative water loss and, thus, more drought stress (Lagergren, Lankreijer, Lindroth, Cienciala, & Mo, 2008).

There are various strategies of drought tolerance utilized by conifers in response to drought, often driven by underlying physiological reactions based on species, life history,

and forest assemblage. Species with adaptations to extreme drought are considered *drought tolerant*. There are two basic physiological pathways of drought-tolerant adaptation – isohydry and anisohydry (Brodribb, Mcadam, Jordan, & Martins, 2014; McDowell et al., 2008). Species belonging to *Pinaceae* are more isohydric, a strategy that involves increasing hormone concentrations, usually abscisic acid, to reduce stomatal conductance (movement of CO₂ and water entering and exiting leaves) and eventually lead to stomatal closure in drought conditions (Brodribb et al., 2014). These species are considered to use the strategy of drought avoidance to tolerate droughts (Moran, Lauder, Musser, Stathos, & Shu, 2017). Drought avoidant species often have high phenotypic plasticity and react physiologically to drought leading to increases in abscisic acid and reductions in photosynthate production (McDowell et al., 2008; Moran et al., 2017). The pathway to mortality for drought avoiders (isohydric species) is often carbon starvation resulting from closed stomata.

The other strategy of drought tolerance is drought avoidance, anisohydry, and it is more common in the *Cupressaceae* family. These species have structural differences that resist drought; for example, their xylem is more resistant to drought-induced cavitation (desiccation of xylem), allowing transpiration without suffering fatalities from cavitation in drought conditions (Brodribb et al., 2014). Anisohydry encompasses the strategy of drought resistance, where trees continue assimilating CO₂ in drought conditions (Moran et al., 2017; Sade, Gebremedhin, & Moshelion, 2012). Like *Pinaceae*, *Cupressaceae* species also respond through changes in stomatal conductance, but these changes are short-lived for *Cupressaceae* and often are followed up with normal levels of transpiration (Brodribb et al., 2014). Species that are anisohydric (drought resisters) will eventually die from embolism-induced hydraulic failure in prolonged drought (McDowell et al., 2008; Sade et al., 2012; Sevanto, McDowell, Dickman, Pangle, & Pockman, 2014). Despite that these basic pathways are common to particular families, it is also possible for individuals of the same species to die from carbon starvation and hydraulic failure (Sevanto et al., 2014). Furthermore, tree mortality is almost always associated with hydraulic failure, while only about half the time it associates with carbon starvation in addition to hydraulic failure (Adams et al., 2017). Tree responses to drought may also increase with ontogeny (Niinemets, 2010), and potentially weaken in mixed forests (Forrester, 2014). Physiological drought responses also change based on stand dynamics, and sensitivity varies depending on shifting limiting factors.

Dendrochronology can be used to identify drought responses in conifers. The correlation between growth and drought (i.e., growth-drought relationships) indicates the level of *drought sensitivity* or *growth-drought sensitivity* (which is not necessarily *drought tolerance*, discussed above). In other words, species with strong drought sensitivity have strong growth-drought correlations between annual growth and drought indices. Growth-drought sensitivity shows to what extent trees are reacting to drought through changes in radial growth (i.e., growth drought sensitivity is the percent of the variability explained by drought). Growth-drought sensitivity is known to change in response to resource availability. (Bertness & Callaway, 1994; Grime, 2006). Reduced stand competition, resulting from thinning, has been shown to increase growth-drought sensitivity because sensitivity to competition is reduced (Niinemets, 2010; Pérez-de-lis et al., 2011). For example, trees in dense stands, like those growing at Priest River (PREF) at the time of thinning, experience high levels of competition for all resources, including nutrients and space, and therefore a smaller percentage of growth is limited by water availability. In other words, during times of high density, trees may be more *sensitive* to interactions in stand dynamics rather than drought, and drought sensitivity would decrease with greater density. Therefore, when trees show weak growth-drought correlations (i.e., weak growth-drought sensitivity), they are possibly experiencing intense inter-tree competition and therefore growth becomes more sensitive to competition in the stand rather than drought. Conversely, trees may become more sensitive to drought stress in high competition situations because trees may reduce competitive/interactive growth-responses in order to continue utilizing water (Callaway, 2007; Carnwath & Nelson, 2016). Other tree and plant species have shown greater competition with exceedingly limiting resources (Martin-Benito et al., 2010; Tielbörger & Kadmon, 2000), where competition for available water increases drought sensitivity. Other studies show that growth-drought sensitivity increases in arid sites (Hember, Kurz, & Coops, 2017), and during drought spells (Fang et al., 2010).

Growth-drought responses in these forests vary and depend on numerous interacting factors, such as species competition and thinning intensity (Sohn et al., 2016; Vernon, Sherri, Mantgem, & Kane, 2018). Therefore, forest management objectives should consider how these variables impact growth when suggesting or implementing silvicultural treatments (Ruzicka, Puettmann, & Brooks, 2017). This study utilizes dendrochronology to investigate

species-specific growth-drought relationships and the role thinning has on impacting drought sensitivity of moist mixed-conifer forests. Specifically, I identify seasonality, strengths, and directions of growth-drought responses. Next, I compare growth-drought responses among treatments to identify potential impacts of thinning on growth-drought sensitivity. Finally, I investigate changes in growth-drought relationships over time to determine whether relationships are stationary or dynamic. Particularly, I focus on the growth-drought sensitivity during a ten year drought from 1986–1995 – a drought I termed the Millennial Drought.

Methods

Sampling

Trees were sampled from the strip clearcut described in *Site Description* from Chapter 1 (Figure 1.1). The same samples described in Chapter 1 *Field Sampling* were used in this analysis. Cores were prepared, measured, and those measurements were checked to assure quality using the methods described in *Tree Ring Analysis* in Chapter 1 (see Table 1.1 for quality control results). A significance level of $P < 0.05$ was used for all analyses. All statistical analyses were conducted in R 3.4.3 unless otherwise stated (R Core Team 2017). The full methods are displayed in a workflow diagram in figure 2.1.

Data Acquisition and Preparation

Chronology Detrending

After assuring the quality of the samples using the methods described in the *Tree Ring Analysis* section in Chapter 1, series were separated into twelve species and treatment combinations based on results from Chapter 1, which show that trees in the sites thinned at Moderate and High intensity were not significantly different from each other in growth. Therefore, I combined the two treatments in the analyses, and refer to the combination of Moderate and High as “High” in this chapter. Trees in High were between 494-988 trees ha⁻¹ (3.0–4.6 m mean spacing). The reference and low-intensity treatments are unchanged from Chapter 1 (Ref = 10,022 ± 2,421 trees ha⁻¹ (1 m mean spacing); Low = 1,976 trees ha⁻¹ (2.1–2.4 m mean spacing)).

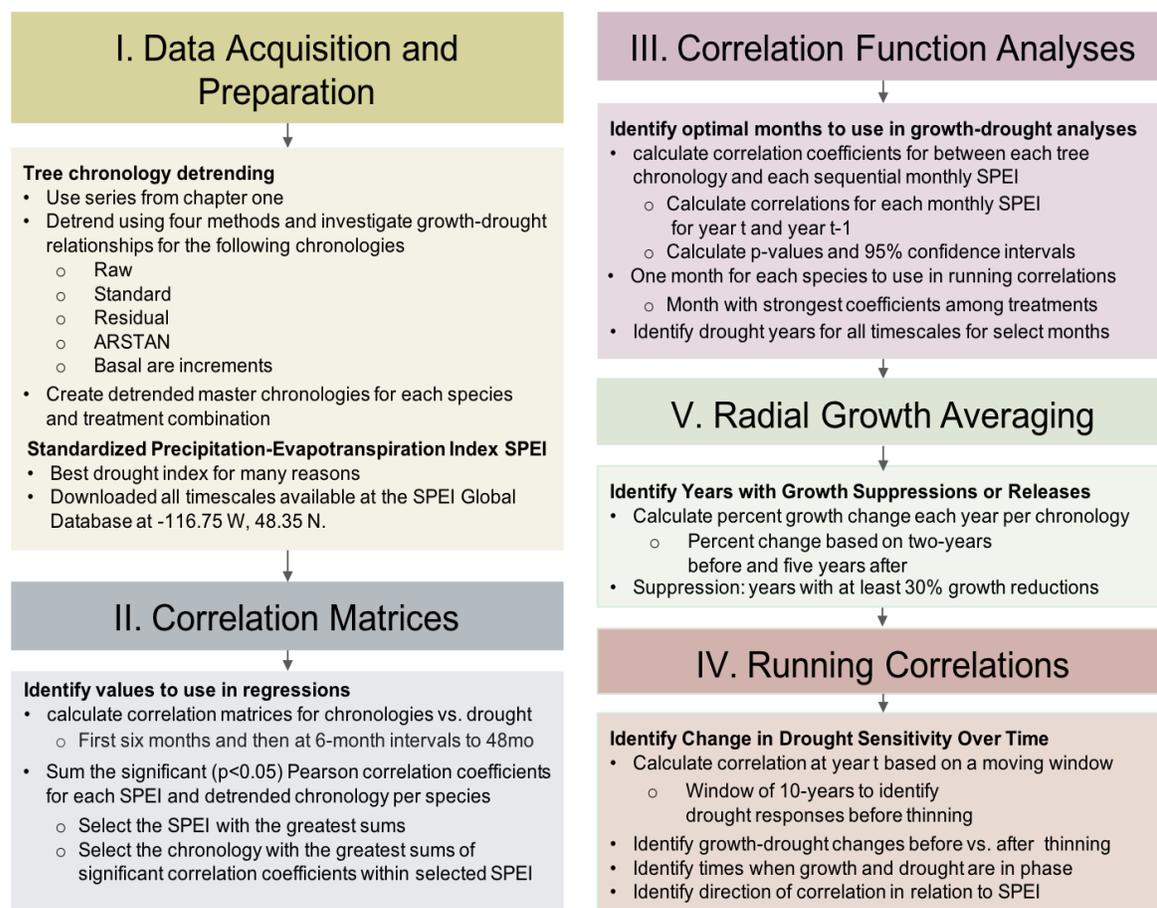


Figure 2. 1 Workflow diagram of statistical methods.

Once series were separated into species-treatment combinations, they were detrended to best characterize growth-drought relationships. Detrending is the process by which unwanted noise in the chronology is removed in order to isolate the desired signals (James Hardy Speer, 2010; Stokes & Smiley, 1968). I selected the four most common detrending methods because they are known to show significant correlations with climate variables – standardized (std.) residual (res.), arstan (ars.), and basal area increments (BAI). Standard, residual, and arstan chronologies were calculated using the computer program ARSTAN (Edward Roger Cook, 1985). The detrending process in ARSTAN involves fitting a growth-curve line to raw ring-width series and removing long-term trends that are often significantly autocorrelated. The growth curve in older trees is usually a negative exponential curve; however, these trees were relatively young (~70-yr), and they did not show any linear trends over time. Therefore, I selected a cubic smoothing spline of 33% the length of the series

because it maintains high inter-series correlation values while maintaining short term variability (Grissino-Mayer, 2001). The standard chronology creates an index from the smoothing spline by subtracting the predicted observation from the observed observation and dividing by the standard deviation. The residual is the difference between the observed minus the predicted value. The arstan detrending method begins with the standard chronology then re-introduces stand-level variability to capture more high-frequency variability (Cook 1985). I also detrended the raw ring widths using basal area increments (BAI; cm²). I used the equation developed by Biondi (1999) to calculate BAI:

$$a_t = \frac{\pi}{100} w_t \left(w_t + 2 \sum_{i=0}^{t-1} w_i \right)$$

where a_t is the ring area in cm². Pith was not estimated in these samples; therefore, w_0 represents the distance from the innermost complete ring to the adjacent bark-side ring (Biondi, 1999). Finally, I created master chronologies for each species-treatment combination by computing the mean growth for each year from each detrended series. I also created a raw ring width master chronology.

Standardized Precipitation Evapotranspiration Drought Index

Numerous drought estimates attempt to identify the magnitude, intensity, and temporal extents of droughts (Heim, 2002). Familiar drought estimates, like Palmer drought severity index (PDSI; Palmer, 1965) and the standardized precipitation index (SPI; (Mckee, Doesken, & Kleist, 1993), are extensively used in system analyses and monitoring (Carnwath, Peterson, & Nelson, 2012; Hidalgo, 2004; Sheffield, Goteti, Wen, & Wood, 2004). However, a new estimate for drought, the standardized precipitation evapotranspiration index (SPEI), is a drought index based on local climate and vegetative demand and is considered the most accurate estimate to date (Vincente-serrano et al., 2012). The SPEI is selected in this study over other drought indices because it (a) incorporates droughts of different timescales, (b) identifies droughts based on vegetative demand by using the Penman-Monteith equation to estimate potential evapotranspiration; (c) identifies drought onsets, and (d) accurately reflects drought variability induced by climate change known as *global-change-type-drought* (Vincente-serrano, Begueri, & Lopez-Moreno, 2009). Recent studies also find that SPEI correlates well with tree rings and can be strong indicators of tree growth-drought relationships (Carnwath et al., 2012; Dai et al., 2018).

The ability to incorporate droughts at different time scales makes the SPEI especially useful when investigating relationships with trees with variable life-history traits and drought tolerances, like the selected species in this study. Short-term droughts, referred to as meteorological droughts, occur at high-frequencies and are associated with soil water and low-order streams. Droughts at medium timescales, or hydrological droughts, show lower frequencies and are associated with reservoir storage and medium-order streamflow. Long time-scale droughts are associated with depletions or high variability in groundwater storage (Vicente-serrano et al., 2012, 2009). Because of the aforementioned qualities, I use this index to investigate species-specific drought responses in mixed coniferous forests. All available timescales of SPEI were downloaded from the Global SPEI Database (Beguería, Vicente-Serrano, & Angulo-Martínez, 2010) for the geographical coordinates for the strip clearcut (-116.75 W, 48.35 N). The data consists of long-term (1901-2016) SPEI values for the Earth at a spatial resolution of $0.5^\circ \times 0.5^\circ$ and a temporal frequency of one month. The standardized precipitation-evapotranspiration index ranges from [-3, 3], where positive values represent moist years and negative values represent years of drought. The typical range of SPEI is [-2, 2] on average (Stagge, Tallaksen, Gudmundsson, & Loon, 2016), but at PREF, a moist forest, -1 ± 0.01 is the lower 10th percentile from 1950-2016 for all monthly observations – an extreme drought year. The 25th percentile is -0.45 ± 0.01 . The value at the upper 90% percentile (moist years) is 1.5 ± 0.01 , and the overall variance is low ($\sigma^2_{(38640)} = 0.90$) from 1950-2016 for all monthly observations. Therefore anything lower than -0.45 is a drought year at PREF.

Correlation matrices

To identify which chronologies and drought timescales should be investigated further, I conducted correlation matrices for each master chronology vs. the following monthly SPEI values to identify the strongest growth-drought signal: SPEI01–SPEI06, SPEI12, SPEI18, SPEI24, SPEI30, SPEI36, SPEI42, SPEI48. The final correlation matrix was conducted for 156 SPEI variables and 72 master chronologies (12 for each of five detrending methods plus 12 for the raw ring width master chronologies). Next, I calculated the sum of significant Pearson correlation coefficients for each SPEI timescale investigated (Table 2.1). I selected the drought timescales that had the greatest counts of significantly correlated relationships based on *p*-values from absolute values of Pearson correlations ($p < 0.05$; Table 2.1 and 2.2).

In this research, I use SPEI-04 (four-month), SPEI-24 (24-month), and SPEI-48 (48-month) to investigate short-, mid-, and long-timescale drought responses, respectively. The population samples did not meet the assumptions of parametric testing; however, Pearson correlations are robust to violations of the assumptions (Havlicek & Peterson, 1976).

Table 2. 1 Counts of statistically significant correlations between growth and drought for each drought timescale investigated (rows) and for each species (columns). Note: Highlighted numbers are used in the following growth-drought analyses.

	Western larch	Grand fir	Western redcedar	Western hemlock	Total
SPEI01	11	16	13	11	51
SPEI02	8	17	24	17	56
SPEI03	4	17	26	21	68
SPEI04	2	18	32	18	70
SPEI05	1	16	28	11	56
SPEI06	2	14	20	8	44
SPEI12	2	0	0	3	5
SPEI18	10	6	9	12	37
SPEI24	16	3	14	15	48
SPEI30	30	12	22	31	95
SPEI36	39	17	31	48	135
SPEI42	59	20	25	66	170
SPEI48	75	19	41	66	201

Table 2. 2. Counts of statistically significant correlations between growth and drought for each master chronology investigated. Note: Highlighted numbers are used in the following growth-drought analyses.

Count	Western larch	Grand fir	Western redcedar	Western hemlock
Raw	129	17	96	208
Standard	25	26	48	36
Residual	49	18	31	59
Arstan	59	22	46	49
BAI	15	98	73	6

Correlation Function Analysis

Correlation function analysis was used to find the optimal time of year where the relationships are strongest (Blasing, Solomon, & Duvick, 1984) in the computer software *Dendro Tools* (Burnette, 2013). Correlation function analysis involves calculating a series of Pearson correlation coefficients between each tree chronology and each sequential monthly SPEI to identify which months show the strongest correlations in the growing year (year t) and in the year prior ($t-1$). The Correlation function analysis is also useful for identifying the season of drought to which trees are sensitive. The month with the greatest overall Pearson correlation coefficient, and lowest Pearson correlation p -value, for all three treatments per species was used in subsequent comparisons and analyses. Based on the results from the correlation function analyses, I identified the drought months of statistical significance and used those in analyses moving forward. Not only does the correlation function analysis help identify seasonality of drought sensitivity, but it also identifies the level of strength and directions of growth-drought correlations, as well as differences among thinning treatments.

Running Correlations

Tree tolerance to drought-stress may increase throughout the life of a tree (Niinemets, 2010), while growth-drought sensitivity may weaken in mixed forests (Forrester, 2014). Therefore, analysis of the changing growth drought relationships over time will ensure a more thorough picture of the dynamics that influence growth responses in this forest (Fang et al., 2010; Ram, 2012). To investigate the change in growth-drought relationships over time, I calculated running Pearson correlations for each species-treatment combination for all three drought timescales using *Dendro Tools* (Burnette, 2013). Running correlations calculate Pearson correlation coefficients and Pearson correlation p -values for growth-drought relationships for each year, depending on a moving window. I used a window of ten years to ensure I could observe at least ten years of pre-thinning growth-drought relationships, because the Millennial Drought (described more in detail later) was ten years long, and because moisture patterns in the region are influenced heavily by the Pacific Decadal Oscillation (Halofsky et al., 2018). Hence, in the year 1970, the correlation coefficient depends on the growth-drought relationship for the prior ten years (1961-1970). For the year 1971 the correlation coefficient is computed for the years 1962-1971 and so on.

Results

Overall patterns in growth-drought relationships

Western larch, the most drought-tolerant deciduous species in this study, was the most sensitive to drought, followed by western hemlock, western redcedar, and finally, grand fir, which shows weak correlations overall and significant negative relationships at times. Western larch was most sensitive to long-term winter drought, while western redcedar responded most to short-term growing-season drought. Grand fir and western hemlock react equally to short- and long- term drought, though seasonality differs from winter to summer, respectively. The high thinning intensity treatment showed greater positive drought relationships compared to low and reference for western larch and grand fir at the long- and short- timescales, respectively. Western hemlock showed a slight increase in sensitivity in high-intensity thinned plots, but only in the short-term; at long timescales sensitivity was higher in the unthinned locations. Western redcedar did not show any notable changes in drought-sensitivity based on thinning intensity, indicating that variables other than drought are more strongly affecting the radial growth of western redcedar.

The Drought of the late 80s and early 90s (a.k.a. The Millennial Drought)

I identified a sustained winter (December—February) drought of significance at all time-scales that occurred from 1986-1995 with one year of release (high moisture) in 1990. The same drought is present in the autumn (September–November), but only at mid- and long-term timescales. This drought overlaps with the 1988–89 North American drought (Trenberth & Branstator, 1992), though feedback loops and other microclimate variability may have allowed the drought to persist through the early 90s in this region (Oglesby & Erickson III, 1989). For simplicity purposes, I will hereafter refer to this drought as the *Millennial Drought*, and it will be compared to the running correlations of all species-treatment combinations to identify changes in growth-drought relationships in response to drought; it will also be used to compare growth-drought sensitivity during drought among thinning treatments. I chose to focus on this drought interval over the other lengthy drought interval that occurred in the late 1970s (1976–1979) because the Millennial Drought was sustained over a greater temporal range. Additionally, the Millennial Drought occurred much later post-thinning (16–18 years, vs. 8–6 years) when compared to the earlier identified

drought; thus, the variability in growth during the Millennial Drought is more likely affected by drought, rather than dynamic post-thinning growth responses (Chapter 1).

All trees greater than 11.5 cm dbh were measured in the transect approximately seven years before the Millennial Drought (11-years post-thinning). Results from those measurements show that there were 988 trees ha⁻¹ in unthinned treatments, 505 trees ha⁻¹ in low-intensity treatments, and 427 trees ha⁻¹ in high-intensity treatments, on average, with greater proportions of seedlings and non-tree species in the thinned locations. Larch made up a much greater proportion of basal area in the reference treatment where sapling density was higher than the thinning treatments (Shen et al., 2019). Thus, significantly less light and precipitation reached the forest floor in the unthinned locations at the time of the Millennial Drought when compared to the thinned locations.

Western larch

Correlation Function Analysis

In all three timescales, larch is sensitive to winter drought. At the short timescale, the most significantly correlated month is February at year t-1, though the average p -value for all treatments in the short-term is not significant ($\bar{r} = 0.25$, $\bar{p} = 0.15$). At mid- and long-term drought timescales, western larch was most significantly sensitive to January from year t-1 ($\bar{r} = 0.32$, $\bar{p} = 0.05$), and year t ($\bar{r} = 0.41$, $\bar{p} = 0.01$), respectively. All treatments were significantly correlated with drought at the 48-month (long-term) timescale (Figure 2.2). At the short timescale, the only significant growth-drought relationship is with February from the year before in High ($r = 0.34$, $p = 0.02$). Overall, high thinning intensity, which resulted in the lowest density plots, was significantly correlated with droughts at all timescales (Figure 2.2). Reference plots were more sensitive (significantly correlated with) to drought than low-intensity plots.

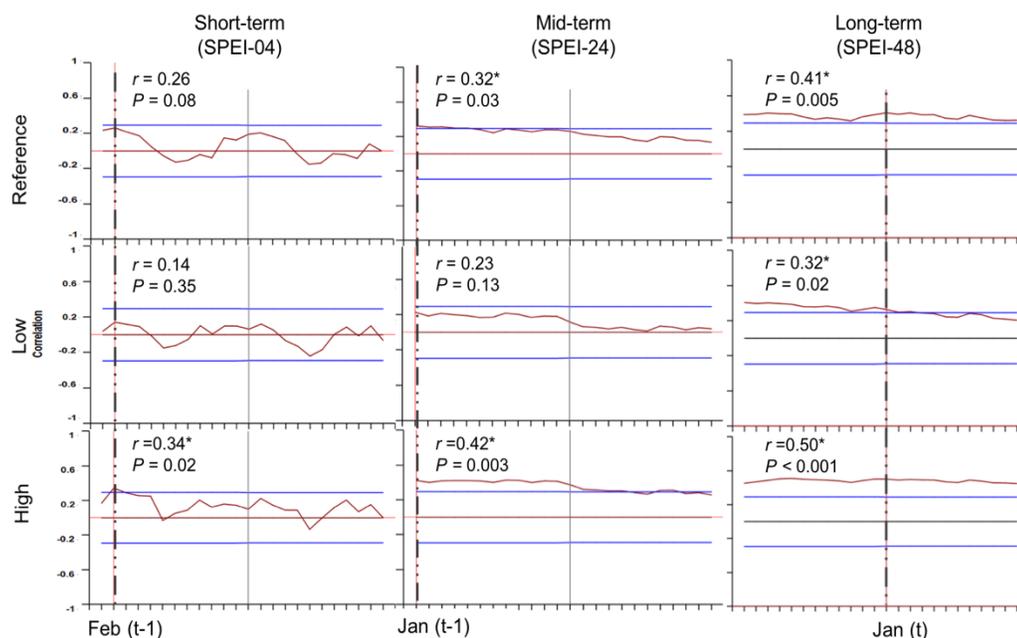


Figure 2. 2. Plots of correlation function analyses for western larch and each SPEI timescale (columns) and treatment (rows). Correlation coefficients are on the y-axis. Asterisks next to correlation coefficients mark statistical significance. The red chronology line is the correlation coefficient for each month. Months are on the x-axis. The vertical grey line in the center of each cell represents January of year (t), and year (t-1) is to the left. The blue horizontal lines represent the 95% confidence interval. Vertical black dashed line is the month with the most significant mean correlation coefficient and lowest mean p -value for each drought timescale.

Running Correlations

There are no significant differences among pre-thinning drought sensitivities (growth-drought correlations) for treatments (Figure 2.3). Recently after thinning, growth-drought relationships strengthen and become more positive. In the years leading up to the Millennial Drought (1976–1984), correlations with drought were significantly positive for mid- and long-term droughts in all treatments ($p < 0.001$). Additionally, the correlation becomes significantly negative during the tail end of the Millennial Drought in the unthinned, reference plots. Sensitivity in reference sites follow the same pattern for all drought timescales, but the positive correlation is most significant in long-term growth-drought relationships. Compared to the thinned plots, the reference plots show greater variability in growth-drought relationships and was the only treatment to show significant negative correlations during the Millennial Drought.

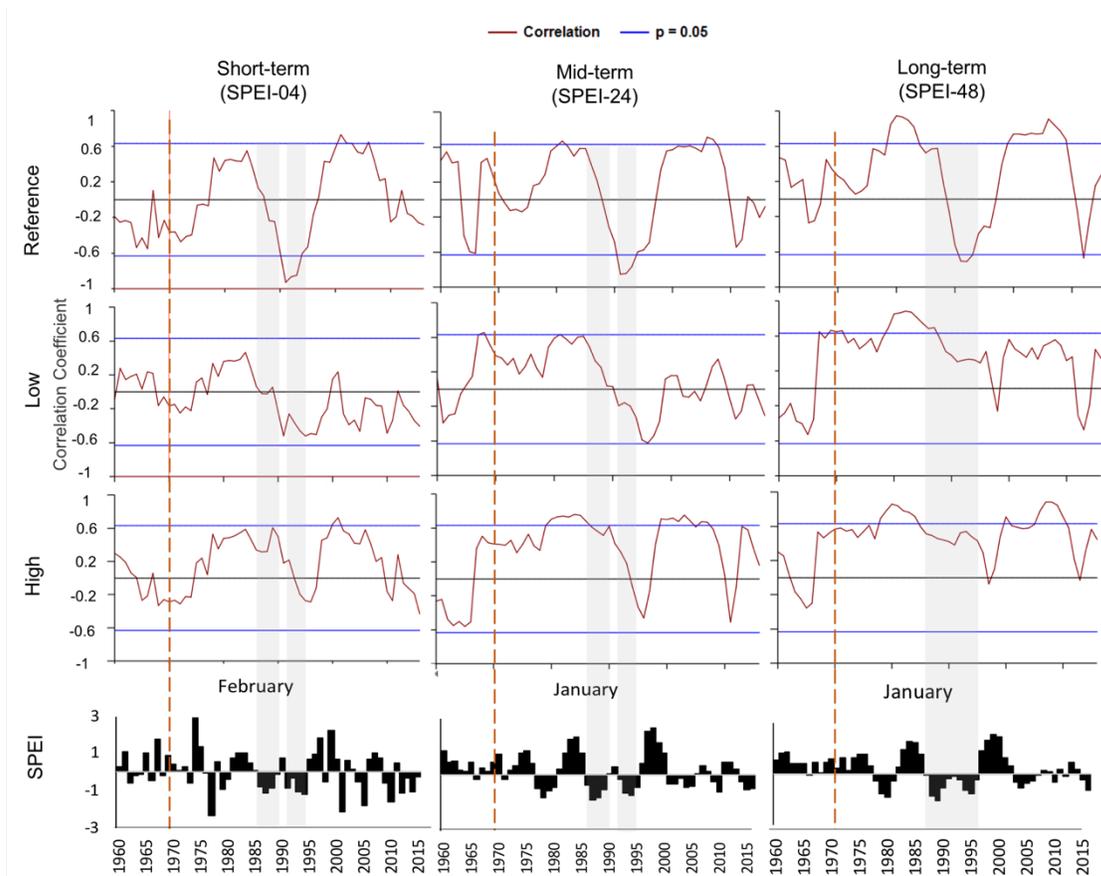


Figure 2. 3. Plots of running correlation analyses for western larch and each drought timescale and treatment combination Note: Drought years related to the Millennium Drought are shaded in grey. Dashed vertical red line is the year of secondary thinning (1971).

Grand fir

Correlation Function Analysis

At short timescales, grand fir is more sensitive to early summer drought (June), which includes the prior three months (March-May), though the average p -value is not significant ($\bar{r} = 0.25$, $\bar{p} = 0.11$; Figure 2.3). In both mid- and long-term drought timescales, grand fir is sensitive to December drought at year $t-1$; these relationships are also primarily negative, but they are not statistically significant ($\bar{r} = -0.13$, $\bar{p} = 0.41$; and $\bar{r} = -0.18$, $\bar{p} = 0.25$, respectively). The only grand fir chronology that is significantly correlated to drought is in the high thinning intensity at short timescales, and the relationship is positive ($r = 0.31$, $p =$

0.04). Although the significance is mild, grand fir does show increasing drought sensitivity in response to high thinning intensity, especially at short timescales (Figure 2.4).

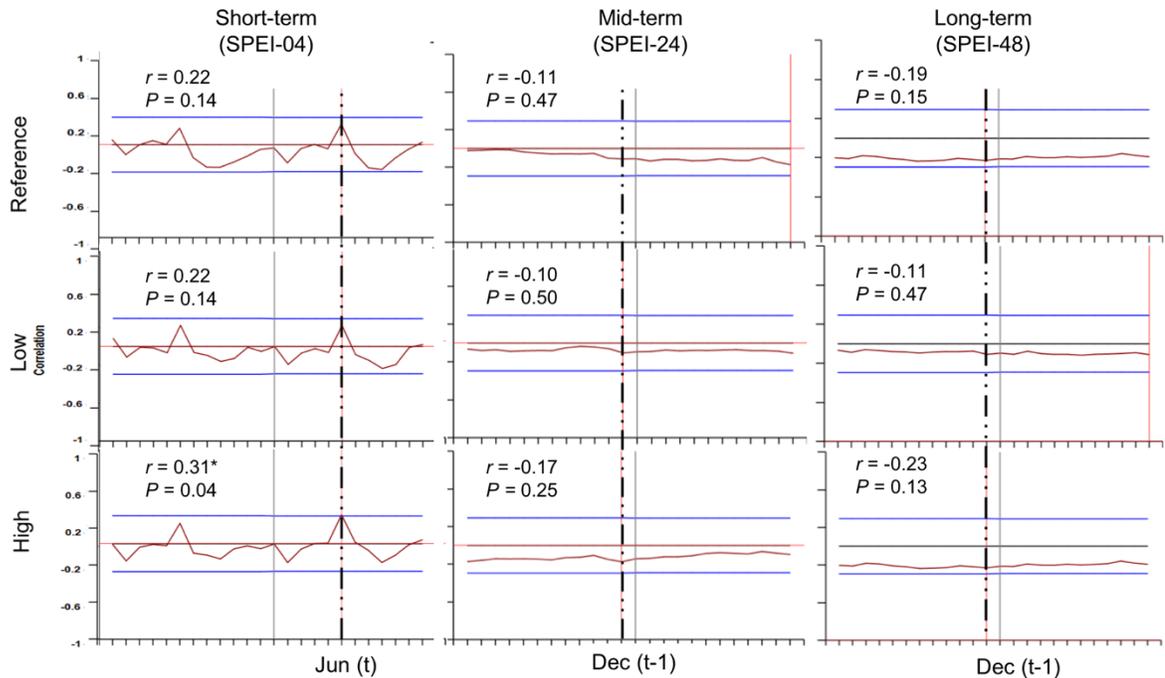


Figure 2. 4. Plots of correlation function analyses for western larch and each SPEI timescale (columns) and treatment (rows). Correlation coefficients are on the y-axis. Asterisks next to correlation coefficients mark statistical significance. The red chronology line is the correlation coefficient for each month. Months are on the x-axis. The vertical grey line in the center of each cell represents January of year (t), and year (t-1) is to the left. The blue horizontal lines represent the 95% confidence interval. Vertical black dashed line is the month with the most significant mean correlation coefficient and lowest mean p -value for each drought timescale.

Running Correlations

There are no significant differences among pre-thinning drought sensitivity (growth-drought correlations) for each treatment (Figure 2.5) for grand fir. Like western larch, mid- and long-term growth-drought relationships strengthen and become significantly positive ($p < 0.05$) after thinning from 1972–1974. However, unlike western larch, these relationships abruptly change direction in 1975/76 toward a negative correlation. This downward trend in the direction of the growth-drought relationship coincided with another drought that occurred from 1975–78 at mid- and long-term timescales, a time when larch was significantly positively correlated with drought (Figure 2.5). Furthermore, grand fir showed a period of

positive correlation with drought throughout a moist period just before the Millennial Drought (1980–84). The correlation becomes significantly negative during the tail end of the Millennial Drought for the high-intensity thinning compared to western larch, which showed more significant negative correlations in the unthinned plots during this time. In the moist years after the Millennial Drought (1995–2000), correlations with drought were significantly positive for mid-term droughts in the reference treatment ($p < 0.05$). After this, the grand fir becomes more sensitive to, and positively correlated with, short-term drought ($p < 0.05$). Sensitivity to short-term drought follows the same general pattern for all treatments, while mid- and long-term drought responses are similar to one another.

