THE GROWTH-CLIMATE RELATIONSHIP OF OREGON WHITE OAK (*QUERCUS GARRYANA*)

A Thesis

Presented to

The Faculty of Graduate Studies

of

The University of Guelph

by

THOMAS BRIAN MAERTENS

In partial fulfillment of requirements

for the degree of

Master of Science

August, 2008

ABSTRACT

THE GROWTH-CLIMATE RELATIONSHIP OF OREGON WHITE OAK (*QUERCUS GARRYANA*)

Thomas Brian Maertens
University of Guelph, 2008

Advisor:
Professor Ze'ev Gedalof

This thesis describes the growth-climate relationship of Oregon white oak, a foundation species in one of the most endangered habitat types in North America. These trees inhabit dynamic forest ecosystems in which climate is especially significant and expected to become increasingly important. In this study, we identify characteristic growth responses of Oregon white oak to its climate and assess their geographic patterns.

We used dendroecological techniques to determine unique correlation functions for each of 18 climatically sensitive stands representing much of the geographic range of the species. Principal components analyses identified important associations between growth and climate. Over 110 years of analysis, 1896-2005, spring conditions have dominated the dendroclimatic response but other significant relationships occur throughout the year. The relative importance of climatic controls varies throughout the species