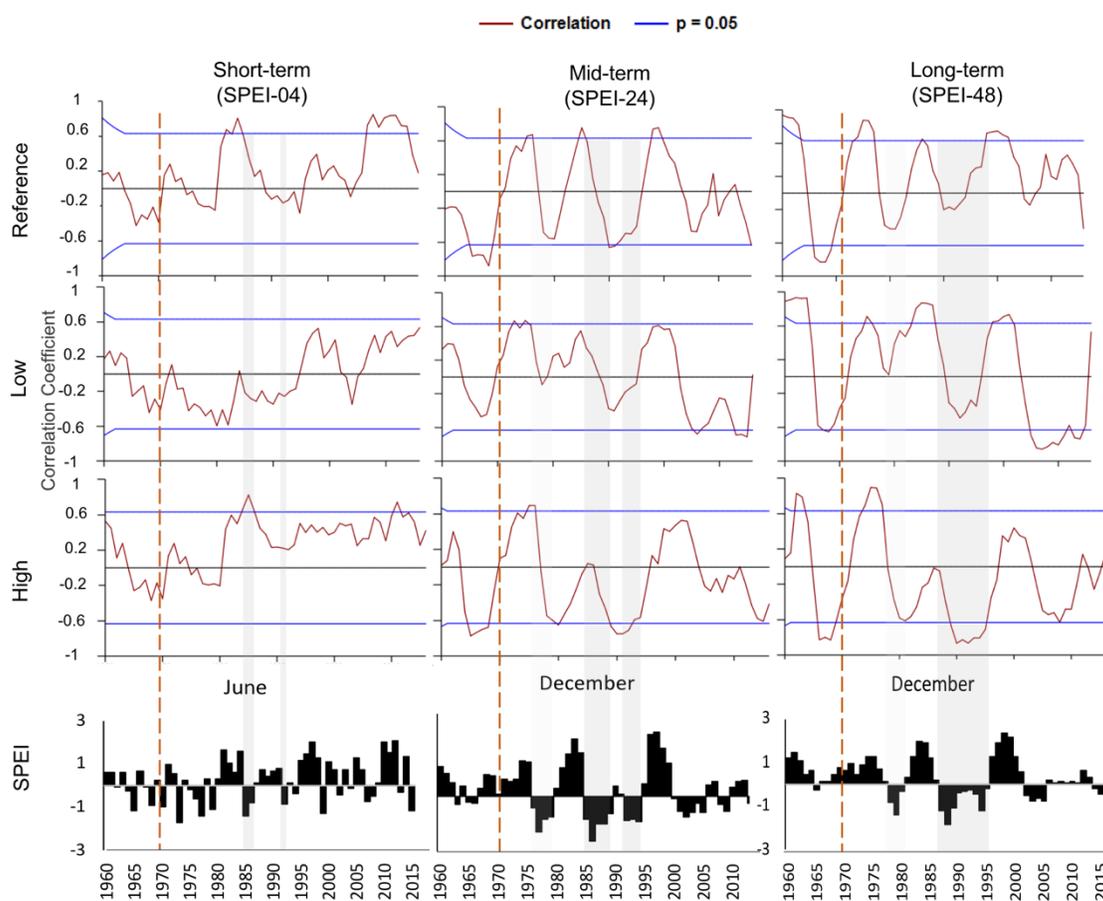


Figure 2. 5. Plots of running correlation analyses for grand fir and each drought timescale and treatment combination. Note: Drought years related to the Millennial Drought are shaded in darker grey, while a notable drought in the mid 70s is shaded in lighter grey. Dashed vertical red line is the year of secondary thinning (1971).

Western Redcedar

Correlation function analysis

In short timescales, western redcedar is most sensitive to growing-season drought (Figure 2.6). In the short and long timescales, the most significantly correlated month is September at year t . Drought responses were not significant overall for long-term scales ($\bar{r} = 0.27$, $\bar{p} = 0.08$). Drought responses were least significant for the mid-term timescale- ($\bar{r} = 0.25$, $\bar{p} = 0.10$). However, western redcedar was significantly correlated with drought at the four month (short-term) timescale for all treatments ($\bar{r} = 0.38$, $\bar{p} = 0.01$) – opposite of western larch, which was more statistically sensitive to long-term drought (Figure 2.2). At long-term drought timescales, the only significant growth-drought correlation is in the high-intensity thinning treatments ($r = 0.31$, $p = 0.03$). Overall, thinning does not appear to impact the growth-drought relationships of western redcedar, as evidenced by nearly identical relationships in all treatments.

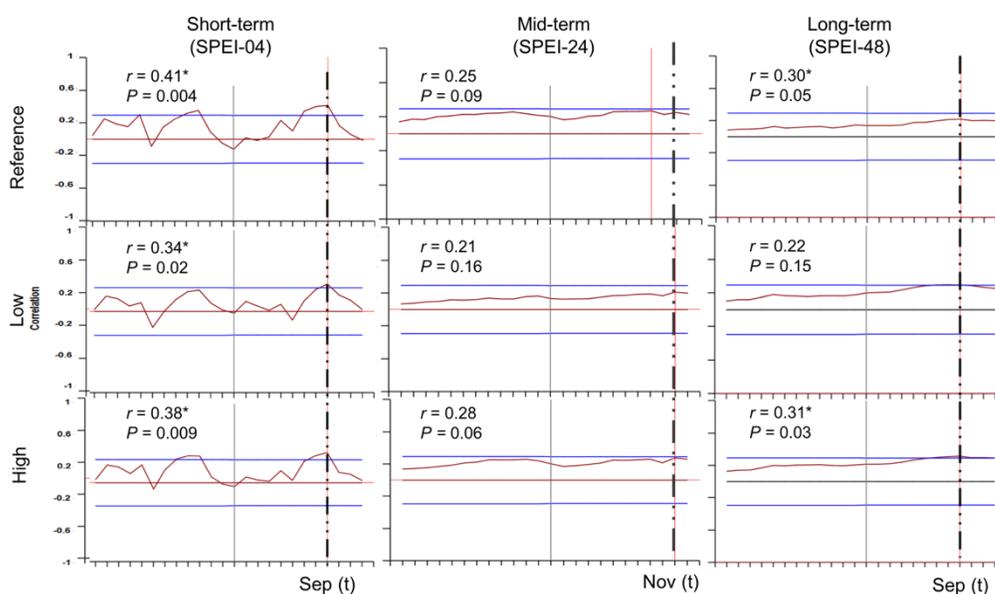


Figure 2. 6. Plots of correlation function analyses for western larch and each SPEI timescale (columns) and treatment (rows). Correlation coefficients are on the y-axis. Asterisks next to correlation coefficients mark statistical significance. The red chronology line is the correlation coefficient for each month. Months are on the x-axis. The vertical grey line in the center of each cell represents January of year (t), and year (t-1) is to the left. The blue horizontal lines represent the 95% confidence interval. Vertical black dashed line is the month with the most significant mean correlation coefficient and lowest mean p -value for each drought timescale.

Running Correlations

There are no significant differences among pre-thinning drought sensitivity for each treatment (Figure 2.7). Like western larch and grand fir, long-term growth-drought relationships strengthened and became significantly positive ($p < 0.05$) after thinning at various years in the 1970s. However, unlike western larch and grand fir, these relationships strengthen to a significant positive relationship with short-term drought during the Millennial Drought. The strong positive growth-drought relationships during the Millennial Drought are opposite the response of western larch, which showed significant negative relationships. Also contrary to larch is that western redcedar switched to a negative growth-drought relationship in the moist years to follow the Millennial Drought (1995–2000). Sensitivity to short-term drought follows the same general pattern for all treatments, while mid- and long-term drought show stronger correlations during the millennial drought in the high thinning intensity treatment ($p < 0.05$).

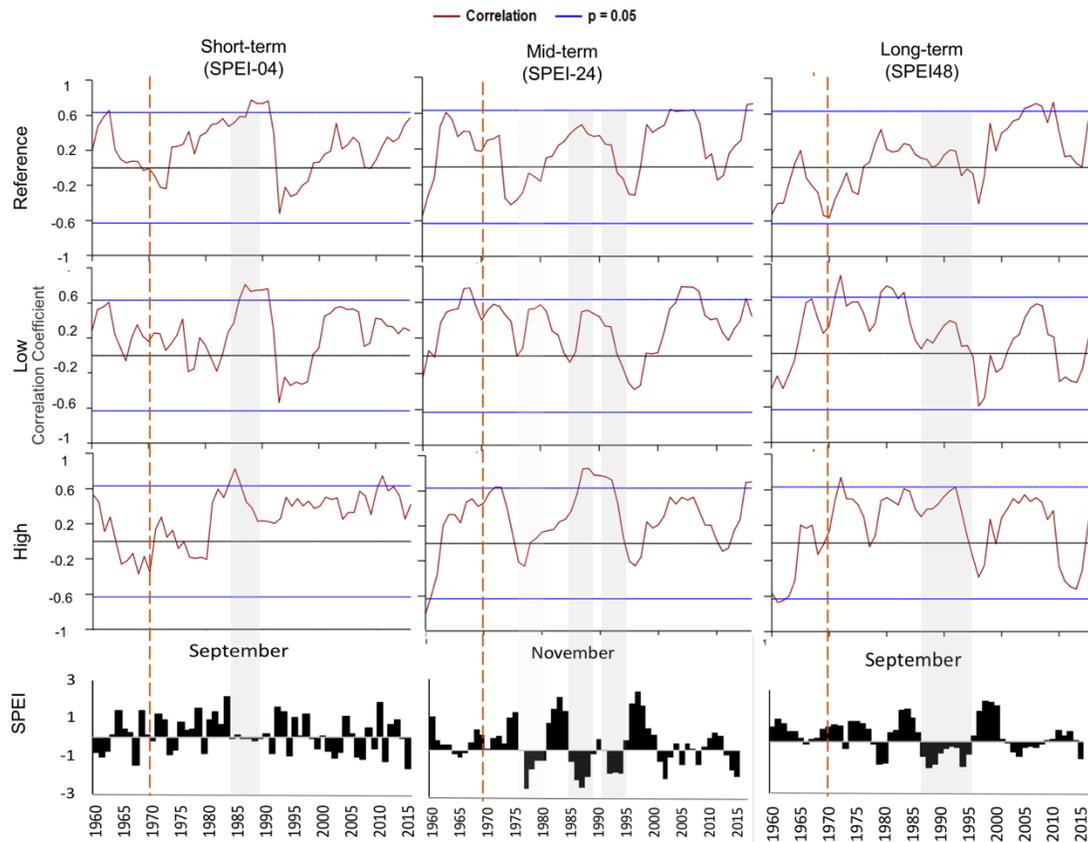


Figure 2. 7. Plots of running correlation analyses for western redcedar and each drought timescale and treatment combination. Note: Drought years related to the Millennial Drought are shaded in grey. Dashed vertical red line is the year of secondary thinning (1971).

Western hemlock

Correlation Function Analysis

Like western redcedar, western hemlock is sensitive to dry-season drought (Figure 2.8). At the short- and long timescale, the most significantly correlated month is September at year t , while the mid-term drought correlated with September at year $t-1$. The strengths of the growth-drought relationships is weakest for mid-term drought ($\bar{r} = 0.34$, $\bar{p} = 0.03$), while responses at short and long-term timescales are similar to one another (Short-term: $\bar{r} = 0.38$, $\bar{p} = 0.01$; Long-term: $\bar{r} = 0.40$, $\bar{p} = 0.01$). The relationships with long- and mid-term drought appear to weaken in response to thinning, as demonstrated by smaller correlation coefficients and bigger p -values (Figure 2.8). On the other hand, sensitivity to short term

drought appears to strengthen in heavily thinned locations, as demonstrated by higher correlation coefficients and smaller p -values.

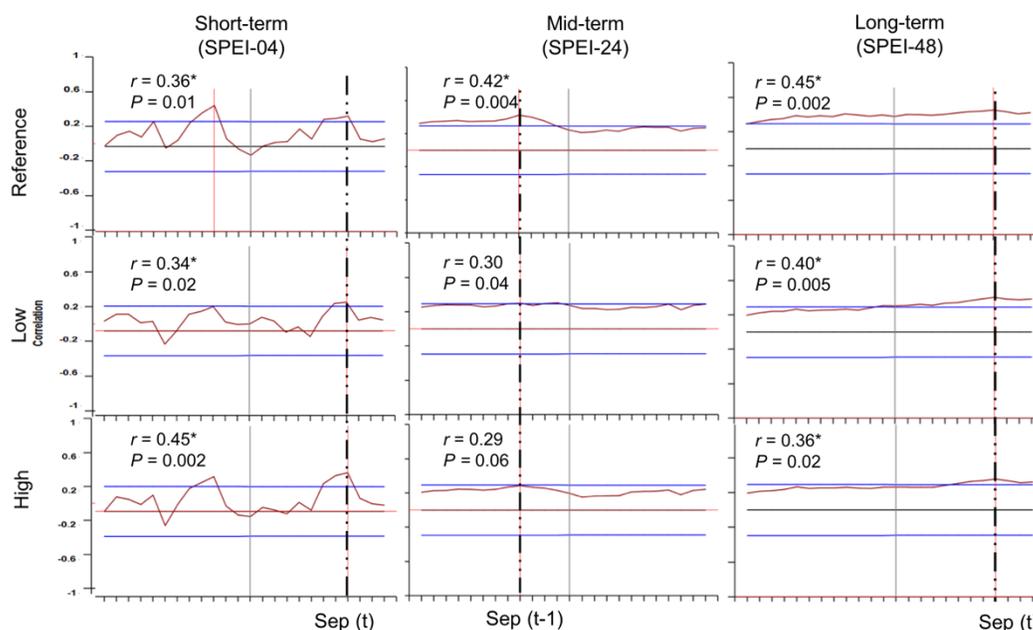


Figure 2. 8. Plots of correlation function analyses for western larch and each SPEI timescale (columns) and treatment (rows). Correlation coefficients are on the y-axis. Asterisks next to correlation coefficients mark statistical significance. The red chronology line is the correlation coefficient for each month. Months are on the x-axis. The vertical grey line in the center of each cell represents January of year (t), and year (t-1) is to the left. The blue horizontal lines represent the 95% confidence interval. Vertical black dashed line is the month with the most significant mean correlation coefficient and lowest mean p -value for each drought timescale.

Running Correlations

Western hemlock shows highly variable relationships with long- and mid-term drought at all timescales before thinning with a significant positive correlation before thinning in the low thinning-intensity treatment. The variability decreases over the entire temporal coverage of the study after thinning. The relationships in the short timescale remain insignificant for low and high thinning intensities throughout the full period of coverage, while there is increased sensitivity over time in unthinned sites until eventually, the relationship becomes significantly positive ($p < 0.01$) about 40-years after thinning (2010). At that same time, growth drought sensitivity decreases for mid- and long-term droughts, but the variability in these relationships makes interpretation difficult. Moreover, there appears to be a slight shift from positive to negative correlations during the two mid-term pulses of the

Millennial Drought, but none are statistically significant ($p > 0.05$). After the Millennial Drought growth became significantly positive in all treatments for mid- and long-term drought timescales.

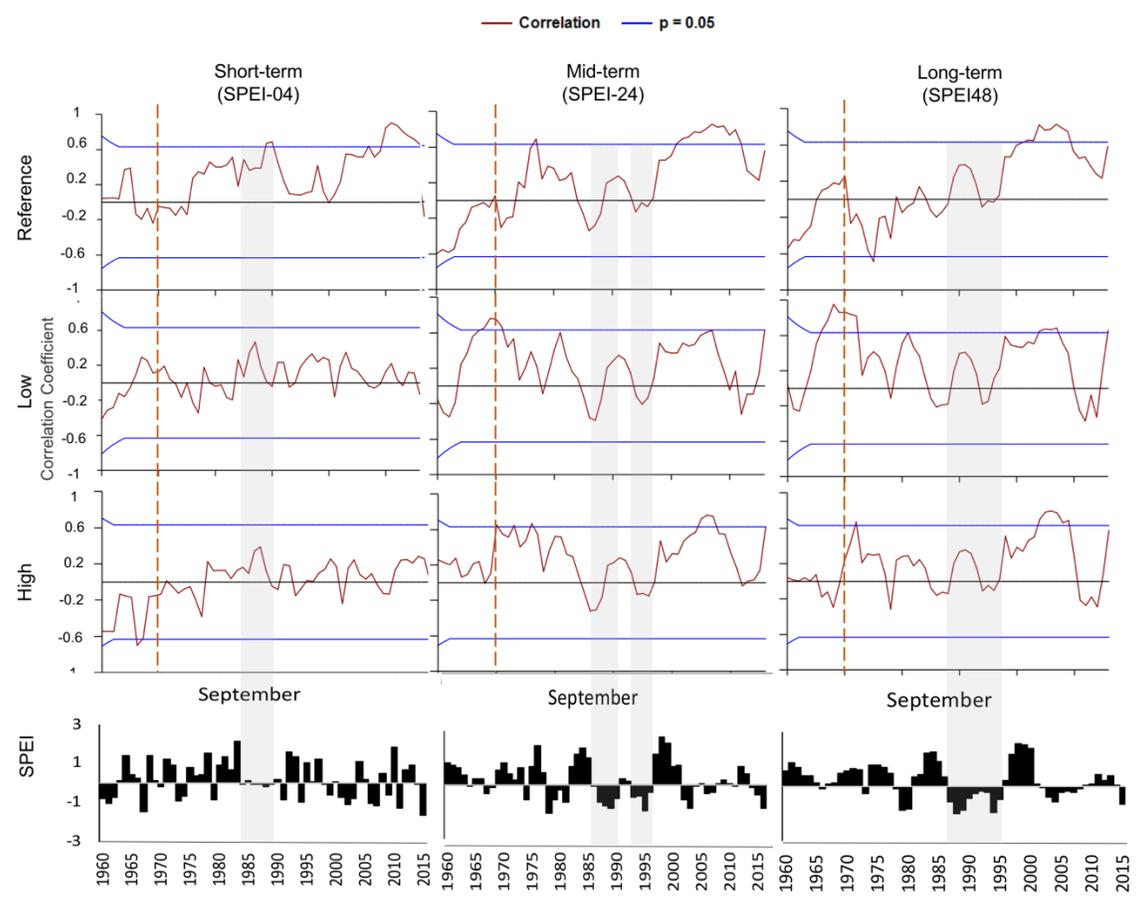


Figure 2. 9. Plots of running correlation analyses for western hemlock and each drought timescale and treatment combination. Note: Drought years related to the Millennial Drought are shaded in grey. Dashed vertical red line is the year of secondary thinning (1971).

Discussion

Seasonality of drought sensitivity

Western larch is most sensitive to winter drought. Sensitivity to winter drought is possibly due to direct influences of winter snow-pack on soil-moisture in the growing season. Snow-melt and snowpack are responsible for most of the soil water recharge in the Pacific Northwest compared with rainwater (Hardy et al., 2001; Maurer & Rowling, 2014). Snowmelt also infiltrates deeper below the root zone and recharges groundwater (Earman, Campbell, Phillips, & Newman, 2006); thus, snow is responsible for preventing agricultural droughts in this region (Vincente-serrano et al., 2012). Soil moisture throughout the growing season also positively correlates with the timing of snowmelt and generally trends toward becoming more xeric as time passes (Harpold et al., 2015). Western larch, which has deep branching roots (Schmidt, Shearer, & Roe, 1976), begins growing in the early spring, before co-existing species (Baker, Tai, Miller, & Johnson, 2019), and may quickly consume available soil water. Therefore, in years with low snowpack, western larch will reduce radial growth in response to lack of recharge, yet moisture inputs from the growing season don't appear to influence radial growth. Other studies support that western larch is sensitive to winter drought variables, for example interactions between winter temperature and summer moisture are shown to strongly impact western larch growth (Rehfeldt & Jaquish, 2010).

Overall growth-drought sensitivity of grand fir was not statistically significant for any timescales; however, it is most positively correlated with short-term February drought. Overall trends show that growth-drought correlations are mostly negative with mid- and long-term winter drought – a trend opposite of western larch, which is positively correlated with winter drought. In other words, with two or more years of consecutive winter drought, grand fir grows at faster rates while western larch reduces radial growth (though running correlations show some parallels in growth-drought sensitivity during the Millennial Drought discussed in detail below). Given that both species are considered to be drought-tolerant (Fiedler & Lloyd, 1995; Minore, 1979), there appears to be growth trade-off between these species, or they are using different drought adaptations from one another. The significantly thicker sapwood of grand fir may allow it to buffer itself in drought years, allowing trees to continue growing in conditions with inadequate moisture (Running, Waring, & Rydell, 1975). Growth increases in drought years might also be a response to greater temperatures

associated with drought, plus the ability to store water in the sapwood. Supporting this hypothesis is the fact that grand fir is limited by cold temperatures in the northern Rocky Mountains (Parker, 1955). Furthermore, it is possible that in years with early snow-melt (resulting in winter drought) that grand fir might grow more because it begins growing earlier in the season after the snow is melted.

Western redcedar and western hemlock are most sensitive to September droughts during the growing year. Sensitivity to late growing-season drought is common and generally expected because summers are hot and dry, trees are growing at greater rates, and vapor pressure deficits are greater in summers than at any other time of year. Most species will be dormant by the end of the summer, but western redcedar continues to have higher water potentials than western larch and grand fir well into October (Baker et al., 2019). Western redcedar also has indeterminate growth allowing it to continue growing later in the season when conditions are favorable (Minore, 1983). These species may also be responding to moisture inputs at the end of the growing season, which prolongs growth (and growth-drought sensitivity) into the fall season (Fang et al., 2010).

Drought sensitivity at different timescales

Western larch is significantly sensitive to long-term droughts while the sensitivity becomes exceedingly insignificant with shorter drought timescales. This shows that multiple years of winter drought are required before western larch will respond with reduced radial growth. These long-term consecutive winter droughts lead to reductions in overall soil water storage (Earman et al., 2006), indicating that in years of drought at short timescales, larch may be avoiding drought by tapping into deep water with extended root lengths (Schmidt et al., 1976), a hypothesis also suggested by Baker et al. (2019). Greater root growth may lead to an inability to respond to short-term changes in soil moisture, particularly from precipitation, because total root mass is reduced in extended droughts (Lagergren et al., 2008; Moran et al., 2017). The isohydric strategies practiced by this species may allow it to avoid immediate drought stress. However, xylem, which functions for several years, may lose transport efficiency after years of drought avoidance. Drought response in the current year can influence future drought responses because xylem growth in drought years results in smaller and thinner-walled tracheids (Moran et al., 2017). Therefore, the accumulation of

drought-stressed xylem, year after year, increases the likelihood of failure under drought conditions (Guérin et al., 2020), and thus exacerbates growth suppressions in the longer-term.

Grand fir was more positively correlated with short-term drought but more negatively correlated with mid- and long-term drought, indicating that after two to four years of snow-droughts, grand fir is able to withstand drought and continue growing despite the fact that species like western larch are unable to grow. These results indicate that grand fir may rely on water stored in the sapwood to survive long-term drought. Additionally, it is known that grand fir can easily become drought stressed making it susceptible to being attacked by secondary agents such as insects and pathogens. Thus, the high variability in growth-drought sensitivity could be due to interactions resulting from shallow roots that are easily damaged by diseases that cause root-rot, such as *Armillaria spp.* (McDonald, Martin, & Harvey, 1987; Minore, 1979).

Western redcedar is significantly sensitive to short term droughts, and sensitivity decreases to insignificant in mid- and long-term. Western redcedar resists drought via anatomical attributes, like cavitation-resistant xylem (Brodribb et al., 2014; Grossnickle, Steven & Russell, 2010). However, western redcedar also responds to short-term drought by reducing stomatal conductance; thus, reducing carbon assimilation (Grossnickle, Steven & Russell, 2010), but these changes are short-lived before resistance sets in (Brodribb et al., 2014; Sevanto et al., 2014). In other words, the short-term drought sensitivity indicates that western redcedar adopts a drought-avoidance strategy in the short term, leading to reductions in radial growth and therefore strong growth-drought relationships; but after continued drought exposure, western redcedar might begin to rely on its ability to resist drought through cavitation-resistant xylem – explaining the lack of sensitivity to mid- and long-term drought.

Western hemlock shows almost equal significant positive sensitivity to droughts at all timescales. This supports the fact that western hemlock is not very drought tolerant, and whatever slight strategy of isohydry implemented by western hemlock is short-lived (Korol, 2001), and drought will eventually lead to hydraulic failure (Adams et al., 2017; K L Kavanagh & Zaerr, 1997). In other words, regardless of drought timescale, radial growth (and likely other growth) significantly reduces in response to drought for western hemlock. As examined in the first paragraph of this Discussion, there are many anatomical and

physiological characteristics of drought-intolerance that may lead to this sensitivity (Ballard & Dosskey, 1985; Bond & Kavanagh, 1999; Secrest, MacAloney, & Lorenz, 1941).

Drought sensitivity among thinning treatments

Western larch showed greater long-term positive drought sensitivity with high thinning intensity compared to low and reference. This is the expected response when resources are freed up for individuals who often grow with heavy inter-specific competition (Niinemets, 2010; Pérez-de-lis et al., 2011). In other words, western larch growth may be more sensitive to neighborhood competition than to drought in high-density forests. The only grand fir chronology that is significantly correlated to drought is the high thinning intensity at short-term timescales. Like western larch, this increasing positive correlation with reduced stand density suggests that grand fir switched from responding to competition in unthinned sites to drought where density was lowest.

Unlike the extreme drought-avoiders (western larch and grand fir), western redcedar, a member of the *Cupressaceae* family, did not show any notable changes in drought-sensitivity based on thinning intensity, indicating that variables other than drought are more strongly affecting radial growth of western redcedar. These findings are not alarming because this species is known to be a nutrient-limited, slow-growing generalist and drought-resister with significant growth releases in response to thinning and fertilization (Joseph A Antos et al., 2016; Baker et al., 2019; Binkley et al., 2004; Blevins et al., 2006; Jackson & Spomer, 1979; Chapter 1). Therefore, it makes sense that western redcedar is able to balance stressors from multiple sources without dramatically changing growth rates. This hypothesis is supported by the fact that western redcedar generally grows slower than associated species under competition (Joseph Avery Antos, 1977; Chapter 1).

Like the other *Pinaceae* (western larch and grand fir), western hemlock showed a slight increase in sensitivity in high-intensity thinned plots, but only in the short-term. Other than isohydric drought strategies, thinning damage might explain the greater sensitivity to short-term drought in the high-intensity treatment plots for western hemlock. As described in the introduction, thinning can lead to greater infection rates, which can lead to the conservation of water via stomatal closure, ultimately reducing radial growth (Fettig et al., 2013). These results also support the hypothesis presented in Chapter 1 that hemlock was potentially damaged by mechanical thinning, which resulted in greater vulnerability to

pathogens (Chapter 1, Discussion). Contrary to the other *Pinaceae*, western hemlock showed the greatest sensitivity in the mid- and long-term drought timescales, which increased in unthinned locations. It is possible that western hemlocks' competitiveness reduces when resources are limited because they need to use their energy reserves for avoiding or resisting drought (Carnwath & Nelson, 2016). Moreover, there is more interception and less throughfall in high-density, unthinned plots compared to thinned locations (Molina & deCampo, 2012). Thus, reference plots may have greater drought sensitivity because individuals are more limited by water. It is also notable that western larch transpires at much higher rates than other species (Baker et al., 2019; Fiedler & Lloyd, 1995) and in the high-density, unthinned plots, there is likely very little water available overall, so it is possible that western larch is consuming more water than other species.

Change in growth-drought sensitivity during the Millennial Drought

The Millennial Drought supplies a reference point to investigate whether growth-drought responses are stationary or if they differ according to moisture availability. Western larch and grand fir show significant inverse relationships with drought during the Millennial Drought, which indicates decoupling between growth inhibition and drought during dry years. This phenomenon is present in western larch during the Millennial Drought only, while grand fir becomes negatively correlated even in less extreme short-lived droughts. The trees are not necessarily growing more than at moist times; however, the interannual variability in moisture content does not reduce growth during the Millennial Drought. These species exhibit high drought-avoidance strategies, which partially explains why tree growth and drought are decoupled in drought situations. Although water use efficiency can increase in response to drought for drought-avoidant species, correlations are weak between efficiency and radial growth (Eilmann et al., 2010; Moran et al., 2017). These results also indicate that western larch and grand fir are responding to other variables, such as neighborhood competition, rather than to moisture limitations in times of drought and competition (Niinemets, 2010; Pérez-de-lis et al., 2011). This is also supported by the fact that growth-drought relationships are more variable in reference plots than thinned plots for these two species. The unthinned plots were extremely overcrowded at the time of thinning; thus, the sensitivity of these species varies between limiting factors of moisture and levels of competitive interaction. Interestingly, western larch shows stronger negative correlations

during the Millennial Drought in the reference plots, while grand fir is stronger in the high-thinning intensity plots. This might be because they are accessing water at different depths. Western larch might have access to water that is inaccessible to competitors in the reference site because of its deep roots (Schmidt & Shearer, 1990). While grand fir, with its shallow roots, is able to utilize more water in the upper soil layers of the high-intensity treatments (Fowells, 1965).

Contrary to western larch and grand fir, western redcedar and western hemlock both showed mostly positive growth-drought relationships during the Millennial Drought, and growth declined throughout the drought. This supports results from Carnwath and Nelson (2016) that when resources become limited in high-density stands, sensitivity to competition decreases, and sensitivity to the limiting resource increases. Western redcedar also showed continued growth reductions and a drop in the correlation coefficient after the Millennial Drought when moisture was abundant. Perhaps this results from a positive feedback loop between growth-reductions in response to drought and the amount of functional xylem, where reduced growth from previous years may lead to reduced transport efficiency in later years (Moran et al., 2017). Indeed, western redcedar demonstrated prolonged reductions in growth throughout the Millennial Drought that extended into the following years after drought (Chapter 1, Figure 1.2). The continued growth reductions might also be because competitiveness increased post-drought, and competition is known to intensify in wet years (Carnwath & Nelson, 2016). These growth reductions might also be a consequence of aging, which is inversely correlated with drought recovery for western redcedar (Hoffmann, Schall, Ammer, Leder, & Vor, 2018).

Conclusion

Overall drought sensitivity relates to different strategies of drought tolerance

Western larch is most sensitive (significantly correlated) to drought followed by western hemlock, western redcedar, and finally grand fir – which shows weak correlations overall and significant negative correlations at times. It appears that the species exhibit differing drought adaptation strategies of avoidance or resistance, and variability in growth involved trade-offs among competitiveness and overall resource availability.

Western larch, the most “drought-tolerant” of all species in this study (Fiedler & Lloyd, 1995; Parent, Mahoney, & Barkley, 2010), was also the most drought-sensitive.

Although these facts seem at odds with each other, they are a clue to the drought-tolerant strategies utilized in response to drought. In other words, despite showing high levels of drought tolerance, western larch reduces radial growth in response to drought, indicating a strategy of drought avoidance. To avoid drought western larch increases concentrations of protective molecules in response to drought reduce carbon assimilation (Mosca et al., 2012) and western larch displays phenotypic plasticity (Rehfeldt, 1995). Evidence supports that western larch uses a drought-avoidance strategy. For example, western larch shows strong stomatal control based on fluctuating moisture levels (Baker et al., 2019; Kavanagh, Pangle, & Schotzko, 2007) and high phenotypic plasticity to variable environmental conditions (Rehfeldt, 1995). Western larch also showed early leaf senescence during a drought in the summer of 2015 (Baker et al., 2019), adding support that it is avoiding drought through physiological responses and plasticity (McDowell et al., 2008; Moran et al., 2017).

Grand fir is the second most drought-tolerant study species. Contrary to western larch, however, grand fir shows highly variable relationships with drought and demonstrates statistically insignificant growth-drought sensitivity overall. Grand fir even shows strong negative correlations to drought at ten year time intervals, indicating it continues to grow rapidly in drought years. Grand fir may be using an extreme drought avoidance and isohydric strategy. Baker et al. (2019) found grand fir to be the most isohydric during a growing-season drought of 2015, supporting that it may be avoiding drought stress through physiological means. Grand fir also has significantly thicker sapwood than western larch (Running et al., 1975), possibly allowing it to maintain higher water storage within the tree, which may be mobilized to maintain respiration and other plant functions when moisture from the soil is minimal. However, it also has shallow roots and an inability to store water in root and leaf cells (Fowells, 1965) and those facts, coupled with my results that show greater sensitivity to short-term drought in low-density sites, indicates grand fir may be more sensitive to immediate fluctuations in temperature or stand dynamics than western larch (McDowell et al., 2008).

Western redcedar, which has moderate drought-tolerance, does not show strong drought-sensitivity, indicating it may be resistant to drought, and therefore, changes in radial growth are not observed and correlations are weak between efficiency and radial growth (Moran et al., 2017). Studies confirm that western redcedar appears to resist drought through greater

cellular water storage-capacity (Jackson & Spomer, 1979) and low daily stomatal conductance (Baker et al., 2019). Cedar has high cell elasticity, which allows it the ability to resist greater fluctuations in water availability (Jackson & Spomer, 1979). It is also in the *Cupressaceae* family, which is known to resist vascular cavitation in response to drought – a strategy of drought-resistance (Brodribb et al., 2014). Western redcedar is able to survive a variety of stressful conditions as a generalist that shows isohydric responses to drought in the current year (Joseph A Antos et al., 2016; Baker et al., 2019; Korol, 2001) and anisohydric responses to long-term drought. Moreover, although western redcedar also shows high transpiration efficiency while experiencing drought, correlations are weak between efficiency and radial growth (Eilmann et al., 2010; Moran et al., 2017).

It comes as no surprise that western hemlock was highly drought-sensitive, given that it is the least drought-tolerant species in this study (Fiedler & Lloyd, 1995). In other words, western hemlock grows significantly less in drought years, and more in moist years. Western hemlock does not implement as effective of adaptation strategies as the other species. It does, however, demonstrate little control over stomatal conductance (Korol, 2001), have high rates of cavitation (Bond & Kavanagh, 1999), and root shrinkage in response to drought (Ballard & Dosskey, 1985). Western hemlock also has a high likelihood of secondary infections after droughts (Secrest et al., 1941) and the lowest rates of photosynthesis among the species (Korol, 2001), which may exacerbate inhibited growth in drought years.

Climate change: each species is vulnerable in a different way.

The four species in this study show a wide range of responses and strategies depending on forest stand density plus seasonality, length, and intensity of droughts. Drought sensitivity in the drought-avoiders involves a trade-off between limited water availability and competition. Yet, drought sensitivity increases in high-density, competitive sites for drought-resisters. Furthermore, growth limiting factors vary with climate or vary throughout the ontogeny of the investigated conifers. Given the multiple growth-drought responses of mixed-species forests and the future predictions of highly variable episodes of short- and long-term drought in the Pacific Northwest (McDowell et al., 2008), responses of these species to climate change in moist mixed-species forests are difficult to predict. Nonetheless, some general conclusions about future growth responses from the study species are conjectured based on the results.

It is predicted that 27% of all forests in the Western United States are susceptible to moderate or severe snow droughts under future climate change scenarios (Dierauer, Allen, & Whitfield, 2019). Thus, western larch may struggle to maintain high levels of growth into the future, given the sensitivity to winter drought and the utilization of drought-avoidance strategies. However, my results show that western larch does not respond to short-term, high frequency, droughts (< 24 mo), and predictions show greater interannual variability of snow-droughts with climate change (Marshall et al., 2019). This indicates that if drought events are less than two years in length, western larch may survive climate change scenarios, and may even thrive with sufficient intermittent years with abundant snowpack – especially because western larch is the most drought-tolerant in these forests. Grand fir, which shows a general inverse relationship with winter drought, may grow faster in years of snow-drought. However, its avoidance strategy, and high isohydry characteristics may lead to carbon starvation over time.

Summer soil moisture, driven significantly by snowpack and summer temperatures in the region, is expected to decline while evaporative demand increases (Halofsky et al., 2018). Western redcedar, which is sensitive to summer drought, may demonstrate short-term drought tolerance and endure increased evaporative demand in summers. However, reduced growth during and after the Millennial Drought indicates that long-term drought might suppress growth well after soil-moisture recovery (Hoffmann et al., 2018). Nonetheless, western redcedar displays generalist qualities that allow it to withstand many stressors and is likely to thrive in the fertile mixed moist forests of the northern Rocky Mountains in future climate scenarios.

Results from this study, of strong coupling of growth and drought for western hemlock, plus low drought-tolerance and reductions in future summer moisture (Ballard & Dosskey, 1985; Bond & Kavanagh, 1999; Fiedler & Lloyd, 1995; Korol, 2001; Secretst et al., 1941), indicate growth likely declines in years to come. Moreover, the elevated summer droughts and heat may increase susceptibility to pathogens for this thin-barked species, which further reduces productivity (Secretst et al., 1941). Nonetheless, western hemlock is extremely shade-tolerant, and when growth is limited, western hemlock will be relegated to lower canopy classes, which may allow this species to survive future climate change-related droughts (Minore, 1979).

Management for diversity in mixed forests is recommended

Findings from this chapter, together with results from Chapter 1, demonstrate that many interacting factors influence tree growth in the mixed moist coniferous forests of the Northern Rocky Mountains. Therefore, forest management objectives should consider these interacting limiting factors, especially given the predictions of increased drought occurrences, and the strong resource- and density-dependent growth-drought relationships (Carnwath & Nelson, 2016). The goal of sustainability is long practiced by foresters, and recent research shows that sustainability and resiliency increase when forests encompass complex adaptive systems (Lansing, 2003; Levin, 1998; Wu, 2013). Complex adaptive systems are ecosystems with numerous interacting parts that lead to emergent, non-linear relationships, where the heterogeneous communities within the systems support adaptability (Lansing, 2003; Levin, 1998). Emergence and non-linearity are crucial components of complex systems where relationships are ever-changing, and patterns of interactions are multifaceted (Liu et al., 2007). Diversity allows systems to adapt to different pressures while maintaining normal functions (Holland, 1995). Diversity can refer to the number, distribution, age, size, and type of players in a system. Generally speaking, greater diversity of players facilitates adaptation and leads to greater resilience and lower vulnerability in a system (Page, 2010). The mixed coniferous forest of the strip clearcut demonstrates the qualities of complex adaptive systems. Natural regeneration resulted in a high diversity of species (Shen et al., 2019). Thinning to favor shade-tolerant species at different residual densities resulted in numerous complex interactions among growth, drought, and competition. These interacting factors led to non-linear relationships that change substantially over time based on species, climate, and density. Therefore, strip clearcutting in moist forest results in diverse conifer species composition and structure that can be further managed to create complexity through mid-rotation thinning.

Chapter 3: Spatial variability in flow-growth relationships for four Pacific Northwest conifers along geographical gradients

Meghan Foard, Andrew S. Nelson, Grant L. Harley

Abstract

Surface water is among the most important and vulnerable resources in the Pacific Northwest United States (PNW). Observations show that water quantity is declining in streams across the region, while extreme flooding events occur more frequently. Historical streamflow models inform probabilities of floods or water scarcities by describing the frequency and duration of past events. While past dendrochronological streamflow reconstructions in and near the PNW region are accurate and complimentary, detailed information pertaining to the effect of geographical variability on the strength and directions of species-specific flow-growth relationships in the region is unknown. Our research examines the spatial variability and spatial-dependency of flow-growth relationships of four species to natural streamflow across geographical gradients in the PNW. We compiled historical flow data from 115 stream gauges and growth rates from 88 tree-ring chronologies accessed via online databases. We used correlation matrices to evaluate the strengths and directions of the flow-growth relationships, spatial regression models to determine if the flow-growth relationships were spatially-dependent upon geographical gradients, and kriging to predict the flow-growth relationship for spatially-dependent species across the region. Streamflow correlated negatively with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) chronologies, species commonly found at cool, moist, high elevation sites. Drier-site species, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) had chronologies that were positively correlated with flow, though a few had significant negative correlations.

Geographical gradients could explain the variability of the flow-growth relationships for all species except ponderosa pine, although spatial correlations only explained between 24 and 29% of the variability. Subalpine fir, mountain hemlock, and Douglas-fir were spatially-dependent on latitude, elevation, and longitude, respectively. Kriging models accurately interpolate correlations across the PNW. Our results will help simplify planning for field collections and strengthen methodologies for future streamflow reconstructions by supplying

knowledge about which streams, species, elevations, and directions will yield the most robust models in the spatially diverse terrain of the PNW.

Introduction

Recent observations confirm that overall water quantity is declining in streams of the Pacific Northwest United States (PNW) (C H Luce, Abatzoglou, & Holden, 2013; Charles H. Luce & Holden, 2009) These reductions in streamflow, which threaten electricity, drinking water, and critical habitat throughout the region (Adger, Arnell, & Tompkins, 2005; Jager et al., 2018), are significantly influenced by reductions in snowfall (Abatzoglou, 2011; Berghuijs, Woods, & Hrachowitz, 2014). Streamflow models may improve preparedness for extreme flow (flood or drought) events by describing the frequency and duration of past events (Brooks, Ffolliott, & Magner, 2012; Hamlet et al., 2013). Tree-rings have been used to create accurate streamflow models – they have also extended historical records back hundred of years, and are used to predict future streamflow (Edward R Cook & Jacoby, 1983; Ho, Lall, Sun, & Cook, 2017; Ravindranath et al., 2019). While past dendrochronological streamflow reconstructions in and near the PNW region are accurate and complimentary (Table 3.1), detailed information pertaining to the effect of geographical variability on the strength and directions of flow-growth relationships in the region is unknown. Knowledge of geographical variability is crucial in the process of selecting locations where trees are sensitive to the climate variable proposed for reconstruction (Larson, Allen, Flinner, Labarge, & Wilding, 2013), especially given that recent research focuses on accruing new tree-ring site collections in the *International Tree Ring Database* (ITRDB) and choosing which chronologies to update to the current year. This research is also timely in the wake of a rapidly changing climate in locations with high spatial variability.

Table 3. 1. Other streamflow reconstructions within (or near) the Columbia River Basin.
 Note: ABAM = *Abies amabilis*, ABLA = *Abies laciniosa*, JUOC = *Juniperus occidentalis*, JUSC = *Juniperus scopulorum*, LALY = *larix lyallii*, PCEN = *Picea engelmannii*, PIFL = *Pinus flexilis*, PIJE = *Pinus jeffreyi*, PILO = *Pinus longaeva*, PIMO = *Pinus monophyla*, PIPO = *Ponderosa pine*, PSME = *Douglas-fir*, QUDG = *Quercus douglasii*, THPL = *Thuja plicata*, TSME = *Mountain hemlock*

Citation	Location(s)	Tree spp.; Chronology source	Streamflow measurement reconstructed	Relevant findings
Graumlich LJ, Pisaric MFJ, Waggoner LA, et al., (2003)	Yellowstone River	PSME; Southwestern Montana	total water year	- Model explained 35% of the variability
Gedalof ZE, Peterson DL, Mantua NJ (2004)	The Dalles Dam on the lower Columbia River	ABLA, JUOC, LALY, PCEN, PIFL, PIPO, PSME; ITRDB and PDO working group	mean water year	- Model explained 30% variance - Described change in relationship over time
Axelson JN, Sauchyn DJ, Barivich J (2009)	Oldman and South Saskatchewan Rivers, Alberta	PIFL and PSME; ITRDB & Collected from associated watershed	mean winter flow (October – December)	- Models explained 37% variance for Oldman R. and 43% of the S. Saskatchewan R. - Mixed species models
Hart S, Smith DJ, Clague JJ (2010)	Chilko River, British Columbia (from an alluvial fan)	PCEN, TSME; West branch Nostetuko, Oval Glacier	June, July, and June/July discharge	- Correlations were 0.4, 0.12, and 0.52, respectively - Single species models were not as strong as mixed models
Wise (2010)	Upper Snake River at Jackson Lake Dam in Washington	PSME, PIFL; Snake River Headwaters	total water year	- Model explains 62% variance - Mixed species models
Allen EB, Rittenour TM, Derose RJ, et al (2013)	Logan River Utah	JUSC, PSME; Collected within 100 km of Logan River	mean annual flow	- Model explains 48% variance - Rocky Mountain juniper better captured the streamflow signal than <i>Douglas-fir</i>
Coulthard B and Smith D (2016)	Tsable River, British Columbia	ABLA, ABAM; ITRDB	mean summer flow (July – August)	- Model explains 63% variance - Mixed species model using forward stepwise multiple linear regression
Coulthard B, Smith D & Meko D (2016)	Kanaka, Chemainus, Tsable & Zeballos Rivers, British Columbia	TSME	mean summer flow (July – August)	- Models explains 64% variance - Reconstruction via stepwise regression - Used reconstructed PDSI, in addition to tree growth, to reconstruct streamflow
Littell JS, Pederson GT, Gray ST, et al (2016)	The Dalles Dam on the lower Columbia River	ABAM, JUOC, LALY, PCEN, PIFL, PIJE, PILO, PIMO, PIPO, PSME, QUDG, THPL, TSME; ITRDB & Collected in CRB	mean annual flow	- 59% variance explained back to 1600CE - 82 chronologies were significantly correlated

Climate and streamflow variability in the Pacific Northwest

The PNW, defined here the states of Washington, Oregon, and Idaho, has highly complex and rugged topography. Glacial mountains occur in the western Cascade Range, while eastern Washington and Oregon are dry intermountain steppe grasslands. This spatial heterogeneity results in stark variation in local climates based on slope, aspect, longitude, latitude, and elevation (Fagre et al., 2003; Mock, 1996). Longitudinally, the climate is more xeric in the east and more hydric in the west. Most precipitation falls in the winter from large maritime frontal systems. These westerly fronts deposit vast amounts of precipitation west of the Cascade crest – leading to rainforests on the Olympic Peninsula that receives at least 6000 mm of annual water equivalent on the top of Mount Olympus (Halofsky et al., 2012). The coastal weather systems move east, where most of the remaining moisture descends in the highest elevations of the Cascade Mountains (Mock 1996). The intermountain west follows on the leeward side of the Cascades and receives little precipitation. The intermountain west has a more continental climate (dry with highly variable temperature fluctuations) and consists of deserts, steppes, and grasslands. East of the intermountain region is the western side of the Northern Rocky Mountains in central and northern Idaho, where total precipitation surges once again as elevation increases to the crest of the Rocky Mountains. Latitudinally, temperatures are generally colder in the north. Moisture also increases slightly from south to north, except for the intermountain zone in central Washington. Like all mountainous landscapes, precipitation increases and temperature decreases with ascending elevation. For example, Mount Rainier can have differences in temperature of up to 27 °C and differences in precipitation of up to 640 mm from the base to the 4367 m summit (Hemstrom, 1983). The streams in the PNW are also highly variable, with low order (headwater) streams functioning as primary sediment transports to higher-order streams that extend into adjacent floodplains (Naiman et al., 1992). The lower order streams have reduced flow, sinuosity, and erosion compared to larger rivers (Brooks et al., 2012) which impacts higher order streams. The diversity of hydrologic and geographic variables across the region creates distinctive localized climates with differing limiting factors on tree growth.

Tree growth variability in the Pacific Northwest.

Due to the complex terrain and the highly variable biophysical environments of the PNW, flow-growth models likely differ across geographical gradients. This variability may, in turn, affect the accuracy and applicability of streamflow models (Brubaker, 1980). For example, little is known about localized flow variability, and tree rings may uncover differential regional vs. local signals. Indeed, growth-climate relationships do vary geographically, and this phenomenon, termed a mixed-response (Brubaker, 1980), is evident in the literature. In the Cascade Mountains, Douglas-fir (*Pseudotsuga menziesii* (Merb.) Franco) showed contrasting responses to annual temperature depending on elevation – with higher elevation trees being positively correlated (M. J. Case & Peterson, 2005). Douglas-fir growth was also found to be more sensitive to winter precipitation at lower elevations and summer precipitation at higher elevations (Martin, Looker, Hoyleman, Jencso, & Hu, 2018). Brubaker (1980) found that Douglas-fir showed negative responses to precipitation west of the Cascades and positive correlations to the east. Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is more correlated with precipitation inland than on coastal sites (McCullough, Davis, & Williams, 2017). In British Columbia and the Yukon, white spruce (*Picea glauca* (Moench) Voss), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) all showed spatially-dependent relationships (Miyamoto, Griesbauer, & Scott Green, 2010). Subalpine fir also showed four distinct growth signals across the Olympic and Cascade Mountains (Peterson, Peterson, & Ettl, 2002). These variations in growth and growth-climate relationships between species along mountainous geographical gradients support the notion that flow-growth relationships will also vary spatially across the PNW landscape.

The literature also supports that flow-growth relationships differ among tree species, and these species-specific responses may lend themselves more favorably for streamflow reconstructions for some species over others. For example, *Pinus flexilis* James (limber pine) showed significant positive correlations with streamflow across the Canadian plains (R. A. Case & MacDonald, 2003). Littell et al. (2016) found that all subalpine larch (*Larix lyalii* Parl.) and Pacific silver fir (*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes) chronologies were negatively correlated with streamflow at the Dalles Dam on the Columbia River, while Douglas-fir and ponderosa pine exhibited positive relationships to streamflow in

91% of the chronologies sampled. Gedalof et al., (2004) found negative correlations for all Engelmann spruce (*Picea engelmannii* Parry ex Engelm) and subalpine fir, while all the significant correlations between streamflow and ponderosa pine were positive. These differential flow-growth relationships among species indicate that some species better represent streamflow variability than others. Indeed, in the Logan River of northeastern Utah, Allen et al. (2013) found that Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) better captured the streamflow signal than Douglas-fir. Conversely, Hart et al. (2010) found that models that combined Engelman spruce and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) were stronger than single-species models. Regardless of the direction of the relationship, species that show stronger correlations with streamflow will perform better in streamflow reconstructions.

Our investigation characterizes the flow-growth relationships of four common coniferous species in the PNW, subalpine fir, mountain hemlock, Douglas-fir, and ponderosa pine, to natural streams (Figure 1). We chose these species because they occur in different environments (subalpine fir and mountain hemlock at higher elevation with greater precipitation and lower temperature; Douglas-fir and ponderosa pine at lower elevation with higher temperature and lower moisture) and because they are abundant species in the PNW. We also identify spatial-dependencies of flow-growth relationships along four geographical gradients – latitude, longitude, elevation, and watershed area. Our research will aid in planning methodologies for future streamflow models by supplying knowledge about which free-flowing streams, species, elevations, and directions will yield the most robust models in the spatially complex terrain of the PNW.

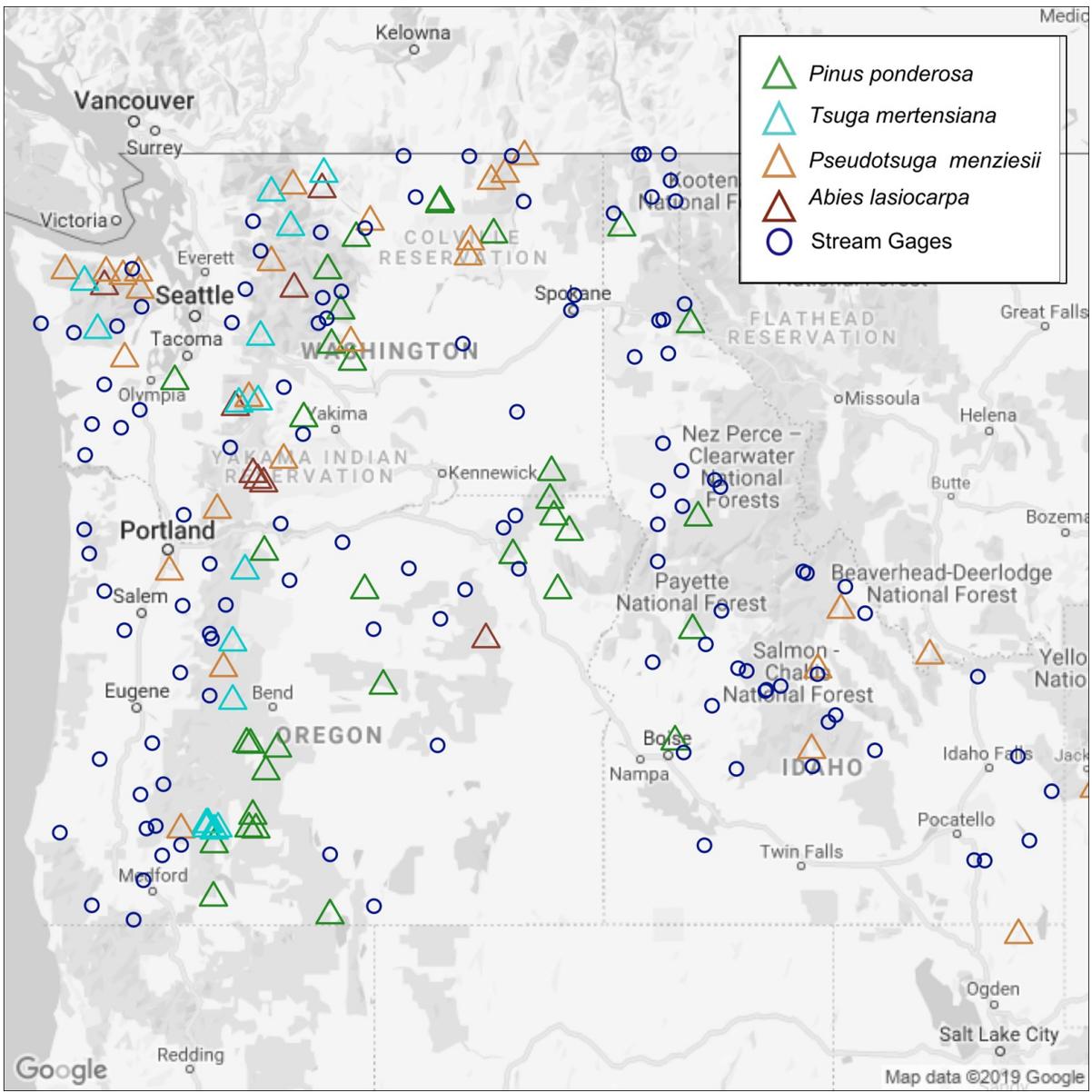


Figure 3. 1. Map of trees and streams across the Pacific Northwest study region. Note: Trees are represented by triangles and stream are circles; there are three states included in this study: Idaho, Oregon, and Washington. *Abies lasiocarpa* = subalpine fir, *Pinus ponderosa* = Ponderosa pine, *Pseudotsuga menzeissii* = Douglas-fir, *Tsuga mertensiana* = Mountain hemlock

Methods

We interpolated the correlation coefficients of spatially dependent flow-growth relationships across the PNW via a series of correlative and spatial statistical techniques. A workflow diagram for the statistical methods implemented in this study is presented in figure 3.1.

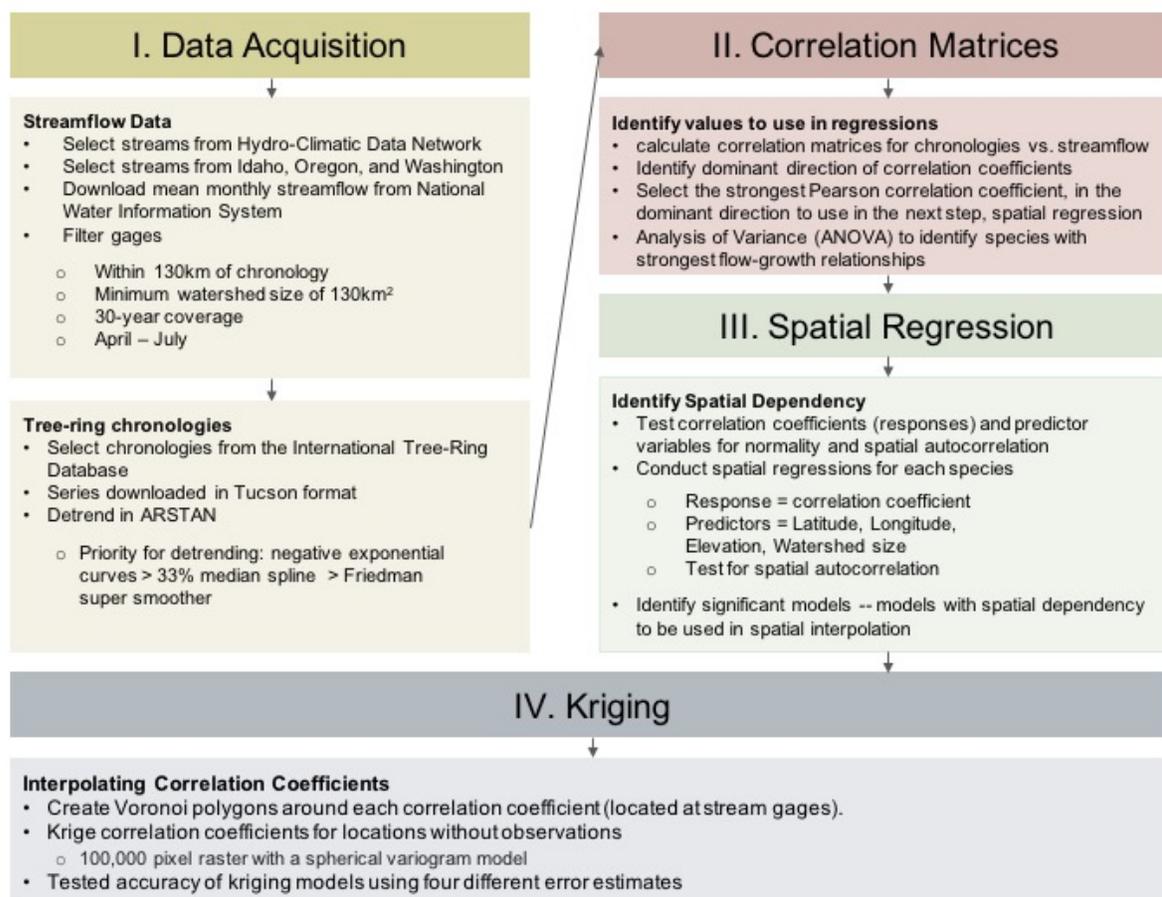


Figure 3. 2. Workflow diagram of statistical methods.

Streamflow Data

Anthropogenic alterations in streamflow such as river channelization or dams might affect the strength of the flow-growth signal (Foard, Burnette, Burge, & Marsico, 2016; Stockton & Jacoby, 1976). Therefore, we attempted to minimize this effect by selecting streams with limited hydrologic alterations from the Hydroclimatic Data Network (HCDN). The HCDN contains a list of United States Geologic Survey (USGS) streamflow gauges with minimal influence of anthropogenic alterations that are used to study climate fluctuations

(Slack & Landwehr, 1992). Stream gauges selected for the HCDN were required to have (a) volumetric flow data available electronically, (b) at least 20 consecutive years of unimpaired recorded flow, and (c) an accuracy rating from the USGS district office of “good” or better. We selected all stream gauges in Idaho, Oregon, and Washington from HCDN, and we downloaded annual, monthly means from the National Water Information System website (US Geological Survey 2019).

We filtered the streams to (a) have a drainage area of at least 129 km², (b) be located within 129 km of a tree-ring chronology source, and (c) have a temporal coverage of at least 20 consecutive years (Figure 1). Streams were filtered using the tidyverse package in R (Wickham et al., 2019). We selected minimum drainage areas to avoid insignificant microclimate signals and flashy hydrographs. Streams were selected to be within at least 129 km to reduce overlap and to ensure the variance of the chronologies represented the climate that locally and directly influences streamflow variability (Wiens, 1989). Distance calculations were completed using the sp package in R (R. S. Bivand, Pebesma, & Gómez-Rubio, 2013; E. Pebesma & Bivand, 2005). Spring snowmelt has a significant influence on overall streamflow in this region (Appleton & St. George, 2018; Leung, Hamlet, Lettenmaier, & Kumar, 1999), and streamflow is positively correlated to snowpack and snowfall (Mote, Hamlet, Clark, & Lettenmaier, 2005); therefore, we also filtered flow for the months April thru July which are known to capture the snowpack signal in the region (Stewart, Cayan, & Dettinger, 2004).

Tree ring chronologies

We downloaded all tree ring-width series from the International Tree Ring Databank (ITRDB; International Tree-Ring Data Bank, 2019). We selected subalpine fir, mountain hemlock, Douglas-fir, and ponderosa pine because they were the most common species in the database, they grow in dissimilar hydroclimates, and they are also sensitive to hydroclimate signals (Peterson et al. 2002; Biondi 2000; Marcinkowski et al. 2015a; Pettit et al. 2018). Raw ring width measurements for all series at 191 locations were downloaded in Tucson format (Stokes & Smiley, 1968). Due to a lack of chronologies in eastern Idaho, we also included chronologies within 129 km of any stream gauge in eastern Idaho. As a result, we added three chronologies (one from Montana, Utah, and Wyoming each). Each series was detrended interactively to avoid negative fit lines using ARSTAN (Edward Roger Cook,

1985). Because trees in the ITDB are at least 100 years old, we assigned priority for detrending starting with negative exponential curves. If there was a negative fit, then a 33% median smoothing spline was selected, and if there was still a negative fit, we used the Friedman super smoother. We analyzed the ARSTAN chronologies because they are sensitive to the high-frequency variability present in PNW streamflow.

Correlation matrices

To capture the signal of the spring pulse onset due to snowmelt, and to control for variations in the timing of the snowmelt signal, we correlated the months of April, May, June, and July to tree growth (Stewart et al., 2004). We calculated correlation matrices for all tree chronologies vs. streamflow from the selected months. Then we calculated the mean correlation coefficient for all trees within 129 km of each stream gauge in order to identify the dominant direction of the relationship. For example, if the mean relationship among all trees of a species for each gage was negative, then the dominant direction was identified as negative. Next, we selected the strongest Pearson correlation coefficient, in the dominant direction, from each stream-tree combination to use in the spatial analyses. Analysis of variance (ANOVA) was then used to assess whether there was any significant difference in the strengths of the flow-growth relationships among species on the correlation coefficients. ARSTAN chronologies remove autocorrelation but reintroduce the variability that is common among all series. Tree competition for limiting factors is higher in closed forests.

Regression of geographical variables

We investigated the correlations between geographical predictors and flow-growth correlation coefficients as an exploratory analysis to determine whether spatial interpolations are appropriate. After testing the data for normality and spatial autocorrelation, we determined geographically weighted regressions would best inform geographic dependency. Two species were not normally distributed according to the Shapiro-Wilk test for normality ($p < 0.05$) so we used log-transformed correlation coefficients for spatial regressions (Figure 3.3). To investigate spatial autocorrelation, we used a Moran's I test with eight nearest neighbors because not all observations are evenly spaced for all species (ESRI, 2019). Moran's I tests support that spatial regressions are appropriate because the dependent and independent variables are spatially autocorrelated. For the spatial regression, we used the `gwr()` function from the `spgwr` package in `r`, and to determine the most robust bandwidths, we

used the `gwr.sel()` function (R. Bivand & Yu, 2020). The geographic predictors tested included latitude, longitude, elevation, and size of watershed. We removed all non-significant predictors from the models, then removed co-linear variables to include the most significant predictor(s) for each species model. Ultimately, all multiple regressions reduced to simple models with only one significant independent predictor variable. To visualize the relationships of correlation coefficients along geographical gradients, we illustrated a scatterplot with a smoothing spline (Figure 4). Significant correlations between flow-growth variability and geographical variables indicate that there is a spatial-dependency of flow-growth responses, and this dependency is present in three species. Only the spatially-dependent species were used in spatial interpolations of flow-growth relationships because the interpolation process requires some level of spatial dependency to be useful and accurate (Lam, 1983).

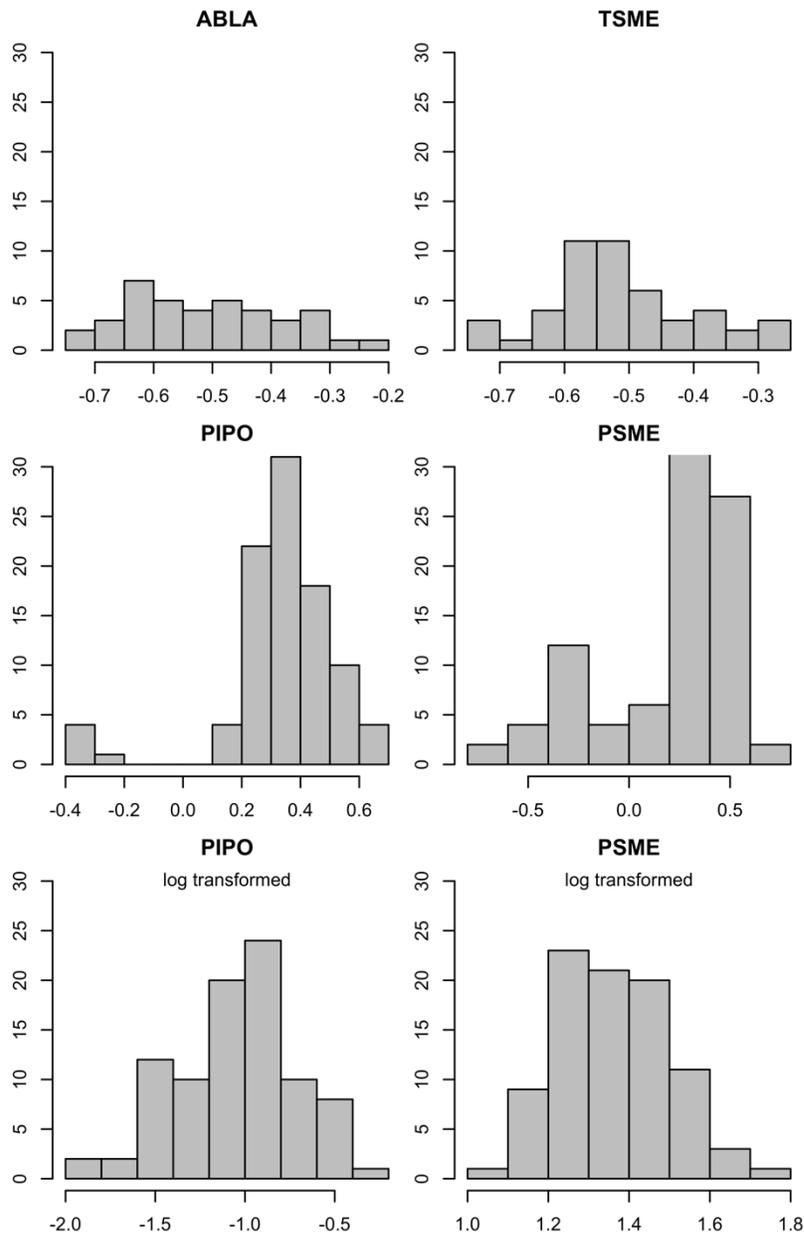


Figure 3.3. Histogram of frequency distributions for species-specific correlation coefficients for flow-growth relationships, plus the log-transformed histograms for species not normally distributed. Note: ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock; x-axes differ.

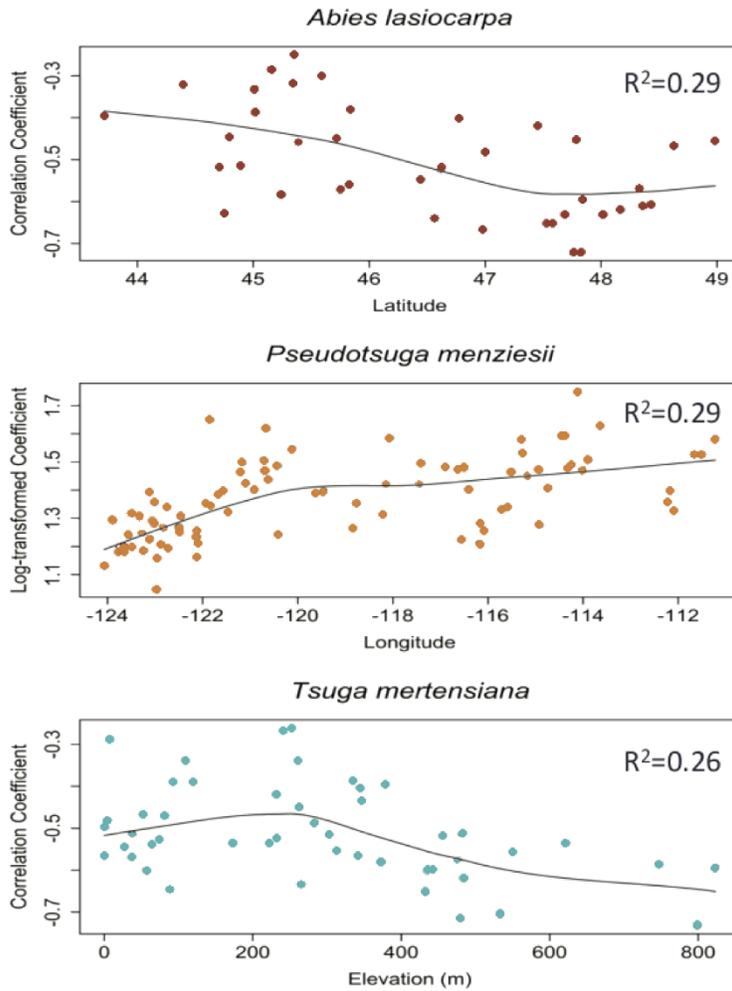


Figure 3. 4. Scatterplot of flow-growth correlation coefficients vs. significant geographic predictors. Note: Only includes species with significant spatial dependence. smoothing splines are calculated by loess for each relationship; latitude and longitude are in decimal degrees and elevation is in meters. *Abies lasiocarpa* = subalpine fir, *Pinus ponderosa* = Ponderosa pine, *Pseudotsuga menzeissii* = Douglas-fir, *Tsuga mertensiana* = Mountain hemlock

Spatial interpolations

We used Kriging to interpolate flow-growth correlation coefficients for spatially-dependent species using the `gstat` package in R (Gräler, Pebesma, & Heuvelink, 2016; E. J. Pebesma, 2004). Although spatial dependence only explained 25%, 17%, and 29% of the variability for subalpine fir, Douglas-fir, and mountain hemlock, respectively, all relationships were significant and suitable for kriging. First, we created Voronoi polygons for stream gauges using the “`voronoi`polygons” function from Brunson and Comber (2015), which creates a polygon around every point observation to ensure that all area within the polygon is nearer to that observation than to other observations (Miles & Maillardet, 1982). We then estimated the correlation coefficients for 100,000 pixels using the ordinary Kriging method, and spherical variogram model. We used Kriging instead of other interpolation methods because it has a lower error than other interpolation methods, it accounts for spatial autocorrelation of observations, and it accounts for the variability of interpolated values (Zimmerman, Pavlik, Ruggles, & Armstrong, 1999). We interpolated filled-contour maps that span the latitudinal and longitudinal ranges of the stream gauges for each tree species. Maps were then restricted to state boundaries in R. We calculated error of kriging models using four different error terms, mean error (ME), mean absolute error (MAE), root mean square error (RMSE), and the correlation coefficient between predicted and observed values (Ponce-hernandez, 2006). Mean error (ME) is a biased estimate that measures the accuracy of the kriging. Mean absolute error is the average absolute measure of the errors in the model. Root mean square error is a measure of the precision of error terms. Together these estimates will help determine the strength of each model. Low error terms with high correlations represent robust models. Three metrics are defined by the following equations:

$$\text{ME} = \frac{1}{n} \sum_{i=1}^n \hat{Z}(x_i) - Z(x_i)$$

$$\text{MAE} = \frac{1}{n} \sum_{i=1}^n |\hat{Z}(x_i) - Z(x_i)|$$

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{Z}(x_i) - Z(x_i))^2}$$

Where $\hat{Z}(x_i)$ is the estimated correlation coefficient at location x_i and $Z(x_i)$ is the observation at location x_i and n is the sample size. Pearson correlation coefficients were calculated with traditional methods (Bolboaca and Jäntschi, 2006).

Results

We analyzed data from a total of 177 stream-gauge flow records (Appendix A) and 195 tree-ring chronologies (Appendix B) in this study. After trees and streams were filtered, a total of 88 tree chronologies remained for spatial interpolations of streamflow from 115 gauges across the PNW (Figure 3.1, Appendix C). There were 46 streams from Idaho, 35 from Oregon, and 34 from Washington. There were 30, 61, 50, and 54 subalpine fir, ponderosa pine, Douglas-fir, and mountain hemlock chronologies used in correlation analyses, respectively. Idaho was the only state that did not have any tree chronologies from subalpine fir and mountain hemlock. The breakdown of the number of streams gauges and chronologies for each species, by state, is in Table 3.2.

The four species differed in their distribution of correlation coefficients (Figure 3.3, Figure A.1). Subalpine fir and mountain hemlock exhibited a normal distribution of observations, the majority of which were negative correlations. Ponderosa pine and Douglas-fir both had slightly bimodal distributions, but in general, were left-skewed towards a greater number of positive observations. The mean correlation coefficient for subalpine fir was -0.51 and ranged from -0.72 to -0.25. The mean correlation coefficient for mountain hemlock was -0.45 and ranged -0.73 to -0.26. The mean correlation coefficient for ponderosa pine and Douglas-fir was 0.33 (range -0.40 to +0.70) and 0.21 (range -0.65 to +0.75), respectively. The species with the greatest range were Douglas-fir (1.4) and ponderosa pine (1.1) The range for subalpine fir and mountain hemlock was the same at is 0.47. Analysis of variance on the absolute values revealed that subalpine fir and mountain hemlock flow-growth correlations are significantly stronger than ponderosa pine and Douglas-fir ($F = 24.72(3,266)$, $p < 0.001$) though they are not different from each other ($p = 0.99$). Subalpine fir and mountain hemlock correlations were greater than ponderosa pine and Douglas-fir by an average of 0.14 and 0.15, respectively. For all species, the month of July had the strongest flow-growth correlation coefficients (Figure 3.5, $n = 152$). April ($n = 44$) and May ($n = 41$) were the next most significantly correlated months, while the fewest correlations were in June ($n = 33$; Table 3.3).

Table 3. 2. Number of streams gauges and chronologies for each species, by state. Note: Many streams correlated with multiple species (and vice versa), thus, the sum of the observations does not total the actual number of stream gauges used in this study; ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock

	Idaho		Oregon				Washington			
<i>SPECIES</i>	<i>PIPO</i>	<i>PSME</i>	<i>ABLA</i>	<i>PIPO</i>	<i>PSME</i>	<i>TSME</i>	<i>ABLA</i>	<i>PIPO</i>	<i>PSME</i>	<i>TSME</i>
NUMBER OF STREAMS	34	28	17	27	25	21	23	33	33	27
NUMBER OF CHRONOLOGIES	12	7	4	13	4	4	4	9	14	5

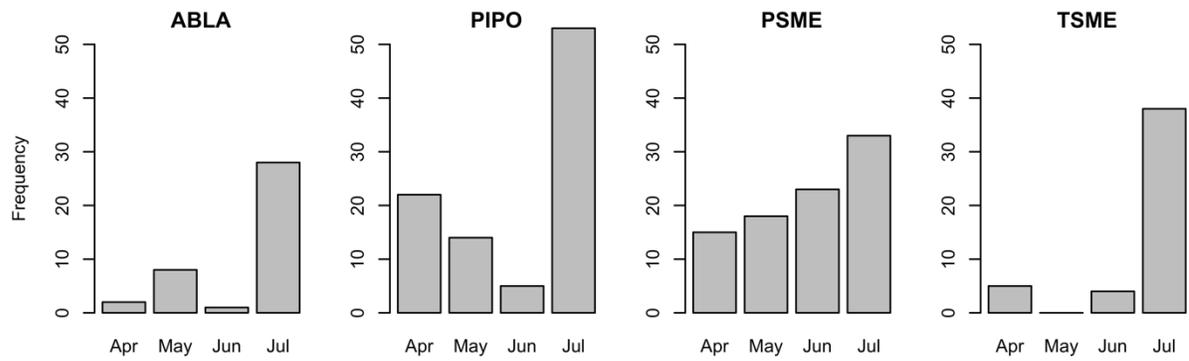


Figure 3. 5. Bar plots of frequency of strongest correlated months for flow growth relationships. ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock

Table 3. 3. Frequency of months with strongest flow-growth correlations for each species. Note: ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock

	April	July	June	May
ABLA	2	28	1	8
PIPO	22	53	5	14
PSME	15	33	23	18
TSME	5	38	4	1

Table 3. 4. Results from Moran's I test for each variable in geographically weighted regressions. Note: All variables are spatially autocorrelated as signified by *p*-values and Moran I statistics; Numbers after variable names show in which model each variable was included; Asterisks after variable names indicate the predictor variables.

VARIABLE	Moran I Statistic	Moran SD	Variance	<i>P</i>-value
ABLA¹	0.37	6.14	4.26e-03	8.54e-10
LATITUDE^{1*}	0.74	11.78	4.26e-03	2.20e-16
PSME²	0.33	7.24	2.20e-03	4.39e-13
LONGITUDE^{2*}	0.93	20.09	2.20e-03	2.20e-16
TSME³	0.15	2.34	5.15e-03	1.94e-02
ELEVATION^{3*}	0.37	5.50	5.16e-03	3.85e-08

Table 3. 5. Results of correlation matrices and geographically weighted regressions. Note: geographically weighted regression models are reported only for species with spatial-dependency; Cor. Coefficient = correlation coefficient; ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock

	Geographical Correlation	Mean Cor. Coefficient	R-Squared	P-Value	F-Statistic	Bandwidth
ABLA	Latitude	-0.51	0.29	$4.52e^{-4}$	14.83 _(1, 37)	8.36
PIPO	None	0.33	-	-	-	-
PSME_{LOG}	Longitude	0.21	0.29	$4.80 e^{-8}$	35.77 _(1,87)	0.91
TSME	Elevation	-0.45	0.26	$4.11e^{-3}$	9.12 _(1, 46)	1.93

There was significant autocorrelation for all variables used in spatial regressions (Table 3.4). Spatial regressions show significant spatial dependence (i.e., correlation with geographic variables) in flow-growth relationships for all species except ponderosa pine (Table 3.5). However, the flow-growth relationships of each species correlated with different geographical variables. Latitude significantly correlated with subalpine fir flow-growth ($F = 14.83(1,37)$, $p < 0.001$), where it explained 29% of the variability. The flow-growth relationship of Douglas-fir correlated significantly with longitude ($F = 35.77(1,87)$, $p < 0.001$), which also explains 29% of the overall variability. The Douglas-fir and longitude relationship exhibited the most significant spatial-dependency among species and spatial variables. Flow-growth correlations were significantly positive in the lower longitudes in the east, and significantly negative in the west. Additionally, all flow-growth relationships between Douglas-fir and longitude were positive east of -117.00 DD (based on the World Geodetic System 1984 geographic coordinate system), where the western piedmont region of the Northern Rocky Mountains begins. Elevation correlated significantly with mountain hemlock flow-growth relationship (i.e. as the stream gauge ascended in elevation, the flow-growth relationship strengthened) ($F = 9.12(1,46)$, $p = 0.006$), and it explained 26% of the variability. Moreover, there is greater variability of flow-growth correlation coefficients in elevations lower than 305 m. The spatial interpolations of the flow-growth correlation coefficients confirm the results of the regression analyses (Figure 3.6), that subalpine fir correlation was stronger farther north, Douglas-fir was more positively correlated farther east, and mountain hemlock correlation was stronger with increasing elevation. Error estimates for the kriging support that models were robust (Table 3.6). The subalpine fir model was the strongest based on having the lowest error and the highest correlation coefficients. The weakest kriging model was for mountain hemlock.

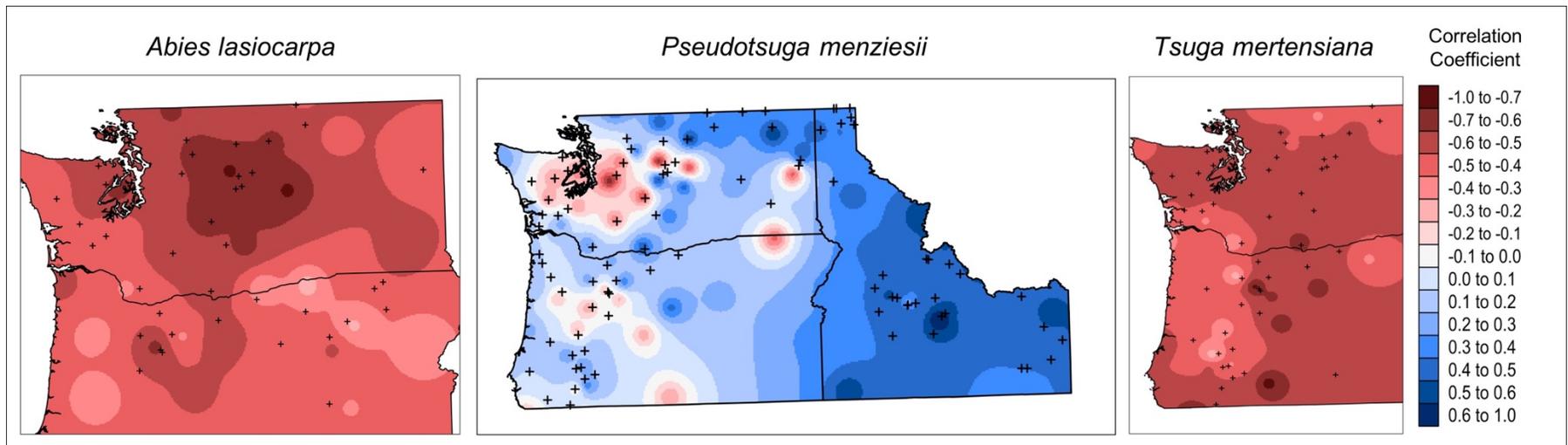


Figure 3. 6. Kriging of correlation coefficients of flow-growth relationships across PNW. Note: Surfaces are only interpolated for species with spatially dependent relationships; black crosses represent the stream gauge locations. *Abies lasiocarpa* = subalpine fir, *Pinus ponderosa* = Ponderosa pine, *Pseudotsuga menzeissii* = Douglas-fir, *Tsuga mertensiana* = Mountain hemlock

Table 3. 6. Error estimates for the kriging models for each species. Note: ME is mean error, MAE is mean absolute error, RMSE is root mean square error, and Corr is the correlation coefficient between predicted and observed values. ABLA = Subalpine fir, PIPO = Ponderosa pine, PSME = Douglas-fir, TSME = Mountain hemlock

	ME	MAE	RMSE	Corr
Subalpine fir	-0.016	0.047	0.066	0.89
Douglas-fir	-0.014	0.128	0.177	0.85
Mountain hemlock	0.0008	0.044	0.068	0.81

Discussion

Scientists have previously described flow-growth relationships between tree-ring chronologies and stream gages for multiple rivers and tree species around the world. However, the effect of geographical gradients on the strength and directions of species-specific flow-growth relationships in the region is unknown. The PNW of the United States is a unique region to study these effects because precipitation and temperature have sharp seasonal fluctuations that are modified by topographic gradients, and there are multiple tributaries to larger rivers fed primarily by snowmelt. Models of streamflow are invaluable in this region because many social-ecological systems depend on surface flow as the main water supply. Our results show that species occurring in high elevation, high moisture and low-temperature environments, such as subalpine fir and mountain hemlock, show strong negative correlations between tree growth and streamflow and a high potential for accurate streamflow models. The high-elevation species also have a small range of correlation coefficients, indicating that they are likely more sensitive to severe environmental variation like those experienced with climate change. In contrast, Douglas-fir and ponderosa pine, which typically occur on drier and warmer sites, exhibit mostly positive flow-growth relationships. They also show larger ranges in flow-growth responses, indicating that they are species with high adaptive capacity. Geographic location in terms of latitude, longitude, and elevation influence flow-growth relationships across the region for all species except the ubiquitously distributed ponderosa pine.

Flow-growth variability of high elevation species

The strong negative flow-growth relationships and small ranges of variability of the alpine mountain species suggest amplified streamflow sensitivity and confirm that subalpine fir and mountain hemlock are suitable for streamflow reconstructions in the PNW. These species are both sensitive to snowpack and interconnected variables such as snow-water

equivalent (SWE) and winter precipitation (Nakawatase & Peterson, 2006; Peterson & Peterson, 2001). Likewise, the growth of these two species is highly correlated (Larocque & Smith, 2005), which is possibly because they are adapted to similar environments and share the same limiting factors. Subalpine fir is more broadly distributed across the region and may be a better surrogate for future flow-growth reconstructions than mountain hemlock, though both are strong candidates. The negative correlations between flow and growth also suggest that the growth of these species may increase in future climate change scenarios, which predict reduced snowpack.

Latitudinal-dependency of flow-growth relationships of subalpine fir

The flow-growth relationship of subalpine fir correlates significantly with latitude – the farther north, the stronger the flow-growth relationship. Subalpine fir chronologies show the highest potential to predict streamflow in the Cascade Mountains, specifically, on the east side of the Cascade Mountains in northern Washington (Figure 3.6). The strong negative flow-growth correlation is likely a result of the shortened growing seasons in high water (deep snowpack with extended melt) years. When the snowpack is high, snowmelt extends over a longer time period resulting in higher streamflow. However, the deep snowpack can delay the onset of the growing season, thus shortening the window for growth. Multiple studies confirm that indicators of snowpack correlate stronger with subalpine fir growth; and in all cases, the relationship is inverse (Larocque & Smith, 2005; Nakawatase & Peterson, 2006; Peterson et al., 2002). Subalpine fir growth correlates negatively with growing season temperature in the north, but positive in the south of the study area (Miyamoto et al., 2010); lending additional evidence that length of the growing season is a growth-limiting factor of subalpine fir growth – where longer days with high temperatures result in summer drought sensitivity. These findings also indicate that subalpine fir is highly sensitive to climate fluctuations and water availability.

Colder annual temperatures associated with latitude mediate flow-growth responses; however, the temperature difference in higher elevations does not influence the flow-growth relationships of subalpine fir. The findings are similar to Peterson et al. (2002), who found that adiabatic temperature changes did not influence growth patterns. The lack of response to temperature changes in high elevation, but a significant correlation with latitude may be a result of longer photoperiods in the north. Peterson et al. (2002) found that when there is little

winter precipitation, summer temperatures are negatively correlated with growth (Peterson et al., 2002). Those findings indicate that while these trees need a long growing season, they do not thrive in warm, extended sunny conditions that lead to low soil moisture. In years where snow melts early, the growing season extends, but in the north, the days are longer, leading to potentially warmer days and more extended periods of radiative soil drying. This extended daytime warming in the north vs. at high elevations helps explain why we do not see an effect of elevation on flow-growth relationships. Higher elevations still have the same day length as lower elevations resulting in similar radiative, warming, and drying periods for all locations at the same latitude. In brief, the results signify that streamflow models with subalpine-fir will strengthen in temperature limiting environments with long summer photoperiods.

Elevational-dependency of flow-growth relationships of mountain hemlock

Like subalpine fir, mountain hemlock correlates negatively with streamflow, snowpack, and climate indicators of winter snowpack (Appleton & St. George, 2018; Gedalof & Smith, 2001; Littell et al., 2016; Marcinkowski & Peterson, 2015; Peterson & Peterson, 2001; Wise, 2010). Moreover, the growth of subalpine fir and mountain hemlock correlate with each other (Larocque & Smith, 2005), showing that both species are likely sensitive to shorter growing seasons that result from prolonged spring snowpack. Nevertheless, the flow-growth relationship of mountain hemlock is not correlated with latitude like subalpine fir but is instead mediated by elevation – as elevation increases, the relationship becomes more negative. This elevational relationship indicates that there is a stronger sensitivity to moisture-limiting environments for mountain hemlock than for subalpine fir. Mountain hemlock is known for thriving in some of the coldest and wettest conditions (Cooper, Neiman, & Roberts, 1991). In other words, mountain hemlock grows in places where there is little to no competition from other trees (Minore, 1979). Adaptations to extreme conditions give this species an advantage over other species that might otherwise be more competitive in more energy-rich environments (Evans, Warren, & Gaston, 2005). However, the inverse sensitivity to wet and cold suggests that mountain hemlock would grow substantially more in warmer and drier conditions.

Climate change and high-elevation species

Our results show that climate change may have varying effects on the growth of the alpine species subalpine fir and mountain hemlock. Alpine species do not grow until conditions in the spring are warm enough, and this synchrony of the spring snowmelt with growth onset has variable implications in relation to climate change. Hydrologists predict that high emissions climate scenarios result in increased snow droughts, and the timing of maximum snow water equivalent will vary more than it did historically (Marshall et al., 2019). Consequently, these consecutive years with little snowpack will result in greater growth and potential range expansion temporarily, but may lead to changes in growth-climate responses where growth limiting factors switch from snowpack to temperature (Marcinkowski et al., 2015). Low snowpack and/or early snowmelt would deplete soil water content, and late summer drought would reduce latewood growth. Another response to future climate change might be repressed growth or even death in places where more precipitation will fall as rain (C. D. Allen et al., 2010). This is because snow acts as an insulating barrier for the ground in the winter and prevents serious frost damage (Hardy et al., 2001). When there is little to no snowpack, the ground temperature may decline to well below freezing and the growth of alpine species might be inhibited.

Douglas-fir and longitude

We found that longitude mediates the flow-growth relationship of Douglas-fir – correlations are significantly positive further east and negative in the west. Brubaker (1980) also found that Douglas-fir showed negative responses to precipitation west of the Cascades with correlations switching to positive in the east. We did not observe an elevational dependency of flow-growth relationships in the PNW, even though elevation was found to mediate the use of winter precipitation by Douglas-fir in the Northern Rockies (Martin et al., 2018). The strong correlation of flow-growth relationships along a longitudinal gradient is likely because the eastern region of the PNW is moisture-limited while the western coast gets more frequent and higher quantities of precipitation throughout the year – where high streamflow years are correlated with hydrometeorological data that limit growth in the west and promote growth in the east (Peel, Finlayson, & McMahon, 2007). Douglas-fir is well-adapted to hydric conditions – especially coastal Douglas-fir, a subspecies that lives along the Pacific coast. This species has shallow roots (Minore, 1979), which increases survival in

anaerobic soils resulting from hydric conditions (Jackson & Spomer, 1979). Though the rooting depths of inland Douglas fir are a bit deeper in the drier conditions of the east, they are still quite shallow and thus cannot access water from the water table (Jackson & Spomer, 1979), or bedrock (Zwieniecki & Newton, 1996) during xeric conditions. Thus, regardless of subspecies, Douglas-fir are dependent on surface flow, and in water-limited areas, this dependency strengthens, which is likely why we see stronger and more positive flow-growth relationships in eastern PNW. Thus, the driest locations to the east of the Cascades would be ideal sampling sites for PNW streamflow reconstruction using Douglas-fir.

Ponderosa pine flow-growth relationship is not spatially dependent

Like Douglas-fir, ponderosa pine shows correlations that are mostly positive with streamflow also the direction and strength of the relationship varies across the region. Unlike Douglas-fir, flow-growth relationships of ponderosa pine are not spatially dependent on longitude, and in fact, flow-growth relationships do not correlate with any geographical variables tested in this study. This lack of spatial dependence is possibly due to the broad geographic distribution of this species – from moderate to arid site conditions. The extended geographic range indicates that spatially dependent variables do not limit growth. Also, the lack of spatial dependency of the flow-growth relationship of ponderosa pine may be due to superior drought adaptations. Ponderosa pine has much longer roots than Douglas-fir in the drier locations of the eastern PNW. The roots of ponderosa pine can access the water table, and it relies less on surface water than Douglas-fir (Jackson & Spomer, 1979). This lack of dependence on surface water indicates that ponderosa pine might not be the best species for streamflow reconstructions despite that it is known to be correlated with other hydroclimate variables in the PNW such as drought (Pettit et al., 2018), precipitation, vapor pressure deficit (McCullough et al., 2017), and moisture-delivering storms (Wise & Dannenberg, 2017).

Chapter 4: Climate change knowledge and gaps in mountainous headwaters: spatial and topical distribution of research in the Columbia River Basin

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Abstract

Climate change is altering mountainous headwaters and the biophysical and social systems that depend on them. While scientific knowledge on climate change abounds, literature syntheses are needed to understand the multidisciplinary impacts, identify critical knowledge gaps, and assess potential management and policy responses. In this study, we systematically map and analyze the topical and spatial distribution of climate change research in the mountainous headwaters of a major transboundary watershed, the Columbia River Basin (CRB). We find that climate change research in the CRB focuses on impacts much more frequently than adaptation, while mitigation is rarely a focus. Most studies assess trends at large spatial extents, use secondary data, and make projections of climate change impacts rather than observations. The spatial distribution and thematic content of research varies across an international border, with greater concentrations of research in the United States than Canada. A general scarcity of social science research and limited interaction between social and biophysical content reinforce the need for increased collaboration between disparate disciplines. Future research focus areas should include research related to climate change adaptation and mitigation, increased integration between social and biophysical sciences, and collaborations that bridge the international border for a more unified basin-wide focus. Focusing on these new directions for research will increase the potential for science and management communities to co-produce actionable science and effective responses to climate change.

Introduction

Study Context

Climate change in mountainous regions is projected to have serious consequences for social and ecological systems due to impacts on snowpack and hydrological dynamics, fire

regimes, biodiversity, and ecosystem function, many of which are already occurring (La Sorte and Jetz, 2010; Nogués-Bravo et al., 2007; Viviroli et al., 2011). These remote environments are critically important for many societies; for example, one-sixth of the global population resides in areas that depend on mountain meltwaters (Parry, 2007). Due to their importance and complexity, research on climate change in mountainous landscapes spans many disciplines, scales, and methodologies. The research that is conducted ultimately shapes the breadth and depth of the body of knowledge influencing governance and natural resource management (Jasanoff, 2004). Moreover, the spatial distribution of research activity is surprisingly difficult to elucidate, yet has important consequences for our understanding of natural systems (Karl et al., 2013; Wallis et al., 2011). It is therefore imperative to understand what research themes are (and are not) well studied, as well as the geographic distribution and disparities of these themes in order to gain a holistic understanding of these systems and develop effective strategies to adapt to change.

The headwaters of the Columbia River Basin (CRB) are an important test case for understanding the state of knowledge about climate change in a mountainous region that is profoundly affected by non-stationary climatology. It serves as an example of a large, transboundary river basin with diverse ecosystems, complex socio-political histories, and a dependency on seasonal snowmelt to maintain water supplies and ecosystem function (Mankin et al., 2015). The region's water resources generate over half of the United States' hydroelectric power production, positioning the CRB as the leading producer of 22 key agricultural commodities, and sustain a population growing at more than twice the rate of the national average (EIA, 2018; USDA, 2018; US Census Bureau, 2017). The region has the scientific and policy-making infrastructure to support a large volume of research and engages in relatively extensive climate change adaptation efforts through, for example, government-led vulnerability assessments (Muccione et al., 2016; Olson, 2017). Because of the broad scope of climate change-related science in the CRB, and the outsized impact of its mountainous natural resources on society at large, rigorous assessment of topical and spatial trends in research is needed to identify critical knowledge gaps.

Motivation for Knowledge Synthesis

Calls for approaches to systematically assess climate change research are ubiquitous (Hulme 2010; Petticrew and McCartney, 2011), yet conducting comprehensive reviews is

challenging because the scope of climate change involves synthesis across multiple disciplines and large bodies of literature (Lenhard et al., 2006). Berrang-Ford et al. (2013) describe the diverse set of approaches used in modern research syntheses, ranging from narrative reviews to scientometrics. While traditional narrative reviews typically provided detailed assessments of the findings of a particular field, science mapping (scientometrics) and systematic review approaches have gained popularity in recent years due to their utility in characterizing interdisciplinary fields and making sense of large, disparate bodies of literature. Specifically, scientometric approaches use data from citation indices to measure scientific activity on specific themes. Systematic reviews vary widely in their implementation but typically apply rule-based methods for document inclusion and emphasize quantitative analyses of a body of research (Berrang-Ford et al., 2013; Gough and Oliver., 2012). Several systematic reviews in recent years have assessed trends and gaps in climate change research, often with focuses on adaptation and impacts (e.g., Ford and Pearce, 2010; Ford et al., 2012; Sud et al., 2015; Tuihedur Rahman et al., 2018).

Research Questions and Objectives

In this study, we blend elements of scientometric approaches with a systematic review in order to identify the thematic content and spatial attributes of peer-reviewed research related to climate change in the mountainous regions of the CRB. The specific questions that we address are: (1) What are the common thematic foci and relative deficiencies in this body of research? (2) What are the spatial scales and distribution of climate change research in the headwater regions of the CRB? (3) Is the thematic content of research clustered spatially or conducted at specific scales in a way that suggests a need for further study of particular topics, specific places, or both?

The primary outcome of this work is the elucidation of knowledge gaps in areas of scientific inquiry that are strategically beneficial to improving our understanding of changing mountain landscapes. These outcomes are accomplished with a systematic review of peer-refereed literature to improve the potential for identifying research needs and untapped opportunities of greatest potential benefit. By extension, this improves the potential for the co-production of actionable science and management-relevant science, and facilitates a more tailored “call and response” relationship among science producers and science consumers or decision makers (DeCrappeo et al., 2018). We expect the results of this review methodology

to be useful to scientists seeking opportunities to advance needed interdisciplinary research, and resource managers crafting management responses to climate change.

Methods

Literature Acquisition

We identified studies that (1) are in the CRB, (2) specifically address climate change impacts, adaptation, or mitigation, and (3) address mountainous environments (Figure 4.1). We used a multi-database search, incorporating literature from the Web of Science, Cabdirect, Proquest, and Crossref databases (table 4.1). We assessed each of the articles for inclusion in the corpus of literature based on their titles and abstracts, referring to full texts when necessary. Articles were included if they were peer-reviewed and included a substantial focus on climate change impacts, mitigation, or adaptation in mountain regions of the CRB. Articles were excluded if they did not address climate change, studied paleoclimate, or were conducted at a spatial extent greater than the western United States (Figure 4.1).

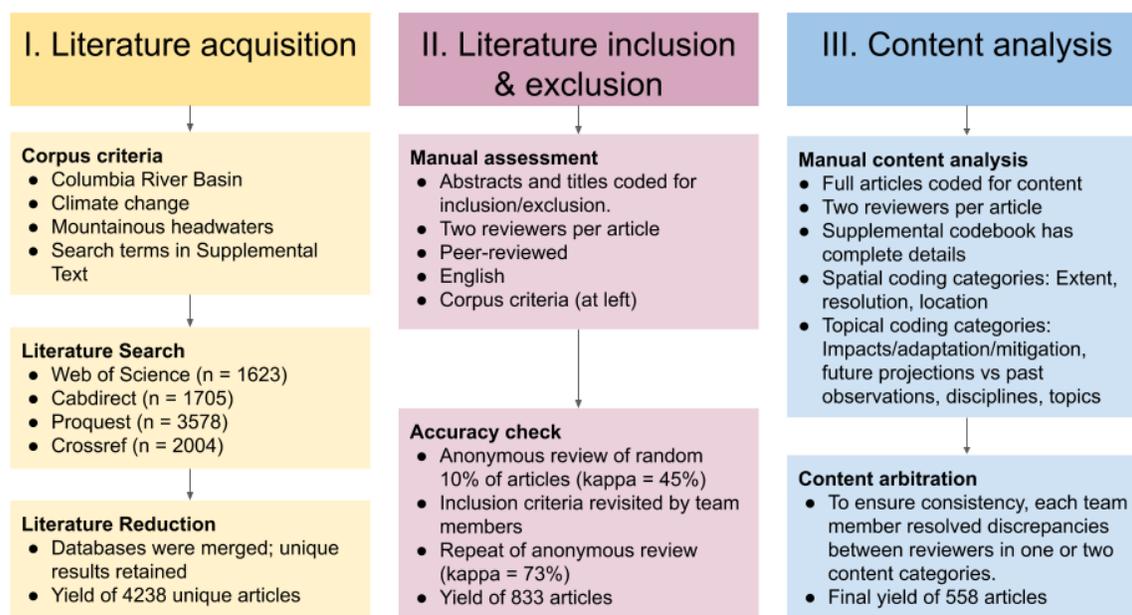


Figure 4. 1. Flowchart for methods of literature acquisition, inclusion, exclusion, and content analysis

Literature Content Analysis

Each article was analyzed to determine its spatial extent, location, and thematic content. We used a Google-form electronic questionnaire and a detailed codebook to ensure consistency among reviewers. To record location, we selected the US Geological Survey six-digit hydrologic unit codes (HUC-6) to identify the watershed(s) where each study took place (Figure B.1). If a study included data from fewer than six individual locations, the latitude(s) and longitude(s) were recorded. Spatial extent, which we defined as the largest area to which findings were extrapolated within the western United States and British Columbia, was selected from seven classifications. We also selected the biome(s) where each study took place from a list of global biomes from Woodward et al. (2004). Freshwater biomes were added to distinguish studies between aquatic and terrestrial biomes.

We developed several categories to analyze the topical and disciplinary content of the research. Using definitions from the Intergovernmental Panel on Climate Change, studies were categorized based on whether the primary knowledge contribution of each article was related to climate change impacts, adaptations, or mitigation (Parry, 2007; Table 4.1). If the article addressed impacts, we determined whether evidence was presented regarding observed historic impacts and/or modeled projected future impacts. Finally, we specified the primary discipline(s) (Table 4.2) and topics addressed in each article. Discipline was determined based on the article and journal titles, primary author's discipline, and the primary knowledge contribution of the article, while topics were selected more inclusively and included any important knowledge contribution. Topics that occurred extremely infrequently were binned into more inclusive categories when possible.

Table 4. 1. Definitions used to assess area of primary knowledge contribution *2007
Intergovernmental Panel on Climate Change definition

Term	Definition used in study
<i>Adaptation</i>	Adjustment in human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.*
<i>Mitigation</i>	An anthropogenic intervention aimed at reducing the anthropogenic forcing of the climate system.*
<i>Impacts</i>	The effects of climate change on natural and human systems.* We categorized impacts as <i>observed</i> , in which trends were noted in empirical data and attribution to climate change was discussed, <i>projected</i> , in which the impacts of climate change were quantitatively modeled for future scenarios, and <i>implications</i> , in which the climate sensitivity of a system was assessed.

Table 4. 2. Definitions of disciplines used in study, listed in alphabetical order

Discipline	Definition used in study
<i>Biology</i>	The study of life, including anatomy, physiology, animal behavior, genetics, morphology, growth, and more.
<i>Climatology</i>	Studies of weather and/or climate, including atmospheric and oceanic patterns and processes.
<i>Ecology</i>	The study of the interaction of biotic and abiotic factors in an ecosystem.
<i>Economics</i>	The study of the production, distribution, and consumption of monetary goods and services.
<i>Engineering</i>	The study of physical design and construction of functional structures.
<i>Forestry</i>	Studies that broadly include forest ecology and forest management.
<i>Geology</i>	The study of earth processes, plus rock & soil science.
<i>Hydrology</i>	The study of water processes, both above and below ground.
<i>Sociology</i>	Any study focused on human populations, human behavior, relationships, culture, and society.
<i>Policy</i>	Any studies related to rulemaking and decision making at an administrative level, including management.
<i>Toxicology</i>	Any branch of chemistry and toxicology that focuses on interactions among biological and chemical processes in the environment.

Data Analysis

Summary statistics were calculated to summarize frequencies for each of the content categories. To assess potential interdisciplinarity, we calculated the frequency of disciplinary co-occurrence to derive a network map. To explore the relationships among topics we conducted a hierarchical cluster analysis (HCA), using topics that occurred in at least five articles. We used Ward's least square error method of clustering because it is less susceptible to noise and outliers, and it yielded the highest agglomerative coefficient (Tan, 2007). This method groups topics into similar nested clusters and minimizes the similarity between

clusters. Topics that co-occur more frequently are joined early in the clustering process. Inclusive clusters are joined together by branches in a dendrogram.

The relationships between different coding categories were also assessed using correspondence analysis. This method calculates factor scores for two categorical variables and converts them to Euclidean distances, which can be mapped together to visualize relationships in two-dimensional space. The proximity in this space between variables indicates the frequency with which they are researched together (Abdi and Williams 2010).

To compare studies that occurred only in Canada, the U.S., or spanning the international boundary, we used a Fisher's exact test. This method identifies whether there are significant differences in the topical distributions of national and transboundary studies. The Fisher's exact test was selected because we had small sample sizes. Results from a Chi-squared test were then used to determine which topics contributed to the differences.

Abstract mining

In order to test the strength of our findings regarding the frequency of disciplinary co-occurrence, we conducted a text mining analysis on the article abstracts. Direct analysis of abstract texts provides a data source that is independent from our coded analysis of the papers, and therefore serves as a check on the data collection process. Abstracts were available for 515 out of our total corpus of 558 studies. Common stop words (commonly used words, such as "and", "also", etc.) and words that occurred less than 20 times were removed, and Pearson correlation coefficients for each remaining pair of words were calculated based on the frequency of co-occurrence in each abstract. Correlations are only reported for cases where Pearson's $p < 0.05$. For cases where other analyses suggested that topics were particularly likely or not to co-occur, we used these correlation coefficients as an additional line of evidence to test our results.

Results and Discussion

Research in the CRB includes an abundance of studies on physical and ecological disciplines and topics.

Articles in the corpus generally focus on physical and ecological disciplines. The most commonly identified disciplines are ecology (204 articles), hydrology (160), climatology (120), and forestry (108), as shown in Figure 4.2. There are 156 (28%) articles with two or more disciplines and 402 single-discipline articles (72%). The most common combinations of disciplines are hydrology and climatology (39), and ecology and forestry (24) (Figure 4.2a).

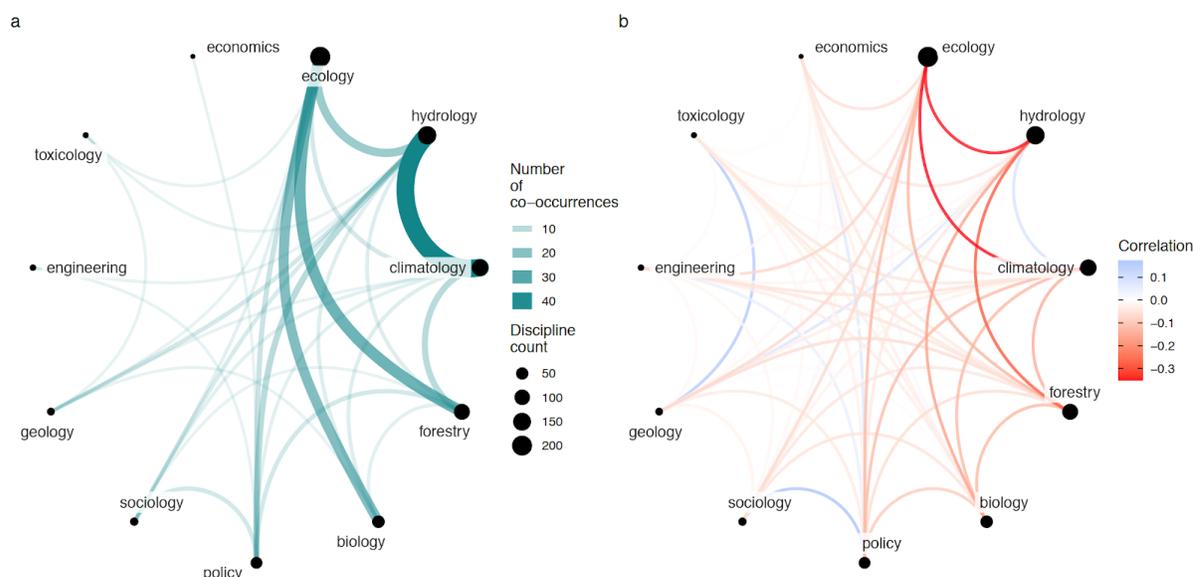


Figure 4. 2. Network map of co-occurring disciplines, showing (a) number of co-occurrences, indicated by edge width and color, and (b) correlation coefficients between disciplines. Size of points indicates number of times each discipline occurred.

There are an average of 6.12 (± 2.5 s.d.) topics per article. The six most common topics are temperature (86% of articles), precipitation (76%), forest ecology (47%), snow (40%), management (40%), and streamflow (37%). The frequency of these topics suggests a dominance of forest ecology and water issues, with fairly frequent discussion of management. The prevalence of management as a topic is important to note, given the paucity of policy or management as a discipline (8%). This discrepancy arises because our methods were relatively exclusive when coding for discipline and inclusive when coding for topic, and suggests that few studies have management or policy as a primary focus, but many

still address management to some extent. The paucity of climate change studies on social science aligns with the global distribution of competitive research funding for climate change, which tends not to support social science studies (Overland and Sovacool, 2020).

The HCA illustrates the tendency for groups of topics to be researched together. Physical science topics related to physical hydrology, precipitation, water quantity, streamflow, and snow cluster together (cluster 1, Figure 4.3). The appearance of these topics in the first cluster demonstrates that hydrological topics are common in the corpus and confirms that they are consequential in relation to climate change in the mountainous regions of the CRB. The word correlation analysis of article abstract text provides supporting evidence for the HCA findings. Indeed, words associated with topics within cluster 1 (precipitation, streamflow, and snow) correlate positively.

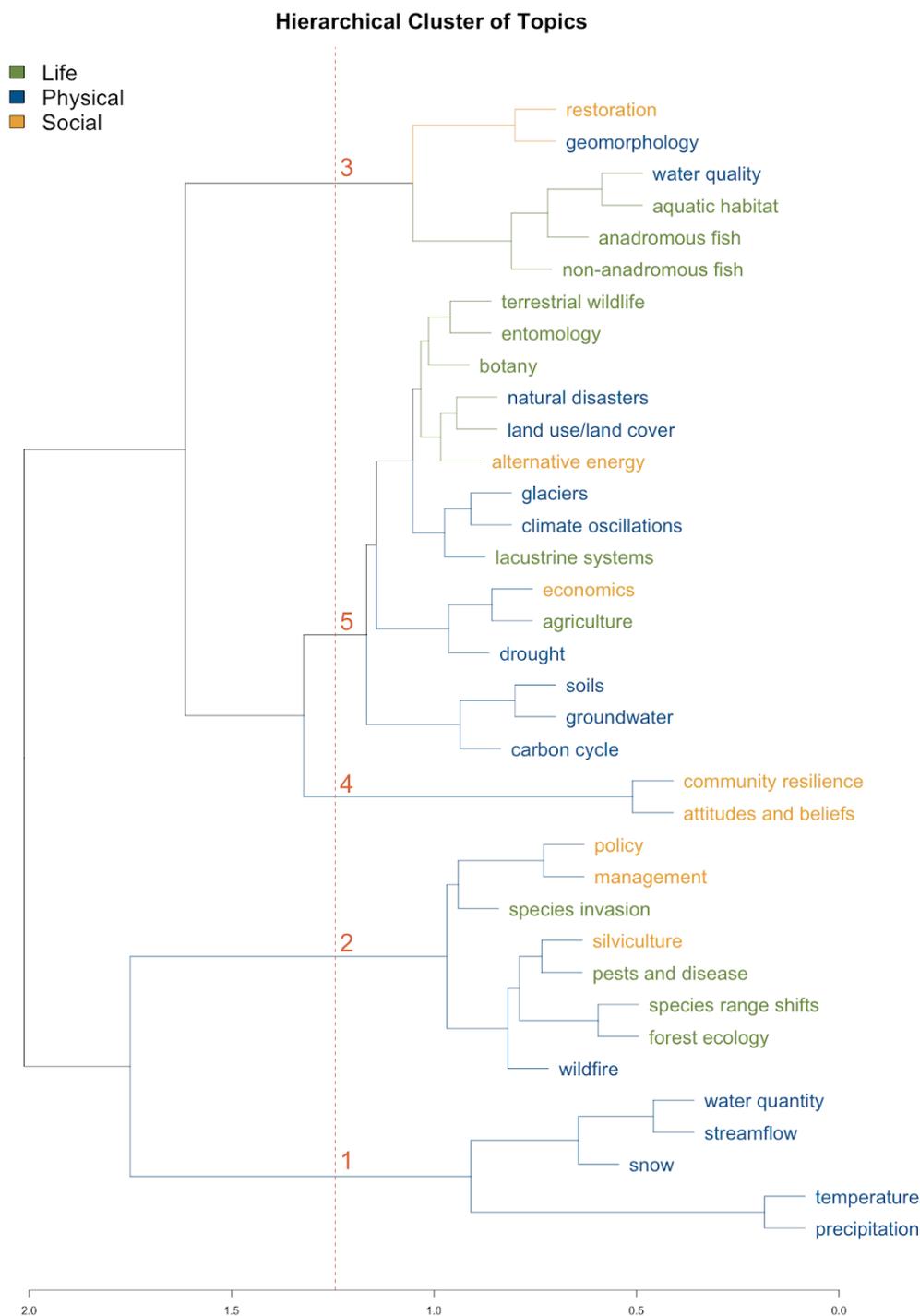


Figure 4. 3. Dendrogram of hierarchical cluster analysis (HCA) of topical co-occurrences. The HCA measures the dissimilarity between variables and represents them in nested clusters. The x-axis shows the dissimilarity between topics. Topics that are grouped together near the right (distance = 0) are frequently coupled in the literature. Cluster numbers in red are referenced in the text. Colors of topics indicate whether each topic was classified as primarily related to the social (yellow), life (green), or physical (blue) sciences.

Some disciplines and topics are infrequently researched together, suggesting an opportunity for further disciplinary integration.

Several lines of evidence indicate that some disciplines and topics are relatively infrequently researched in conjunction with each other. These include the frequency of disciplinary co-occurrence (Figure 4.2), the HCA (Figure 4.3), and correlational analysis of abstract texts. One area of research where deeper disciplinary integration may be needed is the associations between terrestrial and aquatic processes. For example, the disciplines of hydrology and forestry show a fairly strong negative correlation. In the HCA, topics related to forest ecology and water resources form two distinct clusters in branches two and three, also suggesting separation between these topics. The text analysis of abstracts also supports the idea that forest and aquatic issues are not well integrated; for example, word pairs with negative correlations include forest/fish and fire/fish. Of the minority of articles that do integrate topics related to forests, fires, and fish, five out of seven model the additive effects of climate change, altered forest vegetation, wildfire, and/or other disturbances on aquatic habitat (Davis et al., 2013), stream temperatures (Holsinger et al., 2014; Isaak et al., 2010) or sediment delivery (Neupane and Yager, 2013; Rugenski et al., 2014). All five articles conclude that that combined effects of climate change and forest disturbances are detrimental to aquatic habitat. The other two articles focusing on fish, fire, and forests do not directly investigate these topics, but instead consider their confounding influence on stream diversions (Walters et al., 2013) or as determining indicators of climate change (Klos et al., 2015). These studies reinforce the interconnection of forests, fires, and stream habitat and highlight both the necessity and further opportunities to integrate forest disturbances into climate change research on aquatic habitat.

Similarly, studies of fire and snow do not tend to be well integrated, as demonstrated by their distinct clusters in the HCA; these terms are also negatively correlated in the abstract text analysis. The topic of snow appears in 42% (236) of the corpus studies, while the topic of fire appears in 20% (113) of articles. However, articles including both snow and fire make up only 5% (27) of the total. Given that snowpack and summer moisture deficit have been described as leading causes of increases in large wildfire occurrence (Westerling, 2006; 2016), this may indicate an area where further thematic integration is needed to address potential fire-snow feedbacks.

Our findings also suggest that biophysical disciplines are generally not studied in conjunction with social science disciplines, with a few exceptions. Community resilience and attitudes and beliefs are separated from all other clusters in the HCA, indicating that they are more frequently discussed within the same publications than they are with other topics (Figure 4.3). This also appears to be true in the analysis of disciplinary co-occurrence. Of the five most commonly studied disciplines, none show positive correlations with social science disciplines, such as sociology, policy, or economics.

The studies that do demonstrate deep integration of biophysical and social disciplines may provide models for future interdisciplinary research. Several studies link hydrology with policy; these include studies of water resources engineering and supply management issues (e.g., Lee et al., 2009; Hatcher and Jones, 2013). Only five studies address sociology or policy in conjunction with biophysical disciplines. These include agent-based modeling for planning around future watershed conditions (Nolin, 2012), a synthesis of biophysical climate change indicators and feedback from resource managers (Klos et al., 2015), and an analysis of forest managers' responses to climate change (Blades et al., 2016). These findings are generally in agreement with Bjurström and Polk (2011), who analyzed interdisciplinarity within climate change research through a co-citation analysis of the IPCC Third Assessment report and found that closely related disciplines commonly co-occur, while more disparate disciplines are clearly separated.

Studies on climate change impacts are much more common than those on adaptation or mitigation.

Articles analyzing climate change impacts are much more common than those addressing adaptation or mitigation: 88% (489) primarily focus on climate impacts, while 10% (56) focus on adaptation and 2% (13) are on climate change mitigation. Ford and Pearce (2010) observe an increasing “adaptation gap,” where the number of studies addressing climate change impacts is much larger than those addressing mitigation, and the gap between the two has grown over time, particularly as the number of studies on impacts has increased. The studies in our corpus similarly reflect an adaptation gap; comparing the ten year periods from 1996-2005 and 2005-2015 shows that the gap between the number of adaptation and impacts papers has increased from 63 to 302, though adaptation papers represent a larger portion of the corpus in the later period than earlier, increasing from 3% to 11% of papers. A

similar gap exists for mitigation studies; the gap increased from 64 to 334 papers, though the fraction of papers coded as mitigation increased from 1% to 3%. However, while these changes represent fairly small increases in the total number of papers, the three-to-fourfold increase in frequency indicates considerable growth in adaptation and mitigation research.

Studies primarily assessing climate change impacts, adaptation, and mitigation have distinctly different patterns of disciplinary and topical distributions (Figure 4.4). Articles on climate change impacts tend to be associated with the disciplines of hydrology, climatology, and ecology. In contrast, studies of climate change adaptation are most commonly associated with the disciplinary categories of policy, sociology, forestry, biology, ecology. The topics represented by adaptation articles are heavily skewed towards water quantity, silviculture, species range shifts, attitudes and beliefs, and pests and disease. A relatively small percentage of adaptation articles address groundwater (9%), climate oscillations (2%), or carbon cycling (4%); no adaptation articles studied glaciers. The relative lack of adaptation studies on these topics may suggest important knowledge gaps and therefore opportunities for adaptation research.

Mitigation studies are disciplinarily concentrated in biology, ecology and forestry, and topically focused on carbon cycling, forest ecology, wildfire, silviculture, and management. These findings reflect established understanding that forest management and wildfire are large components of carbon budgets in mountainous regions (Schimel et al., 2002). However, this also suggests potential research needs related to, for example, freshwater carbon budgets, the carbon budget of recreational activities, and climate change mitigation policy in mountainous regions (though a few studies address policy related to mitigation; see Wiedinmeyer and Hurteau, 2010; Stockmann et al., 2012; Law et al., 2018).

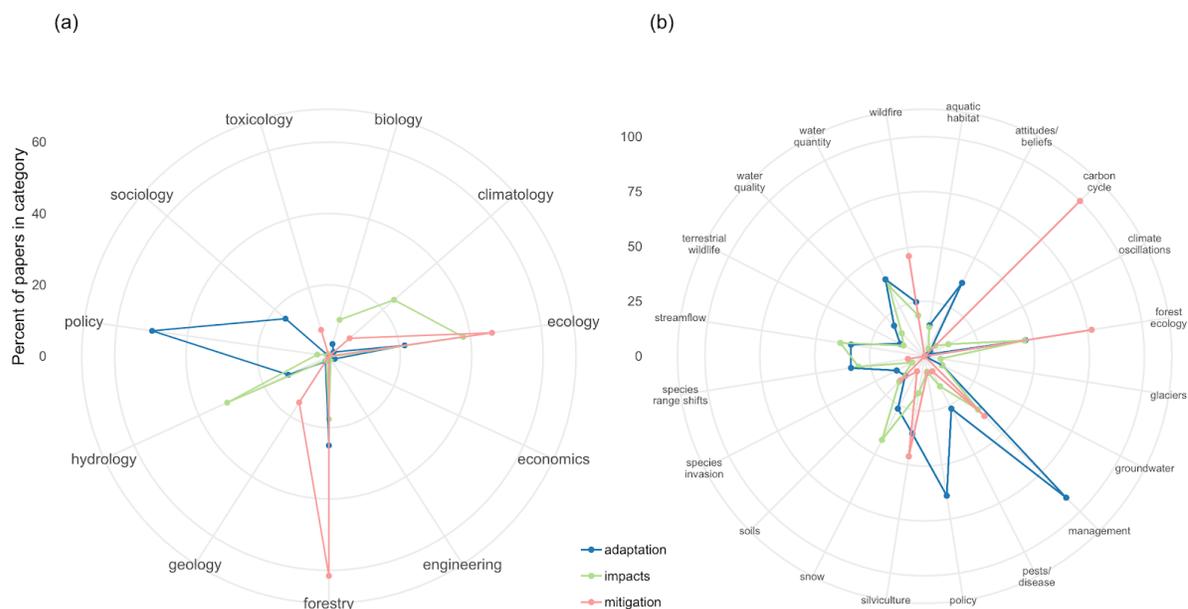


Figure 4.4. Radar plots showing the distribution of adaptation, impacts, and mitigation paper by (a) discipline and (b) topic. Axis displays the percent of papers in the adaptation, mitigation, and impacts categories that address a particular topic or discipline. Figure B.2 shows numbers of papers, rather than percentages.

Research is predominantly focused at relatively large scales, makes projections of future rather than observed conditions, and uses existing rather than new data.

Articles in the corpus range in spatial extent from point or plot scale to the western U.S. The Pacific Northwest (660,000 km²) and the Western U.S. extents are the most common and include 37% of articles (205). Another 22% of articles (121) span between 40,000 km² and the Pacific Northwest (660,000 km²). The remaining 42% of articles (232) report on studies at spatial extents less than 40,000 km². Different disciplines generally associate with different spatial extents (Figure 4.5). For example, articles with climatology as a discipline tend to occur more frequently at larger extents. This is to be expected, given the nature of the discipline, though it may raise questions about whether microclimates and refugia are adequately studied from a climatological perspective (e.g. Curtis et al., 2014; Daly et al., 2010).

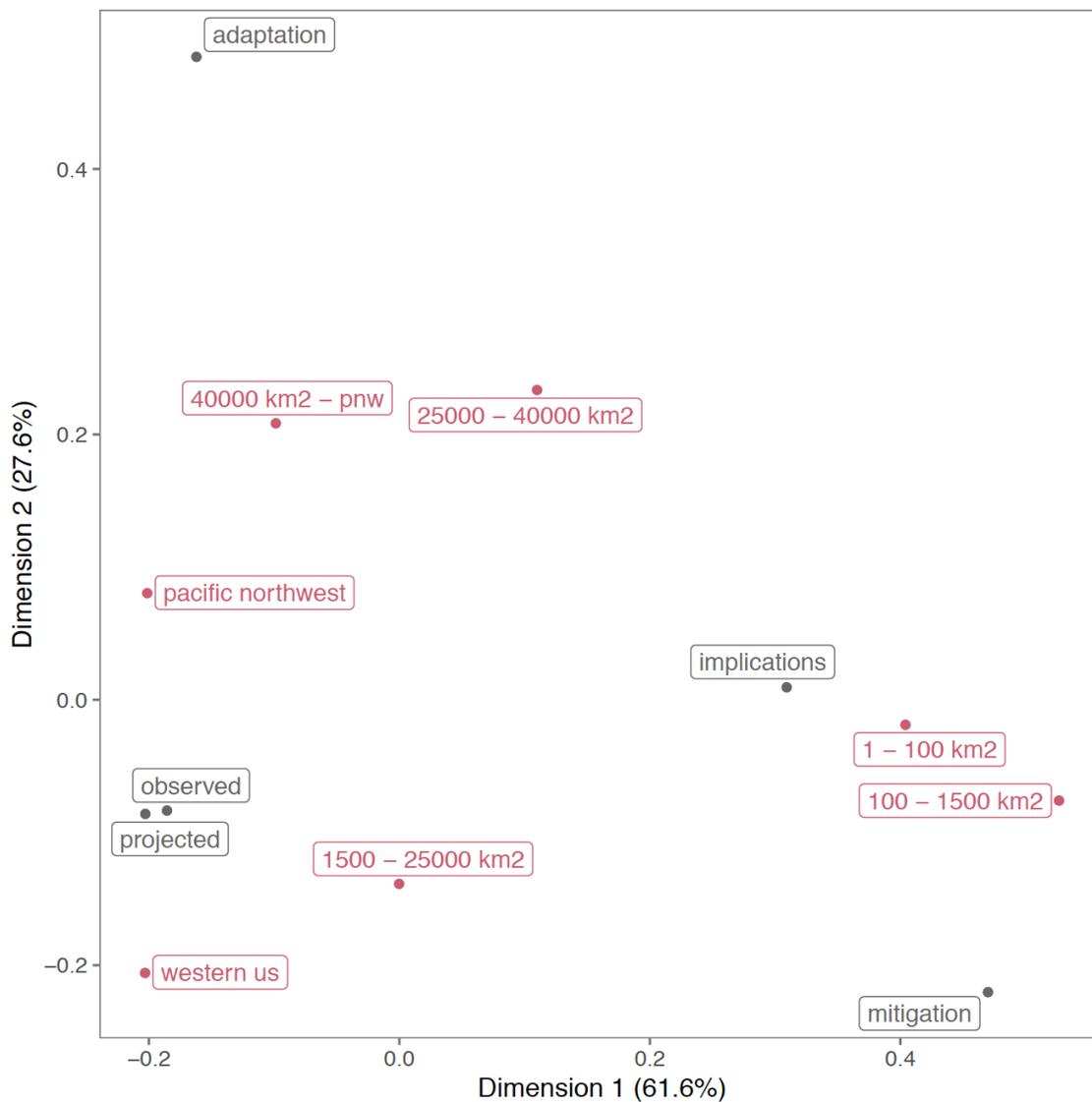


Figure 4. 5. Biplot of correspondence analysis of impacts (observed, projected, or implications) adaptation, and mitigation (black labels) vs. spatial extents (red labels). Variables that are close in Euclidean space are frequently coupled in the literature.

Projections of climate change impacts are more common than observations. Of the 507 articles that study climate change impacts, 35% (171) make formal projections of climate change impacts; 28% (139) focus on observed environmental trends and discuss their attribution to climate change, while 42% (205) assess a climate change impact but do not explicitly discuss observed or projected trends. Reporting on new field data is also relatively uncommon; only 34% (188) of studies include new data. The frequency with which studies include observed or projected impacts vary by discipline (Figure 4.6). Articles with

disciplines categorized as ecology, forestry, biology, policy, or geology tend to reference climate change implications, rather than explicitly making observations or projections of climate change. In contrast, hydrology and climatology have more studies of projected and observed climate change impacts. While trends vary by discipline, the relative preponderance of research based on simulated and/or remotely-sensed data at fairly coarse resolutions and large scales raises questions about whether these large-scale findings are adequately supported by observed data, which is usually collected at much smaller scales and may have important variations within simulation grid cells (e.g. McKelvey et al., 2011).

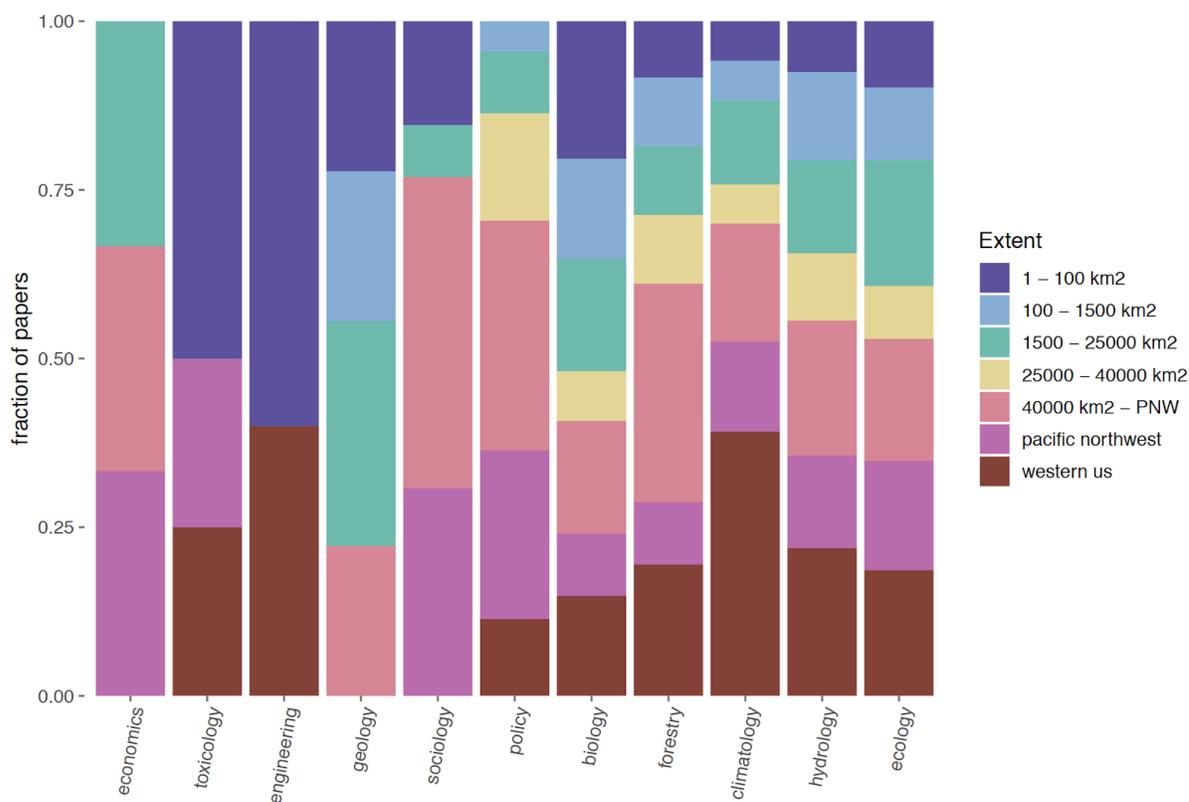


Figure 4. 6. Spatial extent of disciplines. Disciplines are arranged in ascending order of frequency within the dataset.

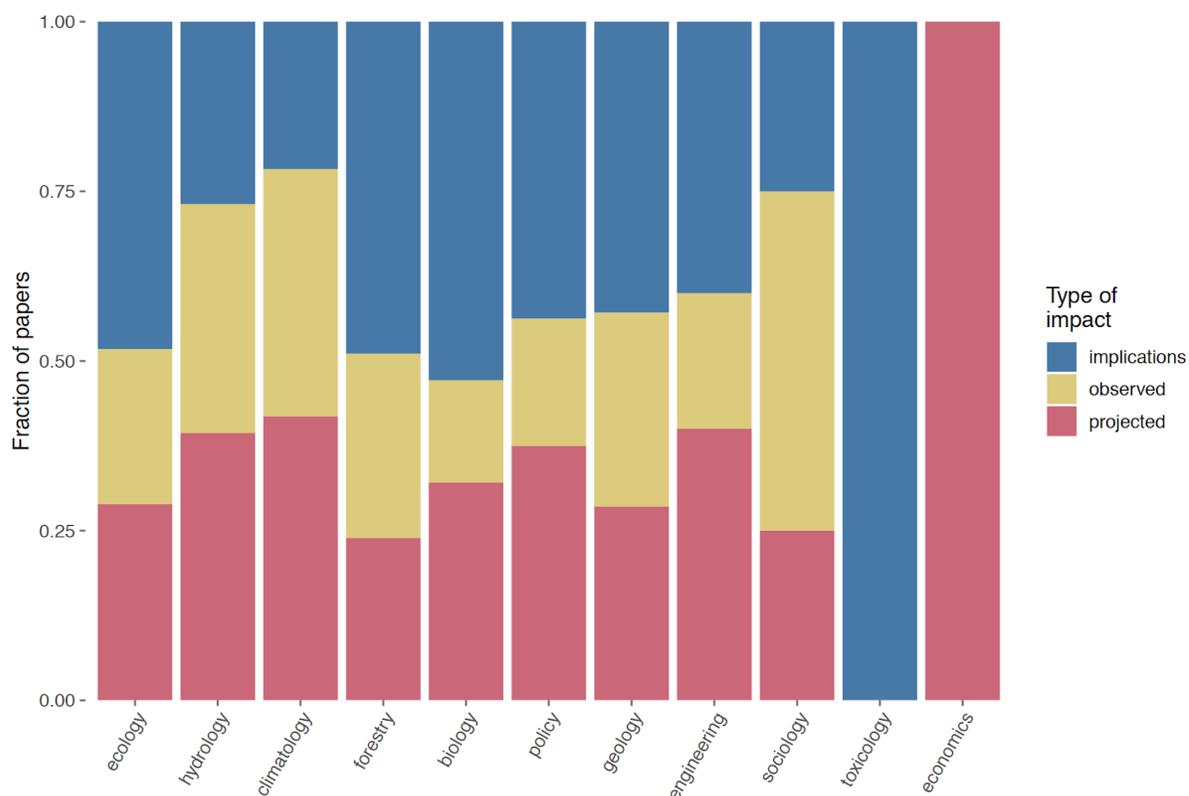


Figure 4. 7. Studies of climate change impacts that identify climate change implications or observed or projected impacts, by discipline

The quantity of research conducted varies spatially, and is concentrated at long-term research sites.

Research is unevenly spatially distributed across the CRB (Figure 4.7). The quantity of research we identified is much less in Canada (84) than in the U.S. (405). For studies conducted at smaller extents, research activities are concentrated at several locations that appear to be fairly well explained by geographical features, such as the location of long-term research sites. For example, notable concentrations of research appear to occur at the H.J. Andrews Experimental Forest in Oregon, Mount Rainier National Park in Washington, and in the Reynolds Creek Experimental Watershed in Idaho. Another relatively high concentration of studies occurs in the Okanagan Basin, Canada, though these are not clustered at a particular research site.

Biophysical context influences the spatial distribution of research themes.

The thematic content of research is unevenly distributed across HUC-6 watersheds (Figure 4.8). Correspondence analysis reveals groupings of watersheds and disciplines. Research in the Upper Snake and Snake Headwaters tends to encompass the same disciplines and is closely associated with policy and ecology. Sociology is frequently coupled with the Okanagan (Canada), Columbia (Canada), and Spokane watersheds, with sociology studies in Canada commonly focused on social issues shaping forest management (Goemans and Ballamingie, 2013; Furness and Nelson, 2015; Carolan and Stuart, 2016). Hydrology is also associated with Okanagan (Canada), Columbia (Canada), Spokane, Yakima, and John Day watersheds. Forestry is closely coupled with the Willamette, Kootenai, and Upper Columbia River watersheds, though the topic's central location within the correspondence analysis graph indicates that it is researched frequently within most watersheds. Maps of the spatial distribution of selected topics support the correspondence analysis and demonstrate that the topical distribution of research varies in space (Figure 4.8). For many topics, the variability between the U.S. and Canada is much larger than within-country differences; however, we focus our discussion here on within-country differences followed by discussion of transboundary differences in the next section.

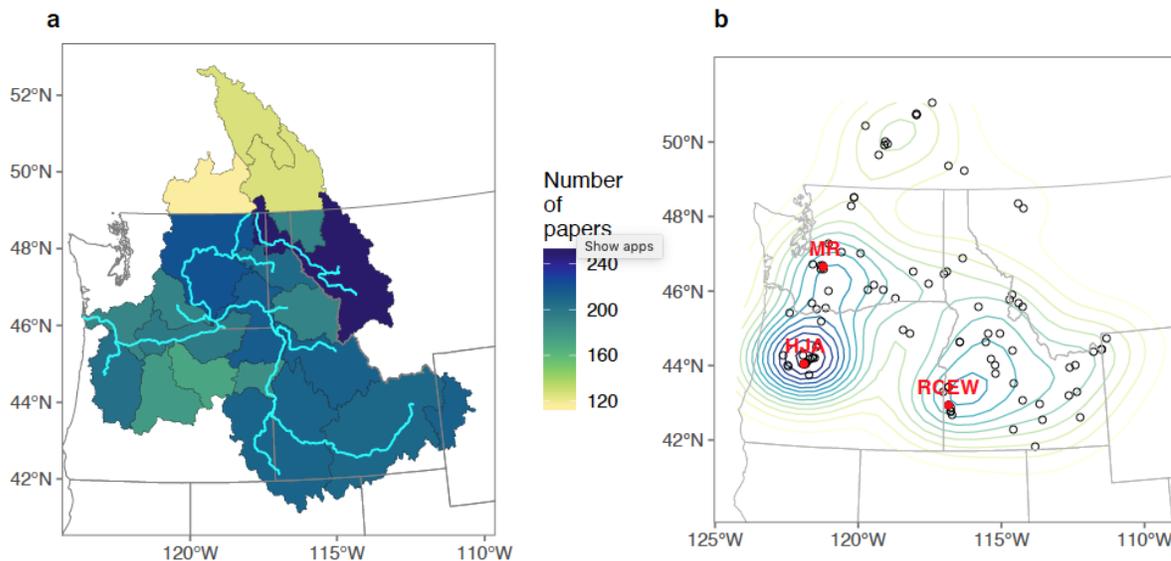


Figure 4. 8. Spatial distribution of literature, displayed as (a) total number of papers per HUC-6 watershed and (b) point locations for studies with spatial extents less than 1500 km². Contours showing estimated density of studies. Rivers are displayed in cyan; points of interest with high concentrations of research are in red. MR = Mount Rainier; HJA = H.J. Andrews Experimental Forest; RCEW = Reynolds Creek Experimental Watershed.

Disturbance history influences the the topical distribution of research. For example, the preponderance of forest ecology and wildfire studies in the Greater Yellowstone Ecosystem may be due to the 1988 Yellowstone Fires, as evident in the many studies that reference these fires (e.g., Romme et al., 2011; Donato et al., 2016; Seidl et al., 2016; Zhao et al., 2016). Studies of pests and disease are also relatively common in the Greater Yellowstone Ecosystem, as well as the Salmon River watershed (Figure 4.9). Many of these studies are focused on bark beetle outbreaks (e.g. Buotte et al., 2016; Logan et al., 2010; Seidl et al., 2016; Simard et al., 2012).

A relatively large portion of the research conducted in the Upper Snake and Snake River Headwaters addresses management implications. Articles addressing management in this area predominantly focus on interactions between water resources management and biophysical conditions under climate change (Loinaz et al., 2014; Qualls et al., 2013; Ryu et al., 2012; Sridhar and Anderson, 2017); forest and terrestrial ecosystem management, often specific to unique species such as whitebark pine (Logan et al., 2010; Macfarlane et al., 2013); or sagebrush steppe communities (West and Yorks, 2006). Interestingly, despite the relative prevalence of management topics in these two watersheds, adaptation studies are about as common (10% of studies) as in the entire corpus. This finding suggests that a high proportion of impacts-focused studies in this region also address management implications, which may be a result of the long history of conservation planning efforts in the Greater Yellowstone Ecosystem (Clark et al., 1991).

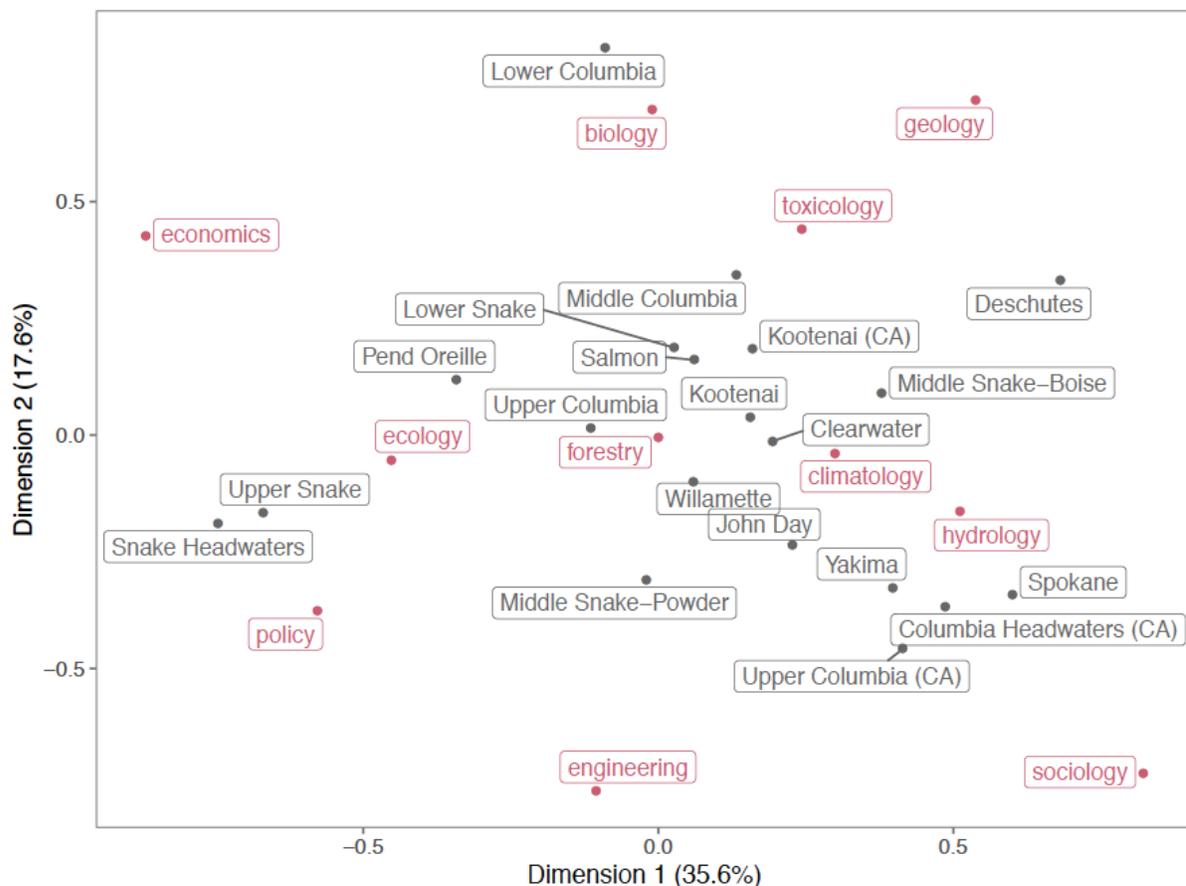


Figure 4. 9. Biplot of correspondence analysis of watersheds (black labels) and disciplines (red labels). When variables appear close in Euclidean space, they are frequently coupled in the literature.

Within Canada, management is frequently researched in the Upper Columbia watershed (85% of Canadian policy articles, $n=18$). Of these management articles, 67% (12) focused on forests (e.g., Nitschke and Innes, 2008; Goemans and Ballamingie, 2013; Seely et al 2015), 17% (3) on wildlife (Bunnell et al., 2011; Festa-Bianchet et al., 2011; McNay et al., 2011), 11% (2) on human dimensions (Turner and Clifton, 2009; Furness and Nelson, 2016), and less than 1% (1) on avalanches (Sinickas and Jamieson, 2016). Water management topics are not addressed in management-related articles in Canada, despite the fact that some research suggests that demand for irrigation water may frequently exceed supply in future climates in the Okanagan basin (Nielsen et al., 2006).

Research themes vary among studies in Canada, the United States, and transboundary studies.

We compared thematic content of articles exclusively in the U.S., in Canada, and those that are transboundary. The comparison suggests that the topical distributions of articles in these three categories are significantly different from each other (Fisher's exact test $p < 0.001$). The prevalence of articles addressing insects and disease and glaciers in Canada are the largest contributors to this difference, though topics related to human dimensions (policy, management, attitudes and beliefs, community resilience) are also more common in Canada than in the U.S. The extensive forested areas and recent pest outbreaks in the Canadian headwaters of the CRB may explain the greater research focus on forest insect and disease impacts. Climate change contributes to the rapid expansion of new bark beetle species at these latitudes, raising concerns for forest health in Canada (Anderegg et al., 2015; Bentz et al., 2010). Concerns about forest health issues due to the close proximity of communities and forests in Canada may influence the more frequent occurrence of topics related to the human dimensions of climate change (e.g., Furness and Nelson, 2016; Parkins, 2008; Parkins and MacKendrick, 2007). The topical focus on glaciers in Canada within the corpus is likely due to the relatively high prevalence and hydrologic importance of glaciers in this area (Moore et al., 2009).

Transboundary studies ($n = 69$) are distinguished by a relatively high frequency of studies addressing climate oscillations, streamflow, anadromous fish and restoration, and a relatively low frequency of studies on policy, forest disturbances, silviculture and carbon cycling. These include studies describing results of climate models across the entire CRB (e.g., Rupp et al., 2016); hydro-climatological models representing downscaled impacts of climate change on hydrology (e.g., Hamlet et al., 2013); comparative streamflow and water temperature modeling (e.g., Ficklin et al., 2014); and models of declining snowpack (e.g., Abatzoglou, 2011). Reconstruction of historical flows or trends are also common across transboundary studies (e.g., Waples et al., 2008). Only five transboundary studies explicitly address policy and management issues (Sopinka and Pitt, 2014; Beechie et al., 2013; Schwandt et al., 2010; Lee et al., 2009; Bisson et al., 2009), and only one of these represents a collaboration between U.S. and Canadian authors (Schwandt et al., 2010). These studies focus on flood control, streamflow, and anadromous fish. A potential issue in interpreting the

thematic content of these transboundary studies is that many transboundary studies tend to occur at relatively large scales (70% were larger than the Pacific Northwest, in contrast to only 37% in the full corpus). Therefore, there may be a confounding effect between topics that tend to be researched at large scales and those that are of particular interest across international borders.

Conclusions

Science produced in mountainous headwaters of the CRB affects our understanding of climate change impacts on social and ecological systems, as well as our understanding of potential adaptation and mitigation strategies. While a number of trends in the thematic and spatial distribution of climate related research in the CRB can be discerned, the relative gaps in knowledge and effort are of the most concern. The following conclusions represent our evaluation of the most important gaps that present significant opportunities for further research:

(1) Only 10% (56) of the articles in our corpus focus on the adaptation of human systems to actual or expected climate change. This may be emblematic of a disconnect between the practice and applications of science - especially applications that build adaptive capacity in social-ecological systems.

(2) Only 2% (13) of the studies included in this review focused on improving knowledge of, or intervening in, carbon cycles to potentially reduce the effects of anthropogenic forcing on the climate system, despite large tracts of forested lands, a significant biomaterials industry, and increasing concerns about climate change feedbacks due to forest disturbance. More research may therefore be needed on climate change mitigation in this region, and potentially in other mountainous regions around the globe.

(3) There is also an opportunity for more climate-related social science research, and more integration of social science with biophysical disciplines. Only five of 558 studies included in this review represented sociology or policy in conjunction with biophysical disciplines, a glaring disparity given the feedbacks between a growing population, climate change, ecosystem services, and land management.

(4) Finally, there is an important opportunity for further transboundary climate change research with an integrated, basin-wide focus. For example, only five of 558 studies explicitly addressed policy and management issues on both sides of the US-Canada border, and only one of these five represents a collaboration between U.S. and Canadian authors. This is surprising, given the interconnectedness of ecological and social systems throughout the watershed and the pervasiveness of observed and predicted climate stressors. In addition to a need for more transboundary research, this suggests a role for further research on the role of international collaborations for understanding climate change impacts, adaptation, and mitigation in this region.

This study quantified thematic and spatial knowledge and gaps in climate change related research for the mountainous headwaters of a large and complex watershed, allowing science and management communities to leverage resources more effectively and, in turn, increasing the potential for the co-production of actionable science and effective responses to climate change. Implementing similar analyses elsewhere could expand understanding of gaps and knowledge structures in the larger body of climate change research for mountainous regions. Moreover, further work could provide important comparisons for models of how to conduct interdisciplinary reviews to advance the management of complex river basins in a changing climate.

Acknowledgements

This work was supported by the National Science Foundation's IGERT Program (Award #1249400). Daniel Hovancsek and Rebecca Witinok-Huber contributed to literature acquisition.

Epilogue

With the utilization of dendrochronological techniques, many of the interacting drivers of species-specific tree growth in the Pacific Northwest were discovered. Shade tolerance, disturbance dynamics, and hydroclimate all influence conifer growth in the region. The relationships between streamflow and growth are heightened for trees growing in extreme climates, and these relationships are driven by geographical features.

The first chapter is an investigation of the impacts of density reductions, via different thinning intensities, on tree growth in moist mixed coniferous forests in northern Idaho, USA. Growth increases in response to stand density are widely recognized, although comparisons of responses among species in mixed-species stands are uncommon (Aldea et al., 2017). Moreover, immediate, short-term, and long-term responses to thinning are not well investigated, especially in mixed-species stands (Pitt & Lanteigne, 2008). Results show all species with immediate growth releases after thinning, signifying an increase in access and utilization of limiting factors and a decrease in competition. Western larch and western redcedar showed significantly higher growth following treatments than in reference plots – both in the short- and long-term. However, no increases in growth for grand fir and western hemlock were present. Species that respond rapidly to available sunlight and/or nutrients, like western larch and western redcedar, show the most significant growth increases. The less consistent responses to thinning by western hemlock and grand fir were likely due to their autecological characteristics and inherent lack of responses to more growing space. Finally, findings support the agreement among forestry science that thinning is a useful tool for increasing growth in most species. However, extra steps must be taken during and after treatment to better ensure growth increases in more injury-prone and less competitive species like western hemlock and grand fir.

There are many aspects of the research design for Chapter 1 that could be improved to help corroborate these findings. If thinning had been implemented at a later date, there would be more pre-thinning temporal coverage and, thus, a greater sample size of data before thinning. Later thinning would also allow for a more balanced design, more confident estimates of pre-thinning growth, and more robust statistical results. Another improvement would include the utilization of the random block design rather than systematic; this would

have ensured that differences among treatments are caused by thinning, and it would have potentially reduced noise from edge effects in the data. Thorough measurements of sampled trees conducted at the time of thinning would allow analyses about changes in growth response as well as enhance abilities to deduce changes in stand structure that may influence growth variability. Nonetheless, findings are still highly significant, and various steps were taken during data analysis to incorporate the experimental design.

With the same tree core samples from Chapter 1, Chapter 2 investigates the temporal variability of growth-drought relationships for these species, and how that relationship is influenced by thinning. The four species in this study show a wide range of responses to drought depending on the timing of drought, length of drought, intensity of drought, and forest stand density. Moreover, drought sensitivity often involves trade-offs, among other limiting factors like direct competition or nutrients. Western larch, the most drought-tolerant deciduous species in this study, was found to be the most sensitive to (correlated with) drought, followed by western hemlock, western redcedar, and finally grand fir – which shows weak correlations overall and significant negative correlations at times. Thus, it appears that the species exhibit differing drought adaptation strategies. Western larch reduces radial growth in response to drought while continuing to transpire at relatively high rates indicating a strategy of drought avoidance. Grand fir shows adaptive decoupling of growth-drought responses during drought years, which also supports a strategy of drought avoidance and isohydry. Western redcedar, which has moderate drought-resistance, does not show strong drought-sensitivity, indicating it may be resistant to drought. Western hemlock, the least drought-tolerant species in this study, was highly drought sensitive. Findings indicate that length and season of drought, species-specific drought tolerance, and stage of stand development, influence growth-drought responses. Thus, drought sensitivity often involves trade-offs among other limiting factors like direct competition or nutrients. Moreover, trees growing in moist forests may not be as highly susceptible to droughts as those in dry forests. Therefore, conclusions suggest stands are managed as complex adaptive systems by prioritizing site diversity (species, age, density) Moreover, results from this chapter (and Chapter 1) demonstrate these management strategies are sustainable.

Findings from the second chapter show that length and season of drought, species-specific drought tolerances, and stage of stand development influence growth-drought

relationships. However, like Chapter 1, a greater temporal coverage before thinning would vastly improve the ability to discern changes in growth-drought relationships before and after thinning. Additionally, pre-thinning and periodic post-thinning measurements of sampled trees would supply insight into interception and transpiration impacts on growth-drought responses. Still, significant growth-drought relationships were identified using robust methods. It is important to note that the dendrochronological techniques used in this study only calculate changes in radial growth. However, trees often respond to drought stress by reducing photosynthesis, producing non-structural carbohydrates, and allocating growth to roots rather than stems and trunks (Brodribb et al., 2014; McDowell et al., 2008; Moran et al., 2017). Finally, trees may respond substantially differently to drought in monocultures vs. mixed forests; therefore, these results are only applicable for mixed forests (Forrester, 2014).

For Chapter 3, the geographical influences of flow-growth relationships were identified for four different conifer species at larger spatial scales. Streamflow correlated negatively with subalpine fir and mountain hemlock, species commonly found at cool, moist, high elevation sites, indicating that they are likely more sensitive to severe environmental variations like those experienced with climate change. Drier-site species, Douglas-fir and ponderosa pine, were mostly positively correlated with flow. However, a few had significant negative correlations, indicating that they are species with high adaptive capacity. Geographical gradients could explain the variability of the flow-growth relationships for all species except ponderosa pine, although spatial correlations were weak. Subalpine fir, mountain hemlock, and Douglas-fir were spatially dependent on latitude, elevation, and longitude, respectively. Knowledge of geographical variability is crucial in the process of selecting locations where trees are sensitive to the climate variable proposed for reconstruction (Larson et al., 2013). Our results help simplify planning for field collections, and strengthen methodologies, for future streamflow reconstructions by supplying knowledge about which streams, species, elevations, and directions will yield the most robust models in the spatially diverse terrain of the PNW.

The results of the third chapter are limited to the Pacific Northwest region of the United States, and based on findings, the variability in flow-growth responses are likely different in other geographical locations. The results are also focused on streamflow from spring snowmelt, and ponderosa pine and Douglas-fir might be better at predicting late

summer streamflow. Ponderosa pine is shown to correlate well with late summer precipitation (Watson & Luckman, 2011), adding evidence that late-season conditions might affect the flow-growth relationships of these species. Nonetheless, annual streamflow in this region is driven by snowpack, so we feel these methods of investigation are justified. The spatial regressions only explained 26-29% of the overall variability in flow-growth relationships. However, the results are still significant, and kriging estimates are accurate. Other possible explanatory predictors that could account for the majority of the variability could include stand dynamics, climate variability, soils, microsites, and disturbance regimes like fires and insects. There may also be bias because trees in the ITRDB were not all selected to show environmental sensitivity. For example, ponderosa pine and Douglas-fir are used frequently for reconstructions of disturbance history, which can distort the environmental signal. Nonetheless, there are still strong flow-growth relationships with some of these chronologies, like the Telephone Draw chronology, which correlates significantly with streamflow despite being collected to predict insect disturbances (James H Speer, Swetnam, Wickman, & Youngblood, 2001). Another limitation is that this study does not account for changing relationships over time. Because our goal was to characterize spatial relationships, we assumed stable temporal relationships, though growth-climate relationships can change over time (Biondi, 2000; Marcinkowski et al., 2015). Despite these limitations, we still feel strongly that this research could benefit scientists who set out to reconstruct streamflow in high-order, as well as lower-order (run-of-the-mill), streams across the PNW.

Chapter four is a collaborative synthesis of climate change research in the Columbia River Basin (CRB). Climate change presents a need for complex adaptation and mitigation strategies to inform new research in mountainous regions and the CRB while increasing the potential for science and management communities to co-produce actionable science and effective responses to climate change. In this study, we systematically map and analyze the topical and spatial distribution of climate change research in the mountainous headwaters of a major transboundary watershed, the Columbia River Basin (CRB). Results show that spatial distribution and thematic content of research varies across an international border, with greater concentrations of research in the United States than Canada. A general scarcity of social science research and limited interaction between social and biophysical content reinforces the need for increased collaboration between disparate disciplines. Future research

focus areas should include research related to climate change adaptation and mitigation, increased integration between social and biophysical sciences, and collaborations that bridge the international border for a more unified basin-wide focus. Focusing on these new directions for research will increase the potential for science and management communities to co-produce actionable science and effective responses to climate change.

For collaborative Chapter 4, several assumptions and limitations should be considered when interpreting our findings. We used multiple rounds of coding and lines of evidence, but as in any such investigation, errors may occur. Our methods required that each article was categorized as either adaptation, mitigation, or impacts. Therefore, while studies that address both mitigation and adaptation may exist, they would have been coded in only one category. Further, we identified several areas of thematic content, which we argue have two important, yet poorly integrated, topics or disciplines. To support these conclusions, we used multiple lines of evidence where possible, but these analytical methods can only identify research integration that is relatively infrequent. Importantly, the identification of geographic disparities or relatively under-studied research themes does not necessarily imply a need for more research. The findings presented here provide a basis to aid experts in the subjective evaluation of areas that may need more research. Moreover, while we used multiple databases to identify research, there are likely some relevant articles that were omitted. In particular, because our study was limited to peer-reviewed literature, grey literature such as legal reviews (e.g., Cosens and Fremier, 2014) is not represented. This may, in part, explain why we identified so few policy-related studies. It is also important to note that the literature search was conducted in December 2016; while there are undoubtedly many new studies available, we expect that the general patterns and trends characterizing the science conducted in this region have remained relatively constant.

Overall, this dissertation can be utilized to provide insight into dendrochronological techniques as well as a guide to silvicultural management in moist mixed-coniferous forests. This study lends support that forest management can assist tree growth and alter growth-drought relationships depending on species. This dissertation also lends evidence to the decades-long theory that trees growing the edges of their ranges show higher sensitivity to limiting factors.

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Appendix A - Supplemental material for Chapter 3

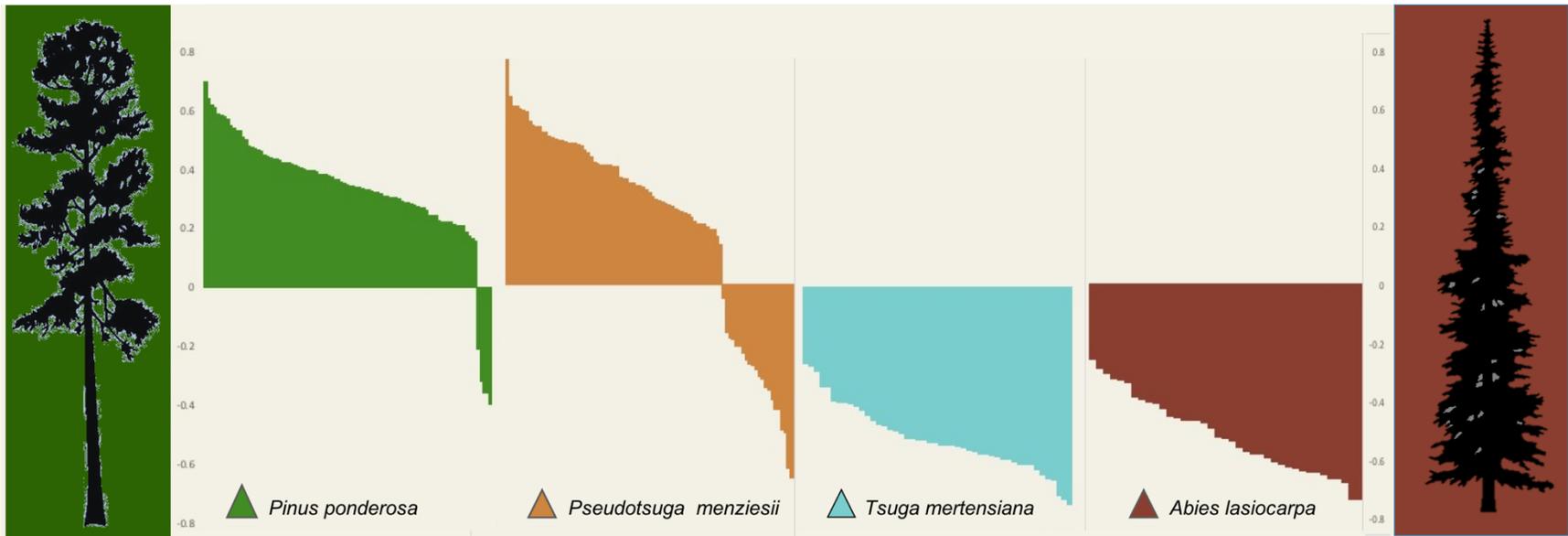


Figure A. 1. Bar plots of correlation coefficients for each chronologies and streamflow combination

Table A. 1. Meta data from Waterdata.USGS.gov for the original 177 stream gauges used in this study. Note: Includes Identification code for the ITRDB (ITRDB#), geographical information, whether each chronology was used in the interpolations (Used in Interpolation?), information pertaining to lead investigators, and literary citations when reported to ITRDB.

Station ID	Station Name	State	Hydrologic Unit Code	Drainage Area (square miles)	Lat	Long	Elevation (m)
10371500	DEEP CREEK ABOVE ADEL	OR	17120007	249	42.1891667	-120.00056	1518.007632
10384000	CHEWAUCAN RIVER NEAR PAISLEY	OR	17120006	275	42.6847222	-120.56889	1350.264
10393500	SILVIES RIVER NEAR BURNS	OR	17120002	934	43.7152778	-119.17639	1278.636
10396000	DONNER UND BLITZEN RIVER NEAR FRENCH GLEN	OR	17120003	200	42.7911111	-118.86667	1296.6192
12010000	NASELLE RIVER NEAR NASELLE	WA	17100106	54.8	46.3741667	-123.74222	7.3152
12013500	WILLAPA RIVER NEAR WILLAPA	WA	17100106	130	46.65	-123.65278	1.088136
12020000	CHEHALIS RIVER NEAR DOTY	WA	17100103	113	46.6175	-123.27639	92.08008
12027500	CHEHALIS RIVER NEAR GRAND MOUNTAIN	WA	17100103	895	46.7761111	-123.03444	37.68852
12035000	SATSOP RIVER NEAR SATSOP	WA	17100104	299	47.0019444	-123.49361	0
12039300	NORTH FORK QUINAULT NEAR AMANDA PARK	WA	17100102	74.1	47.5961111	-123.62306	188.976
12039500	QUINAULT RIVER AT QUINAULT LAKE	WA	17100102	264	47.4577778	-123.88806	56.26608
12040500	QUEETS RIVER NEAR CLEARWATER	WA	17100102	445	47.5388889	-124.31389	4.4196
12048000	DUNGENESS RIVER NEAR SEQUIM	WA	17110020	156	48.0144444	-123.13139	173.52264
12054000	DUCKABUSH RIVER NEAR BRINNON	WA	17110018	66.5	47.6841667	-123.01028	73.606152
12056500	SKOKOMISH RIVER NEAR BLW STAIRCASE RAPIDS	WA	17110017	57.2	47.5144444	-123.32861	232.336848
12134500	SKYKOMISH RIVER NEAR GOLD BAR	WA	17110009	535	47.8375	-121.66556	63.782448
12144500	SNOQUALMIE RIVER NEAR SNOQUALMIE	WA	17110010	375	47.5452778	-121.84111	36.576
12186000	SAUK RIVER AT WHITECHUCK RIVER	WA	17110006	152	48.1688889	-121.46944	283.464
12189500	SAUK RIVER NEAR SAUK	WA	17110006	714	48.4247222	-121.56722	81.0768
12305500	BOULDER CREEK NEAR LEONIA	ID	17010104	56	48.5983333	-116.09167	792.48
12306500	MOYIE RIVER AT EASTPORT	ID	17010105	570	48.9994444	-116.17861	798.594288
12307500	MOYIE RIVER AT EILEEN	ID	17010105	755	48.7741667	-116.15722	647.5476
12311000	DEEP CREEK AT MOTAVIA	ID	17010104	133	48.6333333	-116.4	548.64
12316800	MISSION CREEK NEAR COPELAND	ID	17010104	23	48.9316667	-116.33333	857.8596

12318500	KOOTENAI RIVER NEAR COPELAND	ID	17010104	13400	48.9119444	-116.41639	518.16
12321500	BOUNDARY CREEK NEAR PORTHILL	ID	17010104	97	48.9972222	-116.56806	539.496
12322000	KOOTENAI RIVER AT PORTHILL	ID	17010104	13700	49	-116.50278	518.16
12392300	PACK RIVER NEAR COLBURN	ID	17010214	124	48.42	-116.50056	649.224
12393500	PRIEST RIVER AT OUTLET OF PRIEST LAKE	ID	17010215	572	48.4833333	-116.9	743.099352
12401500	KETTLE RIVER NEAR FERRY	WA	17020002	2220	48.9813889	-118.76528	559.85664
12404500	KETTLE RIVER NEAR LAURIER	WA	17020002	3800	48.9844444	-118.21528	434.4924
12409000	COLVILLE RIVER AT KETTLE FALLS	WA	17020003	1007	48.5944444	-118.06139	426.72
12411000	COEUR D'ALENE RIVER AT SHOSHONE CREEK NEAR PRICHARD	ID	17010301	335	47.7083333	-115.97639	757.428
12413000	COEUR D'ALENE RIVER AT ENAVILLE	ID	17010301	895	47.5722222	-116.25278	640.08
12413500	COUER D'ALENE RIVER NEAR CATALDO	ID	17010303	1220	47.5638889	-116.30694	640.08
12414500	ST JOE RIVER AT CALDER	ID	17010304	1030	47.2747222	-116.18806	661.952448
12414900	ST MARIES RIVER NEAR SANTA	ID	17010304	275	47.1763889	-116.49167	784.725888
12415000	ST MARIES RIVER AT LOTUS	ID	17010304	437	47.2444444	-116.62361	653.296128
12416000	HAYDEN CREEK BELOW NORTH FORK NEAR HAYDEN LAKE	ID	17010305	22	47.8227778	-116.65278	722.376
12422500	SPOKANE RIVER AT SPOKANE	WA	17010305	4290	47.6594444	-117.44806	517.12368
12424000	HANGMAN CREEK AT SPOKANE	WA	17010306	689	47.6527778	-117.44861	523.469616
12427000	LITTLE SPOKANE RIVER AT ELK	WA	17010308	115	48.0222222	-117.27194	569.976
12431000	LITTLE SPOKANE RIVER AT DARTFORD	WA	17010308	665	47.7847222	-117.40333	484.632
12442500	SIMILKAMEEN RIVER NEAR NIGHTHAWK	WA	17020007	3550	48.9847222	-119.61722	346.77096
12445000	OKANOGAN RIVER NEAR TONASKET	WA	17020006	7260	48.6325	-119.46056	262.365744
12447200	OKANOGAN RIVER AT MALOTT	WA	17020006	8080	48.2805556	-119.70306	238.82604
12447390	ANDREWS CREEK NEAR MAZAMA	WA	17020008	22.1	48.8230556	-120.14472	1310.64
12449500	METHOW RIVER AT TWISP	WA	17020008	1301	48.3652778	-120.115	481.584
12449950	METHOW RIVER NEAR PATEROS	WA	17020008	1772	48.0775	-119.98389	274.32
12451000	STEHEKIN RIVER AT STEHEKIN	WA	17020009	321	48.3297222	-120.69056	334.8228
12452800	ENTIAT RIVER NEAR ARDENVOIR	WA	17020010	203	47.8186111	-120.42194	475.783656
12454000	WHITE RIVER NEAR PLAIN	WA	17020011	150	47.8741667	-120.86917	573.609216
12455000	WENATCHEE RIVER BELOW WENATCHEE LAKE	WA	17020011	273	47.8305556	-120.775	566.928
12457000	WENATCHEE RIVER AT PLAIN	WA	17020011	591	47.7630556	-120.665	550.164

12458000	ICICLE CREEK ABOVE SNOW CREEK NEAR LEAVENWORTH	WA	17020011	193	47.5411111	-120.71889	441.96
12459000	WENATCHEE RIVER AT PESHASTIN	WA	17020011	1000	47.5833333	-120.61278	313.346592
12462500	WENATCHEE RIVER AT MONITOR	WA	17020011	1301	47.4994444	-120.42333	207.264
12465000	CRAB CREEK AT IRBY	WA	17020013	1042	47.3605556	-118.84889	422.54424
12465500	WILSON CREEK AT WILSON CREEK	WA	17020013	427	47.4305556	-119.10278	390.144
12488500	AMERICAN RIVER NEAR NILE	WA	17030002	78.9	46.9775	-121.16806	822.96
12500500	NORTH FORK AHTANUM CREEK NEAR TAMPICO	WA	17030003	68.9	46.5611111	-120.91944	746.76
13032000	BEAR CREEK ABOVE RESERVOIR NEAR IRWIN	ID	17040104	77.1	43.2833333	-111.22139	1719.072
13037500	SNAKE RIVER NEAR HEISE	ID	17040104	5752	43.6125	-111.65917	1528.66344
13063000	BLACKFOOT RIVER ABOVE RESERVOIR	ID	17040207	350	42.8166667	-111.50972	1908.048
13073000	PORTNEUF RIVER AT TOPAZ	ID	17040208	570	42.625	-112.08889	1499.0064
13075000	MARSH CREEK NEAR MCCAMMON	ID	17040208	353	42.63	-112.22472	1267.968
13082500	GOOSE CREEK ABOVE TRAPPER CREEK NEAR OAKLEY	ID	17040211	633	42.125	-113.93889	1453.896
13092000	ROCK CREEK NEAR ROCK CREEK	ID	17040212	80	42.3563889	-114.30333	1322.832
13113000	BEAVER CREEK AT SPENCER	ID	17040214	120	44.3555556	-112.17778	1783.08
13120000	NORTH FORK BIG LOST RIVER AT WILD HORSE NEAR CHILLY	ID	17040218	114	43.9330556	-114.11306	2078.736
13120500	BIG LOST RIVER AT HOWELL RANCH NEAR CHILLY	ID	17040218	450	43.9983333	-114.02	2018.37036
13135500	BIG WOOD RIVER NEAR KETCHUM	ID	17040219	137	43.7863889	-114.42417	1901.952
13139510	COMBINATION BIG WOOD RIVER SLOUGH AT HAILEY	ID	17040219	640	43.5180556	-114.31944	1615.796616
13147900	LITTLEWOOD RIVER ABOVE HIGH FIVE CREEK NEAR CAREY	ID	17040221	248	43.4916667	-114.05833	1621.536
13162500	EAST FORK JARBIDGE RIVER NEAR THREE CREEK	ID	17050102	84.6	42.0333333	-115.37222	1569.72
13167500	EAST FORK BRUNEAU RIVER NEAR HOT SPRING	ID	17050102	620	42.5569444	-115.50972	1177.96056
13168500	BRUNEAU RIVER NEAR HOT SPRING IDAHO	ID	17050102	2630	42.7711111	-115.71944	792.0228
13169500	BIG JACKS CREEK NEAR BRUNEAU	ID	17050102	253	42.785	-115.98333	856.488
13178000	JORDON CREEK ABOVE LONE TREE CREEK NEAR JORDAN VALLEY	ID	17050108	440	42.8741667	-116.95333	1371.517704
13185000	BOISE RIVER NEAR TWIN SPRINGS	ID	17050112	830	43.6591667	-115.72611	992.33736
13186000	SOUTH FORK BOISE RIVER NEAR FEATHERVILLE	ID	17050113	635	43.4944444	-115.30556	1285.81404
13200000	MORES CREEK ABOVE ROBIE CREEK NEAR ARROWROCK DAM	ID	17050112	399	43.6480556	-115.98889	950.976

13200500	ROBIE CREEK NEAR ARROWROCK DAM	ID	17050112	15.8	43.6302778	-115.99861	938.784
13214000	MALHEUR RIVER NEAR DREWSEY	OR	17050116	910	43.7847222	-118.33056	1060.438824
13235000	SOUTH FORK PAYETTE RIVER AT LOWMAN	ID	17040120	456	44.0852778	-115.62111	1155.192
13240000	LAKE FORK PAYETTE RIVER ABOVE JUMBO CREEK NEAR MCCALL	ID	17040123	48.9	44.9136111	-115.99639	1566.672
13250600	BIG WILLOW CREEK NEAR EMMETT	ID	17050122	47.4	44.0736111	-116.48611	856.488
13251500	WEISER RIVER AT TAMARACK	ID	17050124	36.5	44.9469444	-116.38194	1243.584
13260000	PINE CREEK NEAR CAMBRIDGE	ID	17050124	54	44.5897222	-116.73667	853.44
13261000	LITTLE WEISER RIVER NEAR INDIAN VALLEY	ID	17050124	81.9	44.4894444	-116.39	990.6
13267000	MANN CREEK NEAR WEISER	ID	17050124	56	44.3916667	-116.89444	862.584
13269000	SNAKE RIVER AT WEISER	ID	17050124	69200	44.2455556	-116.98	636.007872
13295000	VALLEY CREEK AT STANLEY	ID	17060201	147	44.2225	-114.93028	1896.407688
13295500	SALMON RIVER BELOW VALLEY CREEK AT STANLEY	ID	17060201	501	44.2333333	-114.91667	1886.809536
13296000	YANKEE FORK SALMON RIVER NEAR CLAYTON	ID	17060201	195	44.2875	-114.71972	1813.56
13296500	SALMON RIVER BELOW YANKEE FORK NEAR CLAYTON	ID	17060201	802	44.2683333	-114.73194	1798.32
13298500	SALMON RIVER NEAR CHALLIS	ID	17060201	1800	44.3786111	-114.255	1573.984152
13299000	CHALLIS CREEK NEAR CHALLIS	ID	17060201	85	44.5722222	-114.30556	1636.56264
13302500	SALMON RIVER AT SALMON	ID	17060203	3760	45.1833333	-113.89444	1192.115472
13305000	LEMHI RIVER NEAR LEMHI	ID	17060204	895	44.94	-113.63778	1511.808
13306500	PANTHER CREEK NEAR SHOUP	ID	17060203	529	45.3061111	-114.39194	995.159808
13307000	SALMON RIVER NEAR SHOUP	ID	17060203	6270	45.3222222	-114.43972	961.24776
13308500	MIDDLE FORK SALMON RIVER NEAR CAPEHORN	ID	17060205	138	44.4083333	-115.17222	1961.388
13309000	BEAR VALLEY CREEK NEAR CAPE HORN	ID	17060205	183	44.4333333	-115.28333	1932.432
13310500	SOUTH FORK SALMON RIVER NEAR KNOX	ID	17060208	92	44.6541667	-115.70139	1551.526488
13311000	EAST FORK OF SOUTH FORK SALMON RIVER AT STIBNITE	ID	17060208	19.6	44.9058333	-115.32833	1969.008
13313000	JOHNSON CREEK AT YELLOW PINE	ID	17060208	213	44.9622222	-115.49944	1419.0726
13316500	LITTLE SALMON RIVER AT RIGGNS	ID	17060210	576	45.4130556	-116.32472	536.448
13317000	SALMON RIVER AT WHITE BIRD	ID	17060209	13550	45.7502778	-116.32306	430.57572
13319000	GRANDE RONDE RIVER AT LA GRANDE	OR	17060104	678	45.3463889	-118.12389	861.441
13331500	MINAM RIVER AT MINAM	OR	17060105	240	45.62	-117.72556	774.338304

13334700	ASOTIN CREEK BELOW KEARNEY GULCH NEAR ASOTIN	WA	17060103	170	46.3263889	-117.15167	332.232
13336500	SELWAY RIVER NEAR LOWELL	ID	17060302	1910	46.0866667	-115.51278	469.392
13337000	LOCHSA RIVER NEAR LOWELL	ID	17060303	1180	46.1505556	-115.58639	442.868304
13337500	SOUTH FORK CLEARWATER RIVER NEAR ELK CITY	ID	17060305	261	45.8247222	-115.52667	1163.199096
13338000	SOUTH FORK CLEARWATER RIVER NEAR GRANGEVILLE	ID	17060305	865	45.9136111	-116.00472	557.784
13338500	SOUTH FORK CLEARWATER RIVER AT STITES	ID	17060305	1150	46.0866667	-115.97556	396.24
13339000	CLEARWATER RIVER AT KAMIAH	ID	17060306	4850	46.2333333	-116.01667	354.336096
13340000	CLEARWATER RIVER AT OROFINO	ID	17060306	5580	46.4786111	-116.25639	301.99584
13340500	NORTH FORK CLEARWATER RIVER AT BUNGALOW RANGER STATION	ID	17060307	996	46.6313889	-115.50778	682.752
13340600	NORTH FORK CLEARWATER RIVER NEAR CANYON RANGER STATION	ID	17060307	1360	46.8405556	-115.61972	505.968
13341000	NORTH FORK CLEARWATER RIVER AT AHSAHKA	ID	17060308	2440	46.0544444	-116.31944	295.601136
13342500	CLEARWATER RIVER AT SPALDING	ID	17060306	9570	46.4486111	-116.82639	234.845352
13345000	PALOUSE RIVER NEAR POTLATCH	ID	17060108	317	46.9152778	-116.95	748.317528
13348000	SOUTH FORK PALOUSE RIVER AT PULLMAN	WA	17060108	132	46.7325	-117.18	709.05624
13349210	PALOUSE RIVER BELOW SOUTH FORK AT COLFAX	WA	17060108	796	46.8897222	-117.36917	588.940656
13351000	PALOUSE RIVER AT HOOPER	WA	17060108	2500	46.7586111	-118.14778	317.23584
14010000	SOUTH FORK WALLA WALLA RIVER NEAR MILTON FREEWATER	OR	17070102	63	45.83	-118.16889	624.84
14020000	UMATILLA RIVER ABOVE MEACHAM CREEK NEAR GIBBON	OR	17070103	131	45.7197222	-118.32222	565.346088
14034500	WILLOW CREEK AT HEPPNER	OR	17070104	96.8	45.3505556	-119.54889	595.192104
14042500	CAMAS CREEK NEAR UKIAH	OR	17070202	121	45.1569444	-118.81944	1093.808328
14044000	MIDDLE FORK JOHN DAY RIVER AT RITTER	OR	17070203	515	44.8888889	-119.14028	775.581888
14046500	JOHN DAY RIVER AT SERVICE CREEK	OR	17070204	5090	44.7938889	-120.00556	497.561616
14048000	JOHN DAY RIVER AT MCDONALD FERRY	OR	17070204	7580	45.5877778	-120.40833	119.563896
14080500	CROOKED RIVER NEAR PRINEVILLE	OR	17070304	2700	44.1138889	-120.79444	935.99508
14101500	WHITE RIVER BELOW TYGH VALLEY	OR	17070306	417	45.2416667	-121.09389	265.22172
14105700	COLUMBIA RIVER AT THE DALLES	OR	17070105	237000	45.6075	-121.17222	0
14113000	KLICKITAT RIVER NEAR PITT	WA	17070106	1297	45.7566667	-121.20889	88.05672
14137000	SANDY RIVER NEAR MARMOT	OR	17080001	262	45.3916667	-122.12778	222.504

14150300	FALL CREEK NEAR LOWELL	OR	17090001	118	43.9708333	-122.6375	257.379216
14154500	ROW RIVER ABOVE PITCHER CREEK NEAR DORENA	OR	17090002	211	43.7361111	-122.87222	260.957568
14159000	MCKENZIE RIVER AT MCKENZIE BRIDGE	OR	17090004	348	44.1791667	-122.12917	432.523392
14178000	NORTH SANTIAM RIVER BELOW BOULDER CREEK NEAR DETROIT	OR	17090005	216	44.7069444	-122.1	484.653336
14179000	BREITENBUSH RIVER ABOVE FRENCH CREEK NEAR DETROIT	OR	17090005	108	44.7527778	-122.12778	479.73996
14185000	SOUTH SANTIAM RIVER BELOW CASCADIA	OR	17090006	174	44.3930556	-122.50972	231.611424
14185900	QUARTZVILLE CREEK NEAR CASCADIA	OR	17090006	99.2	44.5402778	-122.43472	320.04
14188800	THOMAS CREEK NEAR SCIO	OR	17090006	109	44.7116667	-122.76528	116.080032
14190500	LUCKIAMUTE RIVER NEAR SUVER	OR	17090003	240	44.7833333	-123.23333	52.401216
14191000	WILLAMETTE RIVER AT SALEM	OR	17090007	7280	44.9444444	-123.04167	32.351472
14193000	WILLAMINA CREEK NEAR WILLAMINA	OR	17090008	64.7	45.1430556	-123.49306	96.012
14198500	MOLALLA RIVER ABOVE PC NEAR WILHOIT	OR	17090009	97	45.0097222	-122.47917	241.20348
14201000	PUDDING RIVER NEAR MOUNT ANGEL	OR	17090009	204	45.0630556	-122.82917	36.502848
14208000	CLACKAMAS RIVER AT BIG BOTTOM	OR	17090011	136	45.0166667	-121.91944	621.792
14222500	EAST FORK LEWIS RIVER NEAR HEISSON	WA	17080002	125	45.8369444	-122.465	108.75264
14232500	CISPUS RIVER NEAR RANDLE	WA	17080004	321	46.4416667	-121.86278	372.34368
14233400	COWLITZ RIVER NEAR RANDLE	WA	17080004	1030	46.4702778	-122.0975	243.663216
14245000	COWEMAN RIVER NEAR KELSO	WA	17080005	119	46.1491667	-122.89583	9.144
14251500	YOUNGS RIVER NEAR ASTORIA	OR	17080006	40.1	46.0666667	-123.78889	19.284696
14301000	NEHALEM RIVER NEAR FOSS	OR	17100202	667	45.7041667	-123.75417	9.93648
14301500	WILSON RIVER NEAR TILLAMOOK	OR	17100203	161	45.4847222	-123.68889	21.912072
14303600	NESTUCCA RIVER NEAR BEAVER	OR	17100203	180	45.2666667	-123.84583	13.1064
14306400	FIVE RIVERS NEAR FISHER	OR	17100205	114	44.3375	-123.82639	39.624
14306500	ALSEA RIVER NEAR TIDEWATER	OR	17100205	334	44.3861111	-123.83056	14.679168
14307620	SIUSLAW RIVER NEAR MAPLETON	OR	17100206	588	44.0625	-123.88194	12.4968
14307700	JACKSON CREEK NEAR TILLER	OR	17100302	152	42.9541667	-122.82778	378.0282
14308000	SOUTH UMPQUA RIVER AT TILLER	OR	17100302	449	42.9305556	-122.94722	302.30064
14316700	STEAMBOAT CREEK NEAR GLIDE	OR	17100301	227	43.35	-122.72778	343.98204
14318000	LITTLE RIVER AT PELL	OR	17100301	177	43.2527778	-123.025	252.474984
14321000	UMPQUA RIVER NEAR ELKTON	OR	17100303	3683	43.5861111	-123.55417	27.560016

14325000	SOUTH FORK COQUILLE RIVER AT POWERS	OR	17100305	169	42.8916667	-124.06944	60.173616
14328000	ROGUE RIVER ABOVE PROSPECT	OR	17100307	312	42.775	-122.49861	798.576
14338000	ELK CREEK NEAR TRAIL	OR	17100307	129	42.675	-122.74389	455.343768
14359000	ROGUE RIVER AT RAYGOLD NEAR CENTRAL POINT	OR	17100308	2053	42.4375	-122.98611	341.918544
14362000	APPLEGATE RIVER NEAR COPPER	OR	17100309	225	42.0583333	-123.11389	532.641048
14377000	ILLINOIS RIVER AT KERBY	OR	17100311	364	42.1972222	-123.65556	375.5136
14377100	ILLINOIS RIVER NEAR KERBY	OR	17100311	380	42.2319444	-123.6625	365.39424
14400000	CHETCO RIVER NEAR BROOKINGS	OR	17100312	271	42.1236111	-124.18611	15.24

Table A. 2. Meta data for the original 195 tree-ring chronologies used in this study. Note: Includes Identification code for the ITRDB (ITRDB#), geographical information, whether each chronology was used in the interpolations (Used in Interpolation?), information pertaining to lead investigators, and literary citations when reported to ITRDB

Site Name in ITRDB	Species	State	ITRDB#	Lat	Lon	Elevation (m)	Used in Interpolation?	Investigator	Full Citation
Greenhorn Mountain	ABLA	OR	OR084	44.7	-118.55	2295	Y	King	Technical reports regarding the Greenhorn project are retained by: Vicky Erickson USDA Forest Service Umatilla, Wallowa-Whitman and Malheur National Forests 2517 SW Hailey Ave. Pendleton, OR 97801 541-278-3715
Mt Hood Mid	ABLA	OR	OR080	45.33	-121.67	1790	Y	Peterson	No associated publication or not reported ITRDB
Blue Mountain High	ABLA	WA	WA127	47.95	-123.26	1800	N	Peterson	No associated publication or not reported ITRDB
Blue Mountain Low	ABLA	WA	WA125	47.94	-123.26	1595	N	Peterson	No associated publication or not reported ITRDB
Blue Mountain Mid	ABLA	WA	WA126	47.95	-123.25	1340	N	Peterson	No associated publication or not reported ITRDB
Deer Park	ABLA	WA	WA035	47.85	-123.28	1860	N	Brubaker	No associated publication or not reported ITRDB
Dodger Point High	ABLA	WA	WA118	47.87	-123.51	1725	N	Peterson	No associated publication or not reported ITRDB
Dodger Point Low	ABLA	WA	WA116	47.86	-123.49	1395	Y	Peterson	No associated publication or not reported ITRDB
Dodger Point Mid	ABLA	WA	WA117	47.87	-123.5	1525	N	Peterson	No associated publication or not reported ITRDB
Hart Pass N1	ABLA	WA	WA070	48.7	-120.67	1925	Y	Peterson	No associated publication or not reported ITRDB
Hart Pass N2	ABLA	WA	WA073	48.73	-120.65	2000	N	Peterson	No associated publication or not reported ITRDB
Hart Pass V1	ABLA	WA	WA076	48.68	-120.64	1875	N	Peterson	No associated publication or not reported ITRDB
Hart Pass V2	ABLA	WA	WA077	48.75	-120.61	1825	N	Peterson	No associated publication or not reported ITRDB
Hart's Pass Low	ABLA	WA	WA128	48.72	-120.61	1495	N	Peterson	No associated publication or not reported ITRDB
Hart's Pass S1(H)	ABLA	WA	WA080	48.68	-120.6	1825	N	Peterson	No associated publication or not reported ITRDB
Klahhane Ridge High	ABLA	WA	WA124	47.99	-123.42	1820	N	Peterson	No associated publication or not reported ITRDB
Klahhane Ridge Low	ABLA	WA	WA122	47.99	-123.42	1375	N	Peterson	No associated publication or not reported ITRDB

Klahhane Ridge Medium	ABLA	WA	WA123	47.99-123.41	1560	N	Peterson	No associated publication or not reported ITRDB
Lake Minotaur Low	ABLA	WA	WA098	47.84-121.04	1130	N	Peterson	No associated publication or not reported ITRDB
Lake Minotaur M	ABLA	WA	WA099	47.84-121.03	1465	Y	Peterson	No associated publication or not reported ITRDB
Lake Mnotaur H	ABLA	WA	WA100	47.85-121.04	1740	N	Peterson	No associated publication or not reported ITRDB
Mt Adams High	ABLA	WA	WA106	46.2 -121.57	1890	Y	Peterson	No associated publication or not reported ITRDB
Mt Adams Low	ABLA	WA	WA104	46.12-121.43	1495	Y	Peterson	No associated publication or not reported ITRDB
Mt Adams Mid	ABLA	WA	WA105	46.15-121.51	1735	Y	Peterson	No associated publication or not reported ITRDB
Mt Dana High	ABLA	WA	WA121	47.79-123.49	1860	N	Peterson	No associated publication or not reported ITRDB
Mt Dana Low	ABLA	WA	WA119	47.79-123.49	1540	N	Peterson	No associated publication or not reported ITRDB
Mt Dana Mid	ABLA	WA	WA120	47.79-123.49	1675	N	Peterson	No associated publication or not reported ITRDB
Mt Rainier High	ABLA	WA	WA112	46.81-121.79	1830	N	Peterson	No associated publication or not reported ITRDB
Mt Rainier Low	ABLA	WA	WA110	46.79-121.81	1425	N	Peterson	No associated publication or not reported ITRDB
Mt Rainier Mid	ABLA	WA	WA111	46.8 -121.8	1645	Y	Peterson	No associated publication or not reported ITRDB
Clearwater River	PIPO	ID	ID019	45.81-115.8	1060	Y	Pettit	Joseph L. Pettit, R. Justin Derosé, James N. Long. 2018. Climatic Drivers of Ponderosa Pine Growth in Central Idaho. Tree-Ring Research, Vol. 74, No. 2, pp. 172-185. DOI: 10.3959/1536-1098-74.2.172
East Side	PIPO	ID	ID015	43.75-116.1	1825	Y	Wilkins	Cutter, A. and Wilkins, D. (2012). Development of a tree-ring chronology for the Boise Front. Idaho NSF EPSCoR REU Summer Research Conference, Boise State University, July 29, 2012.
Kenally Creek	PIPO	ID	ID018	44.78-115.87	1800	Y	Pettit	Joseph L. Pettit, R. Justin Derosé, James N. Long. 2018. Climatic Drivers of Ponderosa Pine Growth in Central Idaho. Tree-Ring Research, Vol. 74, No. 2, pp. 172-185. DOI: 10.3959/1536-1098-74.2.172
Laird Park	PIPO	ID	ID003	46.95-116.63	1219	N	Brubaker	No associated publication or not reported ITRDB
Lake Couer d'Alene	PIPO	ID	ID001	47.63-116.47	960	N	Brubaker	No associated publication or not reported ITRDB
Wallace	PIPO	ID	ID002	47.53-115.9	1395	Y	Brubaker	No associated publication or not reported ITRDB

Wellner Cliffs Research Natural Area	PIPO	ID	ID016	48.37-116.79	903	Y	Knapp	No associated publication or not reported ITRDB
Bally Mountain	PIPO	OR	OR033	45.28-118.57	NA	N	Wickman	No associated publication or not reported ITRDB
Big Sink	PIPO	OR	OR038	45.78-117.92	1206	N	Wickman	No associated publication or not reported ITRDB
Blue Jay Springs	PIPO	OR	OR055	42.92-121.53	1490	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Calimus Butte	PIPO	OR	OR059	42.63-121.53	2020	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Crater Lake	PIPO	OR	OR058	42.78-122.07	1370	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Cross Canyon	PIPO	OR	OR029	45.97-117.68	1317	N	Swetnam	No associated publication or not reported ITRDB
Deschutes	PIPO	OR	OR051	43.47-121.4	1420	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Diamond Lake	PIPO	OR	OR054	43.05-121.57	1510	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Drumhill Ridge	PIPO	OR	OR031	45.47-118.2	NA	Y	Wickman	No associated publication or not reported ITRDB
Emigrant Springs	PIPO	OR	OR034	45.5 -118.48	1169	N	Wickman	No associated publication or not reported ITRDB
Experimental Forest	PIPO	OR	OR049	43.72-121.6	1530	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The Univeristy of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.

Fish Lake	PIPO	OR	OR039	45	-117.07	1600	N	Wickman	No associated publication or not reported ITRDB
Grizzly Bear	PIPO	OR	OR030	45.97	-117.72	1231	Y	Swetnam	No associated publication or not reported ITRDB
Indian Crossing	PIPO	OR	OR032	45.12	-117.02	NA	N	Wickman	No associated publication or not reported ITRDB
Junction HW 51 & 57	PIPO	OR	OR052	43.32	-121.75	1420	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Lakeview	PIPO	OR	OR002	42.1	-120.57	1829	Y	Parker	No associated publication or not reported ITRDB
Lava Cast Forest	PIPO	OR	OR090	43.68	-121.25	1500	Y	Pohl	Pohl, K.A., K.S. Hadley, and K.B. Arabas. 2002. A 545-Year drought reconstruction for Central Oregon. <i>Physical Geography</i> 23(4): 302-320.
Little Aspen Butte	PIPO	OR	OR027	42.27	-122.08	1650	Y	Graumlich	No associated publication or not reported ITRDB
Long Prairie	PIPO	OR	OR001	45.15	-120.12	1224	Y	Brubaker	No associated publication or not reported ITRDB
Lookout Pass	PIPO	OR	OR035	45.83	-117.8	1372	N	Wickman	No associated publication or not reported ITRDB
Lookout Pass Low	PIPO	OR	OR046	43.75	-121.65	1320	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Lugar Spring	PIPO	OR	OR040	45.77	-117.97	1200	N	Wickman	No associated publication or not reported ITRDB
Mill Creek	PIPO	OR	OR085	45.5	-121.42	1002	Y	Knapp	Soulé, P.T. and Knapp, P.A. 2006. Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO2 fertilization effect? <i>New Phytologist</i> 171:379-390.
Paulina	PIPO	OR	OR005	44.27	-119.88	1311	Y	Parker	No associated publication or not reported ITRDB
Pringle Falls Fire	PIPO	OR	OR047	43.73	-121.65	1320	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Skookum Butte	PIPO	OR	OR053	43.23	-121.65	1670	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Summit Spring	PIPO	OR	OR037	45.68	-117.47	1354	Y	Wickman	No associated publication or not reported ITRDB

Surveyor Flow	PIPO	OR	OR050	43.62-121.3	1550	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Telephone Draw	PIPO	OR	OR056	42.93-121.62	1550	Y	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Telephone Draw South	PIPO	OR	OR057	42.75-121.52	1550	N	Speer	Speer, J.H. 1997. A dendrochronological record of pandora moth (<i>Coloradia pandora</i> , Blake) outbreaks in central Oregon. MS thesis, The University of Arizona. Tucson, 159pp.; Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A., 2000. Changes in pandora moth outbreak dynamics during the past 622 years. Submitted to Ecology.
Union	PIPO	OR	OR004	45.15-117.62	1433	Y	Parker	No associated publication or not reported ITRDB
Wenaha	PIPO	OR	OR041	45.82-117.67	738	Y	Wickman	No associated publication or not reported ITRDB
Aenas Mountain	PIPO	WA	WA011	48.57-119.15	1285	Y	Brubaker	No associated publication or not reported ITRDB
Bear Creek	PIPO	WA	WA037	48.28-120.23	1085	Y	Brubaker	No associated publication or not reported ITRDB
Bear Creek Ridge	PIPO	WA	WA136	46.7 -120.91	910	Y	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602263
Blewett Pass	PIPO	WA	WA059	47.35-120.55	1240	Y	Graumlich	No associated publication or not reported ITRDB
Boulder Creek	PIPO	WA	WA043	48.58-120.17	701	N	Ferguson	No associated publication or not reported ITRDB
Winthrop Box Canyon	PIPO	WA	WA026	45.98-120.6	775	N		No associated publication or not reported ITRDB
Burge Mountain	PIPO	WA	WA137	48.78-120.27	1100	N	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602264
Colockum Pass	PIPO	WA	WA038	47.2 -120.28	1651	Y	Brubaker	No associated publication or not reported ITRDB
Foggy Dew	PIPO	WA	WA138	48.18-120.26	1230	N	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602265
Fort Lewis	PIPO	WA	WA018	47.03-122.58	61	Y	Brubaker	No associated publication or not reported ITRDB
Government Camp	PIPO	WA	WA015	47.65-120.43	1775	Y	Brubaker	No associated publication or not reported ITRDB

Indian Ridge	PIPO	WA	WA013	46.22-117.7	918	Y	Brubaker	No associated publication or not reported ITRDB
Kamiak Butte	PIPO	WA	WA012	46.85-117.17	765	N	Brubaker	No associated publication or not reported ITRDB
Lucky Point	PIPO	WA	WA010	48.5 -118.8	765	N	Brubaker	No associated publication or not reported ITRDB
North Fork Campground	PIPO	WA	WA060	48 -120.6	915	Y	Graumlich	No associated publication or not reported ITRDB
Rattlesnake Ridge	PIPO	WA	WA139	48.31-118.45	965	Y	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602264
Sneed Mountain	PIPO	WA	WA140	48.59-119.14	1150	Y	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602265
Sugar Loaf Lake	PIPO	WA	WA141	48.6 -119.7	850	N	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602266
Tronson Meadow Ridge	PIPO	WA	WA142	47.34-120.56	1400	N	Wise	Wise, E.K. and M.P. Dannenberg. 2017. Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. <i>Science Advances</i> , 3, e1602263, doi: 10.1126/sciadv.1602267
War Creek	PIPO	WA	WA009	48.42-120.4	1224	N	Brubaker	No associated publication or not reported ITRDB
Windy Meadows	PIPO	WA	WA014	45.32-118.8	1071	N	Brubaker	No associated publication or not reported ITRDB
Windy Point Ridge	PIPO	WA	WA016	46.67-120.93	1337	N	Brubaker	No associated publication or not reported ITRDB
Ketchum East	PSME	ID	ID004	43.67-114.33	1829	Y	Ferguson	No associated publication or not reported ITRDB
Salmon River South	PSME	ID	ID005	44.97-113.95	1402	Y	Ferguson	No associated publication or not reported ITRDB
Salmon River Valley	PSME	ID	ID014	44.42-114.25	1700	Y	Biondi	Biondi, F. 1997. Evolutionary and moving response functions in dendroclimatology. <i>Dendrochronologia</i> 15: 139-150.; Biondi, F., D.L. Perkins, D.R. Cayan, and M.K. Hughes. 1999. July temperature during the second millennium reconstructed from Idaho tree rings. <i>Geophysical Research Letters</i> 26: 1445-1448.; Biondi, F. 2000. Are climate-tree growth relationships changing in north-central Idaho? <i>Arctic, Antarctic, and Alpine Research</i> 32: 111-116.
Wellner Cliffs Research Natural Area	PSME	ID	ID017	48.37-116.79	903	N	Knapp	No associated publication or not reported ITRDB
Dell Sheep Creek	PSME	MT	MT002	44.55-112.8	2084	Y	Ferguson	No associated publication or not reported ITRDB
Abbot Creek RNA	PSME	OR	OR026	42.92-122.5	1448	Y	Graumlich	No associated publication or not reported ITRDB
Barlow Pass	PSME	OR	OR043	45.32-122.65	1300	Y	Briffa	No associated publication or not reported ITRDB

Santiam Pass	PSME	OR	OR096	44.43-121.95	1139	Y	Ratcliff	No associated publication or not reported ITRDB
Santiam Pass SNOTEL	PSME	OR	OR096	44.43-121.95	1139	Y	Ratcliff	No associated publication or not reported ITRDB
Naomi Peak	PSME	UT	UT538	41.91-111.65	2730	Y	Allen	Eric B. Allen, Tammy M. Rittenour, R. Justin DeRose, Matthew F. Bekker, Roger Kjelgren, Brendan M. Buckley. 2013. A tree-ring based reconstruction of Logan River streamflow, northern Utah. Water Resources Research, 49(12), 8579-8588. doi: 10.1002/2013WR014273
Annete Lake Trail	PSME	WA	WA085	47.37-121.33	798	N	Earle	No associated publication or not reported ITRDB
Big Boulder Creek	PSME	WA	WA003	48.83-118.3	3200	Y	Brubaker	No associated publication or not reported ITRDB
Big Quilcene River Trail	PSME	WA	WA086	47.83-123.03	867	Y	Earle	No associated publication or not reported ITRDB
Boulder Creek	PSME	WA	WA053	47.6 -123.58	988	N	Graumlich	No associated publication or not reported ITRDB
Boulder Shelter	PSME	WA	WA031	47.82-123.15	1550	N	Brubaker	No associated publication or not reported ITRDB
Churchill	PSME	WA	WA001	48.98-118.05	1372	Y	Brubaker	No associated publication or not reported ITRDB
Colville Reservation A	PSME	WA	WA008	48.12-118.78	1253	Y	Brubaker	No associated publication or not reported ITRDB
Colville Reservation B	PSME	WA	WA007	48.25-118.75	988	Y	Brubaker	No associated publication or not reported ITRDB
Cougar Creek	PSME	WA	WA049	48.07-121.33	747	Y	Graumlich	No associated publication or not reported ITRDB
Deer Creek Pass	PSME	WA	WA087	48.33-121.72	1052	N	Earle	No associated publication or not reported ITRDB
Deer Park Burn	PSME	WA	WA020	47.95-123.25	1550	Y	Brubaker	No associated publication or not reported ITRDB
Dry Creek	PSME	WA	WA033	45.88-122.03	810	Y	Brubaker	No associated publication or not reported ITRDB
Eagle Point	PSME	WA	WA036	47.97-123.47	1550	N	Brubaker	No associated publication or not reported ITRDB
Elliot Creek	PSME	WA	WA047	48.05-121.4	805	N	Graumlich	No associated publication or not reported ITRDB
Frying Pan Creek	PSME	WA	WA048	46.88-121.62	1170	Y	Graumlich	No associated publication or not reported ITRDB
Hurricane Ridge	PSME	WA	WA032	47.98-123.47	1550	Y	Brubaker	No associated publication or not reported ITRDB
Lava Beds	PSME	WA	WA027	45.97-121.98	930	N	Brubaker	No associated publication or not reported ITRDB
Long Lake	PSME	WA	WA004	48.48-118.8	1120	N	Brubaker	No associated publication or not reported ITRDB
Mt Angeles	PSME	WA	WA084	47.97123.43	1360	N	Briffa	No associated publication or not reported ITRDB

Mt Pilchuck	PSME	WA	WA034	48.13-121.63	710	N	Brubaker	No associated publication or not reported ITRDB
Nooksak Flass	PSME	WA	WA019	48.9 -121.8	550	N	Brubaker	No associated publication or not reported ITRDB
North Fork White Creek	PSME	WA	WA050	47.02-121.7	914	N	Graumlich	No associated publication or not reported ITRDB
Olympic Road	PSME	WA	WA088	48 -124	267	Y	Earle	No associated publication or not reported ITRDB
Pipeston Canyon Twisp	PSME	WA	WA045	48.42-120.05	914	Y	Ferguson	No associated publication or not reported ITRDB
Rainy Pass	PSME	WA	WA023	48.48-120.73	1468	N	Brubaker	No associated publication or not reported ITRDB
Rimrock Valles	PSME	WA	WA4	46.33-121.17	810	Y	Kaiser	No associated publication or not reported ITRDB
Ross Lake	PSME	WA	WA025	48.73-121.05	612	Y	Brubaker	No associated publication or not reported ITRDB
San Juan Hill	PSME	WA	WA090	47.88-121.33	967	N	Earle	No associated publication or not reported ITRDB
Segelson Pass	PSME	WA	WA041	48.35-121.75	1180	N	Brubaker	No associated publication or not reported ITRDB
Silver Creek	PSME	WA	WA089	46.63-121.83	900	N	Earle	No associated publication or not reported ITRDB
Snackout Road	PSME	WA	WA005	48.83-117.55	1219	Y	Brubaker	No associated publication or not reported ITRDB
Soleduck	PSME	WA	WA055	47.98-123.05	750	Y	Graumlich	No associated publication or not reported ITRDB
St Peters Creek	PSME	WA	WA002	48.77-118.48	1676	Y	Brubaker	No associated publication or not reported ITRDB
Summit Load Road	PSME	WA	WA017	46.67-121.53	1224	N	Brubaker	No associated publication or not reported ITRDB
Swauk Pass	PSME	WA	WA3	47.37-120.3	1250	Y	Kaiser	No associated publication or not reported ITRDB
Tahoma Creek	PSME	WA	WA091	46.8 -121.88	970	N	Earle	No associated publication or not reported ITRDB
The Dalles	PSME	WA	WA62	47.07-121.57	790	N	Graumlich	No associated publication or not reported ITRDB
Tunnel Creek	PSME	WA	WA054	47.23-123.23	830	Y	Graumlich	No associated publication or not reported ITRDB
White Pass	PSME	WA	WA2	46.63-121.48	1120	N	Kaiser	No associated publication or not reported ITRDB
Hoback Ridge	PSME	WY	WY055	43.3 -110.67	1997	Y	Brown	Wise, E.K. 2010. Tree ring record of streamflow and drought in the upper Snake River. Water Resources Research 46 (W11529): doi:10.1029/2010WR009282.
Castle Rock	TSME	OR	OR098	42.92-122.05	2198	N	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. Dendrochronologia, doi: 10.1016/j.dendro.2018.09.003
Crater Lake	TSME	OR	OR042	42.97-122.17	2200	Y	Briffa	No associated publication or not reported ITRDB

Crater Lake East High	TSME	OR	OR075	42.83-122	2300	N	Peterson	No associated publication or not reported ITRDB
Crater Lake East Low	TSME	OR	OR073	42.83-122	1910	N	Peterson	No associated publication or not reported ITRDB
Crater Lake East Mid	TSME	OR	OR074	42.83-122	2075	N	Peterson	No associated publication or not reported ITRDB
Crater Lake West High	TSME	OR	OR078	43 -122.33	2210	N	Peterson	No associated publication or not reported ITRDB
Crater Lake West Low	TSME	OR	OR076	43 -122.33	1950	N	Peterson	No associated publication or not reported ITRDB
Crater Lake West Mid	TSME	OR	OR077	43 -122.33	2017	N	Peterson	No associated publication or not reported ITRDB
Husband Lake	TSME	OR	OR086	44.13-121.83	1820	Y	Heyerdahl	No associated publication or not reported ITRDB
Lane Plateau	TSME	OR	OR087	44.15-121.83	1945	N	Heyerdahl	No associated publication or not reported ITRDB
Lightning Springs	TSME	OR	OR100	42.93-122.17	2186	Y	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.004
Llao Rock	TSME	OR	OR099	42.97-122.15	2221	Y	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.003
McKenzie Pass SNOTEL	TSME	OR	OR097	44.22-121.87	1454	N	Ratcliff	No associated publication or not reported ITRDB
Mt Hood High	TSME	OR	OR066	45.33-121.67	1920	Y	Peterson	No associated publication or not reported ITRDB
Mt Hood Low	TSME	OR	OR064	45.33-121.67	1585	N	Peterson	No associated publication or not reported ITRDB
Mt Hood Timberline Lodge	TSME	OR	OR045	45.33-121.68	1600	N	Briffa	No associated publication or not reported ITRDB
Mt Jefferson High	TSME	OR	OR069	44.67-121.83	1950	N	Peterson	No associated publication or not reported ITRDB
Mt Jefferson Low	TSME	OR	OR067	44.67-121.83	1585	N	Peterson	No associated publication or not reported ITRDB
Mt Jefferson Mid	TSME	OR	OR068	44.67-121.83	1785	Y	Peterson	No associated publication or not reported ITRDB
Mt Scott	TSME	OR	OR101	42.93-122.02	2352	Y	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.005
Obsidian Lava Flow	TSME	OR	OR088	44.18-121.83	1700	N	Heyerdahl	No associated publication or not reported ITRDB

Palisade	TSME	OR	OR104	42.97-122.07	2050	N	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.005
Pinnacle	TSME	OR	OR103	42.91-122.07	2198	Y	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.006
Pumice	TSME	OR	OR102	42.98-122.1	2075	N	Appleton	Sarah Appleton and Scott St. George. 2018. High-elevation mountain hemlock growth as a surrogate for cool-season precipitation in Crater Lake National Park, USA. <i>Dendrochronologia</i> , doi: 10.1016/j.dendro.2018.09.004
Sheridan Mountain High	TSME	OR	OR072	43.83-121.67	2090	N	Peterson	No associated publication or not reported ITRDB
Sheridan Mountain Low	TSME	OR	OR070	43.83-121.67	1755	N	Peterson	No associated publication or not reported ITRDB
Sheridan Mountain Mid	TSME	OR	OR071	43.83-121.67	1920	N	Peterson	No associated publication or not reported ITRDB
Wizard Island	TSME	OR	OR079	43 -122.17	2215	N	Peterson	No associated publication or not reported ITRDB
Bagley Lakes	TSME	WA	WA143	48.86-121.69	1297	N	Marcinkowski	Marcinkowski, Kailey W. and Peterson, David L. 2015. A 350-year Reconstruction of the Response of South Cascade Glacier to Interannual and Interdecadal Climatic Variability. <i>Northwest Science</i> , Vol. 89, issue 1, pp. 14-33, https://www.fs.fed.us/pnw/pubs/journals/pnw_2015_marcinkowski.pdf ; Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. <i>Canadian Journal of Forest Resources</i> , Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231.
Baker Ski	TSME	WA	WA039	48.83-120.65	1330	Y	Brubaker	No associated publication or not reported ITRDB
Chinook Pass	TSME	WA	WA063	46.85-121.5	1660	Y	Graumlich	No associated publication or not reported ITRDB
Easy Pass	TSME	WA	WA144	48.57-120.83	1540	N	Marcinkowski	Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. <i>Canadian Journal of Forest Resources</i> , Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231
Findley Lake	TSME	WA	WA030	47.38-121.5	1270	N	Brubaker	No associated publication or not reported ITRDB
Granite Mountain	TSME	WA	WA056	47.42-121.47	1530	Y	Graumlich	No associated publication or not reported ITRDB
Heather Meadows	TSME	WA	WA134	48.87-121.68	1310	N	Bunn	No associated publication or not reported ITRDB
Hidden Lake	TSME	WA	WA145	48.5 -121.21	1769	N	Marcinkowski	Marcinkowski, Kailey W. and Peterson, David L. 2015. A 350-year Reconstruction of the Response of South Cascade Glacier to Interannual and Interdecadal Climatic

									Variability. Northwest Science, Vol. 89, issue 1, pp. 14-33, https://www.fs.fed.us/pnw/pubs/journals/pnw_2015_marcinkowski.pdf ; Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. Canadian Journal of Forest Resources, Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231.
Hoh Lake High	TSME	WA	WA097	47.9 -123.75	1465	Y	Peterson	No associated publication or not reported ITRDB	
Hoh Lake Low	TSME	WA	WA095	47.9 -123.75	1220	N	Peterson	No associated publication or not reported ITRDB	
Hoh Lake Mid	TSME	WA	WA096	47.9 -123.75	1315	N	Peterson	No associated publication or not reported ITRDB	
Lake Minotaur High	TSME	WA	WA100	47.85-121.04	1740	N	Peterson	No associated publication or not reported ITRDB	
Lake Minotaur Low	TSME	WA	WA098	47.84-121.04	1130	N	Peterson	No associated publication or not reported ITRDB	
Lake Minotaur Mid	TSME	WA	WA099	47.84-121.03	1465	N	Peterson	No associated publication or not reported ITRDB	
Minotaur Lake	TSME	WA	WA146	47.84-121.04	1703	N	Marcinkowski	Marcinkowski, Kailey W. and Peterson, David L. 2015. A 350-year Reconstruction of the Response of South Cascade Glacier to Interannual and Interdecadal Climatic Variability. Northwest Science, Vol. 89, issue 1, pp. 14-33, https://www.fs.fed.us/pnw/pubs/journals/pnw_2015_marcinkowski.pdf ; Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. Canadian Journal of Forest Resources, Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231.	
Mt Rainier High	TSME	WA	WA103	46.83-121.75	1830	Y	Peterson	No associated publication or not reported ITRDB	
Mt Rainier Mid	TSME	WA	WA102	46.83-121.75	1645	N	Peterson	No associated publication or not reported ITRDB	
Mt RainierLow	TSME	WA	WA101	46.83-121.75	1425	N	Peterson	No associated publication or not reported ITRDB	
Oakes Peek	TSME	WA	WA051	48.63-121.37	1140	N	Graumlich	No associated publication or not reported ITRDB	
South Cascade Glacier	TSME	WA	WA147	48.37-121.08	1613	Y	Marcinkowski	Marcinkowski, Kailey W. and Peterson, David L. 2015. A 350-year Reconstruction of the Response of South Cascade Glacier to Interannual and Interdecadal Climatic Variability. Northwest Science, Vol. 89, issue 1, pp. 14-33, https://www.fs.fed.us/pnw/pubs/journals/pnw_2015_marcinkowski.pdf ; Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North	

Thornton Lakes	TSME	WA	WA148	48.68-121.32	1473	N	Marcinkowski	Cascade Range, Washington, USA. Canadian Journal of Forest Resources, Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231.
Thornton Lakes High	TSME	WA	WA094	48.67-121.33	1525	Y	Peterson	Marcinkowski, Kailey; Peterson, David L.; Ettl, Gregory J. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. Canadian Journal of Forest Resources, Vol. 45, pp. 676-699. doi: 10.1139/cjfr-2014-0231
Thornton Lakes Low	TSME	WA	WA092	48.67-121.33	1220	N	Peterson	No associated publication or not reported ITRDB
Thornton Lakes Mid	TSME	WA	WA093	48.67-121.33	1370	N	Peterson	No associated publication or not reported ITRDB
White Pass	TSME	WA	WA066	46.62-121.42	1750	N	Graumlich	No associated publication or not reported ITRDB
Wynoochee Falls	TSME	WA	WA058	47.48-123.58	1140	Y	Graumlich	No associated publication or not reported ITRDB

Table A.3. Meta data used for each spatially interpolated stream-tree combination for all species. SPP. Corr = Correlation coefficients, SPP. Chron = ITRDB name for chronology, and SPP.Month = streamflow month

USGS Station ID	Station Name	State	Subalpine Fir Corr	Subalpine Fir Chron	Subalpine Fir Month	Ponderosa Pine Corr	Pondersa Pine Chron	Ponderosa Pine Month	Douglas-fir Corr	Douglas-fir Chron	Douglas-fir Month	Mountain Hemlock Corr	Mountain Hemlock Chron	Mountain Hemlock Month
12452800	ENTIAT RIVER NEAR ARDENVOIR	WA	-0.7217	Lake Minotaur Mid	Jul	0.6111	Aenas Mountain	May	-0.4868	Cougar Creek	Apr	-0.5744	Baker Ski	Jul
12027500	CHEHALIS RIVER NEAR GRAND MOUNTAIN	WA	-0.4016	Dodger Point Low	Jul	0.4116	Fort Lewis	Jul	-0.2878	Frying Pan Creek	Jul	-0.513	Chinook Pass	Jul
12035000	SATSOP RIVER NEAR SATSOP	WA	-0.4804	Dodger Point Low	Jul	0.3417	Fort Lewis	Jul	-0.3189	Hurricane Ridge	Jul	-0.566	Chinook Pass	Jul
12457000	WENATCHEE RIVER AT PLAIN	WA	-0.7217	Lake Minotaur Mid	Jul	0.4479	Blewett Pass	Apr	-0.6183	Frying Pan Creek	Jul	-0.5567	Chinook Pass	Jul
14307700	JACKSON CREEK NEAR TILLER	OR	NA	NA	NA	0.3505	Deschutes	Apr	0.2673	Abbot Creek RNA	May	-0.3957	Crater Lake	Jul
14328000	ROGUE RIVER ABOVE PROSPECT	OR	NA	NA	NA	0.4139	Deschutes	Jul	-0.2711	Abbot Creek RNA	Jun	-0.7327	Crater Lake	Jul
14308000	SOUTH UMPQUA RIVER AT TILLER	OR	NA	NA	NA	0.2909	Drumhill Ridge	Jul	0.1587	Abbot Creek RNA	May	-0.5152	Crater Lake	Jul
12186000	SAUK RIVER AT WHITECHUCK RIVER	WA	-0.6195	Lake Minotaur Mid	Jul	0.2238	Blewett Pass	Apr	0.3236	Ross Lake	Jun	-0.4862	Granite Mountain	Jul
12189500	SAUK RIVER NEAR SAUK	WA	-0.6064	Lake Minotaur Mid	Jul	-0.2098	North Fork Campground	Jun	0.3991	Ross Lake	Jun	-0.4709	Granite Mountain	Jul
12144500	SNOQUALMIE RIVER NEAR SNOQUALMIE	WA	NA	NA	NA	-0.3584	Blewett Pass	Apr	-0.6498	Frying Pan Creek	Jul	-0.5691	Granite Mountain	Jul
12451000	STEHEKIN RIVER AT STEHEKIN	WA	-0.5698	Lake Minotaur Mid	Jul	0.4399	Colockum Pass	Apr	0.4697	Swauk Pass	Jul	-0.3864	Granite Mountain	Jul
12054000	DUCKABUSH RIVER NEAR BRINNON	WA	-0.6301	Lake Minotaur Mid	Jul	0.1758	Fort Lewis	Apr	-0.3555	Olympic Road	Apr	-0.5264	Hoh Lake High	Jul
12048000	DUNGENESS RIVER NEAR SEQUIM	WA	-0.6318	Lake Minotaur Mid	Jul	0.2238	Fort Lewis	Jul	0.3933	Big Quilcene River Trail	Jun	-0.5343	Hoh Lake High	Jul
12040500	QUEETS RIVER NEAR CLEARWATER	WA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.4808	Hoh Lake High	Jul

12039500	QUINULT RIVER AT QUINULT LAKE	WA	-0.4183	Mt Rainier Mid	Jul	0.2459	Fort Lewis	Jul	0.2929	Soleduck	Jul	-0.6002	Hoh Lake High	Jul
12056500	SKOKOMISH RIVER NEAR BLW STAIRCASE RAPIDS	WA	NA	NA	NA	0.1649	Fort Lewis	Apr	-0.3074	Deer Park Burn	Apr	-0.5236	Hoh Lake High	Jul
14198500	MOLALLA RIVER ABOVE PC NEAR WILHOIT	OR	-0.3303	Mt Hood Mid	Apr	0.3254	Mill Creek	Jul	0.2495	Santiam Pass	Jul	-0.2686	Husband Lake	Apr
14318000	LITTLE RIVER AT PELL	OR	NA	NA	NA	0.3588	Diamond Lake	Jun	0.2781	Abbot Creek RNA	Jun	-0.2607	Lightning Springs	Apr
14338000	ELK CREEK NEAR TRAIL	OR	NA	NA	NA	0.2722	Blue Jay Springs	Apr	0.3391	Abbot Creek RNA	Apr	-0.5186	Llao Rock	Jul
14359000	ROGUE RIVER AT RAYGOLD NEAR CENTRAL POINT	OR	NA	NA	NA	0.4715	Telephone Draw	Jul	-0.048	Abbot Creek RNA	Apr	-0.5655	Llao Rock	Jun
14154500	ROW RIVER ABOVE PITCHER CREEK NEAR DORE	OR	NA	NA	NA	0.3058	Crater Lake	Jul	-0.2075	Santiam Pass	Apr	-0.3388	Llao Rock	Jul
14316700	STEAMBOAT CREEK NEAR GLIDE	OR	NA	NA	NA	0.5343	Summit Spring	Jul	0.1929	Abbot Creek RNA	May	-0.4038	Llao Rock	Apr
14232500	CISPUS RIVER NEAR RANDLE	WA	-0.5473	Mt Hood Mid	Jul	0.2244	Fort Lewis	Jul	-0.3479	Frying Pan Creek	May	-0.5803	Mt Hood High	Jun
14222500	EAST FORK LEWIS RIVER NEAR HEISSON	WA	-0.3795	Mt Adams Mid	Jul	0.2461	Mill Creek	Jul	0.3039	Rimrock Valles	May	-0.3376	Mt Hood High	Apr
14048000	JOHN DAY RIVER AT MCDONALD FERRY	OR	-0.3006	Mt Adams Low	Jun	0.3992	Long Prairie	Jul	0.2415	Rimrock Valles	Jul	-0.3888	Mt Hood High	Jul
14113000	KLICKITAT RIVER NEAR PITT	WA	-0.5696	Mt Hood Mid	Jul	0.3458	Bear Creek	May	0.4638	Rimrock Valles	Jun	-0.6456	Mt Hood High	Jun
14179000	BREITENBUSH RIVER ABOVE FRENCH CREEK NEAR DETROIT	OR	-0.6278	Mt Hood Mid	Jul	0.1551	Pringle Falls Fire	Apr	-0.1611	Dry Creek	May	-0.7152	Mt Jefferson Mid	Jul
14208000	CLACKAMAS RIVER AT BIG BOTTOM	OR	-0.3879	Mt Hood Mid	Jul	0.2702	Mill Creek	Jul	0.3522	Barlow Pass	Jul	-0.5352	Mt Jefferson Mid	Jun
14190500	LUCKIAMUTE RIVER NEAR SUVER	OR	NA	NA	NA	NA	NA	NA	-0.1858	Santiam Pass	Jun	-0.4659	Mt Jefferson Mid	Apr
14159000	MCKENZIE RIVER AT MCKENZIE BRIDGE	OR	NA	NA	NA	NA	NA	NA	-0.2543	Santiam Pass SNOTEL	Apr	-0.6523	Mt Jefferson Mid	Jul

14178000	NORTH SANTIAM RIVER BELOW BOULDER CREEK NEAR DETROIT	OR	-0.5174	Mt Hood Mid	Jul	0.2277	Experimental Forest	Jul	-0.2101	Santiam Pass SNOTEL	Apr	-0.6181	Mt Jefferson Mid	Jul
14137000	SANDY RIVER NEAR MARMOT	OR	-0.4584	Mt Hood Mid	Jul	0.2095	Mill Creek	Jul	0.2346	Dry Creek	Jul	-0.5355	Mt Jefferson Mid	Jul
14185000	SOUTH SANTIAM RIVER BELOW CASCADIA	OR	-0.3204	Mt Hood Mid	Jul	0.2453	Lava Cast Forest	Jul	-0.2679	Santiam Pass	Apr	-0.4185	Mt Jefferson Mid	Jul
14321000	UMPQUA RIVER NEAR ELKTON	OR	NA	NA	NA	NA	NA	NA	0.2387	Abbot Creek RNA	Jul	-0.5437	Mt Jefferson Mid	Jul
14101500	WHITE RIVER BELOW TYGH VALLEY	OR	-0.5831	Mt Hood Mid	Jul	0.1888	Mill Creek	Jul	0.4253	Rimrock Valles	Jul	-0.6335	Mt Jefferson Mid	Jul
12488500	AMERICAN RIVER NEAR NILE	WA	-0.666	Lake Minotaur Mid	Jul	0.284	Government Camp	Apr	-0.4973	Cougar Creek	Apr	-0.5927	Mt Rainier High	Jul
12458000	ICICLE CREEK ABOVE SNOW CREEK NEAR LEAVENWORTH	WA	-0.6519	Lake Minotaur Mid	Jul	0.3832	Bear Creek	Jul	0.5073	Soleduck	Jul	-0.5986	Mt Rainier High	Jul
12500500	NORTH FORK AHTANUM CREEK NEAR TAMPICO	WA	-0.6396	Mt Adams High	Jul	0.385	Bear Creek Ridge	May	0.3996	Rimrock Valles	Jun	-0.5842	Mt Rainier High	Jul
12134500	SKYKOMISH RIVER NEAR GOLD BAR	WA	-0.5945	Lake Minotaur Mid	Jul	-0.395	Colockum Pass	Jun	-0.3871	Frying Pan Creek	May	-0.5386	Mt Rainier High	Jul
12459000	WENATCHEE RIVER AT PESHASTIN	WA	-0.6511	Lake Minotaur Mid	Jul	0.3959	Colockum Pass	Apr	0.4377	Swauk Pass	Jul	-0.553	Mt Rainier High	Jul
10384000	CHEWAUCAN RIVER NEAR PAISLEY	OR	NA	NA	NA	0.4442	Deschutes	Apr	NA	NA	NA	-0.5995	Mt Scott	Jul
13032000	BEAR CREEK ABOVE RESERVOIR NEAR IRWIN	ID	NA	NA	NA	NA	NA	NA	0.5831	Hoback Ridge	Jul	NA	NA	NA
13309000	BEAR VALLEY CREEK NEAR CAPE HORN	ID	NA	NA	NA	0.3083	Kenally Creek	Jun	0.5332	Salmon River South	May	NA	NA	NA
13113000	BEAVER CREEK AT SPENCER	ID	NA	NA	NA	NA	NA	NA	0.3999	Dell Sheep Creek	Jun	NA	NA	NA
13120500	BIG LOST RIVER AT HOWELL RANCH NEAR CHILLY	ID	NA	NA	NA	NA	NA	NA	0.4706	Ketchum East	Jul	NA	NA	NA

13063000	BLACKFOOT RIVER ABOVE RESERVOIR	ID	NA	NA	NA	NA	NA	NA	0.5251	Hoback Ridge	Apr	NA	NA	NA
12305500	BOULDER CREEK NEAR LEONIA	ID	NA	NA	NA	0.4753	Wellner Cliffs Research Natural Area	May	0.2582	Snackout Road	May	NA	NA	NA
12321500	BOUNDARY CREEK NEAR PORTHILL	ID	NA	NA	NA	0.3414	Wellner Cliffs Research Natural Area	Jul	0.2233	Churchill	Jul	NA	NA	NA
13168500	BRUNEAU RIVER NEAR HOT SPRING IDAHO	ID	NA	NA	NA	0.3445	Kenally Creek	Apr	NA	NA	NA	NA	NA	NA
14042500	CAMAS CREEK NEAR UKIAH	OR	-0.2844	Greenhorn Mountain	May	0.3945	Lava Cast Forest	Jul	NA	NA	NA	NA	NA	NA
13339000	CLEARWATER RIVER AT KAMIAH	ID	NA	NA	NA	0.2638	Clearwater River	Jul	NA	NA	NA	NA	NA	NA
13340000	CLEARWATER RIVER AT OROFINO	ID	NA	NA	NA	0.3645	Wallace	Apr	NA	NA	NA	NA	NA	NA
12413000	COEUR D'ALENE RIVER AT EVILLE	ID	NA	NA	NA	-0.3574	Wallace	May	NA	NA	NA	NA	NA	NA
12411000	COEUR D'ALENE RIVER AT SHOSHONE CREEK NEAR PRICHARD	ID	NA	NA	NA	0.214	Wellner Cliffs Research Natural Area	Jul	NA	NA	NA	NA	NA	NA
12409000	COLVILLE RIVER AT KETTLE FALLS	WA	NA	NA	NA	0.6983	Sneed Mountain	Jul	0.585	St Peters Creek	Jul	NA	NA	NA
13139510	COMBITION BIG WOOD RIVER SLOUGH AT HAILEY	ID	NA	NA	NA	NA	NA	NA	0.4784	Ketchum East	Jul	NA	NA	NA
12413500	COUER D'ALENE RIVER NEAR CATALDO	ID	NA	NA	NA	0.3206	Wellner Cliffs Research Natural Area	Jul	NA	NA	NA	NA	NA	NA
12465000	CRAB CREEK AT IRBY	WA	NA	NA	NA	0.2767	Blewett Pass	Jul	0.2642	Colville Reservation A	Jul	NA	NA	NA
10371500	DEEP CREEK ABOVE ADEL	OR	NA	NA	NA	0.4239	Lakeview	Jul	NA	NA	NA	NA	NA	NA
12311000	DEEP CREEK AT MOTAVIA	ID	NA	NA	NA	0.5334	Wellner Cliffs Research Natural Area	May	0.4036	Churchill	May	NA	NA	NA
13319000	GRANDE RONDE RIVER AT LA GRANDE	OR	-0.3187	Greenhorn Mountain	May	0.3039	Long Prairie	Jul	NA	NA	NA	NA	NA	NA

12424000	HANGMAN CREEK AT SPOKANE	WA	NA	NA	NA	0.3241	Rattlesnake Ridge	Jul	-0.4215	Colville Reservation B	Jun	NA	NA	NA
14377000	ILLINOIS RIVER AT KERBY	OR	NA	NA	NA	NA	NA	NA	-0.1799	Abbot Creek RNA	Jun	NA	NA	NA
14046500	JOHN DAY RIVER AT SERVICE CREEK	OR	-0.4454	Greenhorn Mountain	May	0.5113	Paulina	Jul	NA	NA	NA	NA	NA	NA
13313000	JOHNSON CREEK AT YELLOW PINE	ID	NA	NA	NA	0.3341	Clearwater River	May	0.4649	Salmon River Valley	Jul	NA	NA	NA
12401500	KETTLE RIVER NEAR FERRY	WA	NA	NA	NA	0.573	Sneed Mountain	Jul	0.352	Pipeston Canyon Twisp	May	NA	NA	NA
12404500	KETTLE RIVER NEAR LAURIER	WA	NA	NA	NA	0.5842	Sneed Mountain	Jul	0.3139	Big Boulder Creek	Jun	NA	NA	NA
12322000	KOOTENAI RIVER AT PORTHILL	ID	NA	NA	NA	0.3837	Wellner Cliffs Research Natural Area	Jul	0.4799	Snackout Road	Jul	NA	NA	NA
13305000	LEMHI RIVER NEAR LEMHI	ID	NA	NA	NA	NA	NA	NA	0.6286	Dell Sheep Creek	May	NA	NA	NA
13316500	LITTLE SALMON RIVER AT RIGGNS	ID	NA	NA	NA	0.3802	Union	Apr	NA	NA	NA	NA	NA	NA
12431000	LITTLE SPOKANE RIVER AT DARTFORD	WA	-0.4544	Greenhorn Mountain	Apr	0.4383	Rattlesnake Ridge	Jul	0.4954	Snackout Road	Jul	NA	NA	NA
13261000	LITTLE WEISER RIVER NEAR INDIAN VALLEY	ID	NA	NA	NA	0.2863	Kenally Creek	May	NA	NA	NA	NA	NA	NA
13337000	LOCHSA RIVER NEAR LOWELL	ID	NA	NA	NA	0.2085	Clearwater River	Jul	NA	NA	NA	NA	NA	NA
13075000	MARSH CREEK NEAR MCCAMMON	ID	NA	NA	NA	NA	NA	NA	0.3575	Naomi Peak	Apr	NA	NA	NA
14044000	MIDDLE FORK JOHN DAY RIVER AT RITTER	OR	-0.5126	Greenhorn Mountain	May	0.4666	Paulina	Jul	NA	NA	NA	NA	NA	NA
13308500	MIDDLE FORK SALMON RIVER NEAR CAPEHORN	ID	NA	NA	NA	0.3683	Kenally Creek	May	0.4499	Ketchum East	Jun	NA	NA	NA
13200000	MORES CREEK ABOVE ROBBIE CREEK NEAR ARROWROCK DAM	ID	NA	NA	NA	0.2877	Kenally Creek	May	NA	NA	NA	NA	NA	NA

12306500	MOYIE RIVER AT EASTPORT	ID	NA	NA	NA	0.3037	Wellner Cliffs Research Natural Area	Jul	0.2114	Snackout Road	May	NA	NA	NA
12307500	MOYIE RIVER AT EILEEN	ID	NA	NA	NA	0.5876	Wellner Cliffs Research Natural Area	May	0.2819	Snackout Road	May	NA	NA	NA
14301000	NEHALEM RIVER NEAR FOSS	OR	NA	NA	NA	NA	NA	NA	0.2003	Barlow Pass	May	NA	NA	NA
13120000	NORTH FORK BIG LOST RIVER AT WILD HORSE NEAR CHILLY	ID	NA	NA	NA	NA	NA	NA	0.7514	Ketchum East	Jul	NA	NA	NA
13341000	NORTH FORK CLEARWATER RIVER AT AHSAHKA	ID	NA	NA	NA	0.4645	Indian Ridge	May	NA	NA	NA	NA	NA	NA
13351000	PALOUSE RIVER AT HOOOPER	WA	NA	NA	NA	0.4243	Grizzly Bear	Jul	-0.4215	Colville Reservation B	Jun	NA	NA	NA
13306500	PANTHER CREEK NEAR SHOUP	ID	NA	NA	NA	0.4796	Kenally Creek	Apr	0.5948	Salmon River South	Jun	NA	NA	NA
13073000	PORTNEUF RIVER AT TOPAZ	ID	NA	NA	NA	NA	NA	NA	0.3289	Naomi Peak	Apr	NA	NA	NA
12393500	PRIEST RIVER AT OUTLET OF PRIEST LAKE	ID	NA	NA	NA	0.5808	Wellner Cliffs Research Natural Area	Jul	0.4832	Churchill	Jul	NA	NA	NA
13302500	SALMON RIVER AT SALMON	ID	NA	NA	NA	NA	NA	NA	0.5073	Salmon River Valley	Jul	NA	NA	NA
13317000	SALMON RIVER AT WHITE BIRD	ID	NA	NA	NA	0.2998	Union	Jul	NA	NA	NA	NA	NA	NA
13295500	SALMON RIVER BELOW VALLEY CREEK AT STANLEY	ID	NA	NA	NA	0.4245	Clearwater River	Jul	0.2762	Salmon River Valley	Jul	NA	NA	NA
13296500	SALMON RIVER BELOW YANKEE FORK NEAR CLAYTON	ID	NA	NA	NA	0.2786	Clearwater River	May	0.4087	Ketchum East	May	NA	NA	NA
13307000	SALMON RIVER NEAR SHOUP	ID	NA	NA	NA	0.3542	Kenally Creek	Apr	0.5944	Salmon River South	Jun	NA	NA	NA
13298500	SALMON RIVER NEAR CHALLIS	ID	NA	NA	NA	NA	NA	NA	0.4885	Ketchum East	Jul	NA	NA	NA
13336500	SELWAY RIVER NEAR LOWELL	ID	NA	NA	NA	0.2223	Clearwater River	Jul	NA	NA	NA	NA	NA	NA
10393500	SILVIES RIVER NEAR BURNS	OR	-0.3948	Greenhorn Mountain	May	0.6186	Paulina	Jul	NA	NA	NA	NA	NA	NA
13037500	SNAKE RIVER NEAR HEISE	ID	NA	NA	NA	NA	NA	NA	0.5275	Hoback Ridge	Jun	NA	NA	NA

13186000	SOUTH FORK BOISE RIVER NEAR FEATHERVILLE	ID	NA	NA	NA	0.208	East Side	Apr	0.5788	Ketchum East	Jul	NA	NA	NA
13338000	SOUTH FORK CLEARWATER RIVER NEAR GRANGEVILLE	ID	NA	NA	NA	0.5501	Kenally Creek	Jul	NA	NA	NA	NA	NA	NA
14325000	SOUTH FORK COQUILLE RIVER AT POWERS	OR	NA	NA	NA	NA	NA	NA	0.1336	Abbot Creek RNA	Jul	NA	NA	NA
13235000	SOUTH FORK PAYETTE RIVER AT LOWMAN	ID	NA	NA	NA	0.3332	Kenally Creek	Apr	0.3385	Salmon River Valley	Jul	NA	NA	NA
13310500	SOUTH FORK SALMON RIVER NEAR KNOX	ID	NA	NA	NA	0.4189	Clearwater River	Jun	0.3312	Salmon River Valley	Jun	NA	NA	NA
14010000	SOUTH FORK WALLA WALLA RIVER NEAR MILTON FREEWATER	OR	-0.5591	Greenhorn Mountain	Jul	-0.3159	Wenaha	Apr	NA	NA	NA	NA	NA	NA
12414500	ST JOE RIVER AT CALDER	ID	NA	NA	NA	0.3228	Wellner Cliffs Research Natural Area	Jul	NA	NA	NA	NA	NA	NA
12415000	ST MARIES RIVER AT LOTUS	ID	NA	NA	NA	0.5413	Wellner Cliffs Research Natural Area	Jul	0.4757	Churchill	Jul	NA	NA	NA
14020000	UMATILLA RIVER ABOVE MEACHAM CREEK NEAR GIBBON	OR	-0.4491	Greenhorn Mountain	May	0.3952	Union	Jul	NA	NA	NA	NA	NA	NA
13295000	VALLEY CREEK AT STANLEY	ID	NA	NA	NA	0.3755	East Side	Jul	0.4701	Salmon River Valley	Jun	NA	NA	NA
14193000	WILLAMINA CREEK NEAR WILLAMINA	OR	NA	NA	NA	NA	NA	NA	0.1996	Barlow Pass	May	NA	NA	NA
14034500	WILLOW CREEK AT HEPPNER	OR	-0.2497	Greenhorn Mountain	May	0.4334	Paulina	Apr	NA	NA	NA	NA	NA	NA
14301500	WILSON RIVER NEAR TILLAMOOK	OR	NA	NA	NA	NA	NA	NA	0.1812	Barlow Pass	Apr	NA	NA	NA
14362000	APPLEGATE RIVER NEAR COPPER	OR	NA	NA	NA	0.3326	Little Aspen Butte	Apr	-0.229	Abbot Creek RNA	Jun	-0.7041	Pinnacle	Jul

12449500	METHOW RIVER AT TWISP	WA	-0.611	Lake Minotaur Mid	Jul	0.5009	Bear Creek	Jul	0.5469	Ross Lake	Jun	-0.5131	South Cascade Glacier	Jul
12445000	OKANOGAN RIVER NEAR TONASKET	WA	-0.4664	Hart Pass N1	May	0.438	Sneed Mountain	Jul	0.3984	Ross Lake	Jun	-0.4509	South Cascade Glacier	Jul
12442500	SIMILKAMEEN RIVER NEAR NIGHTHAWK	WA	-0.4552	Hart Pass N1	Jul	0.3976	Bear Creek	Jul	0.3919	Ross Lake	Jun	-0.435	Thornton Lakes High	Jul
12020000	CHEHALIS RIVER NEAR DOTY	WA	-0.5246	Dodger Point Low	Jul	0.4055	Fort Lewis	Jul	0.2474	Dry Creek	May	-0.3896	Wynoochee Falls	Jul
12010000	NASELLE RIVER NEAR NASELLE	WA	NA	NA	NA	0.3112	Fort Lewis	May	0.1808	Dry Creek	Apr	-0.2865	Wynoochee Falls	Jul
12013500	WILLAPA RIVER NEAR WILLAPA	WA	NA	NA	NA	0.6406	Fort Lewis	Jul	0.2022	Tunnel Creek	Jul	-0.4969	Wynoochee Falls	May

Appendix B - Supplemental material for Chapter 4

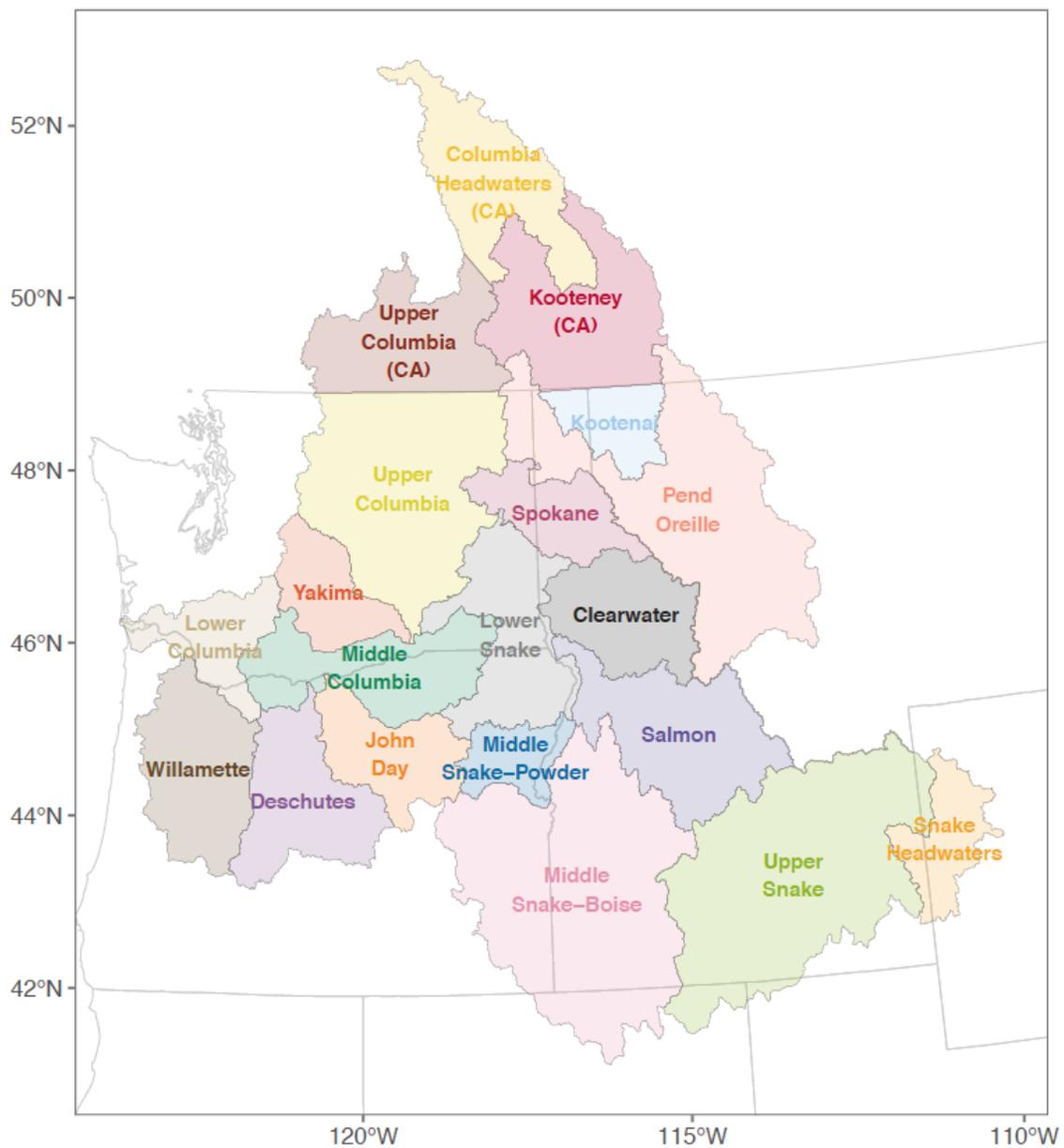


Figure B. 1. HUC-6 units with names.

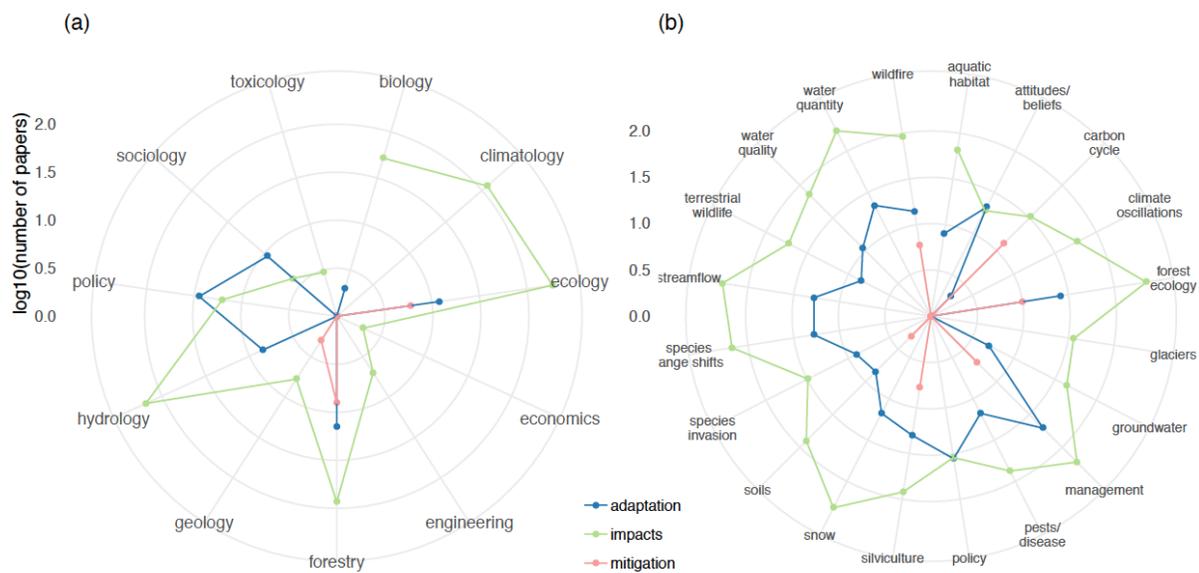


Figure B. 2. Similar to Figure 4.6 but with number of papers, rather than percentages by category.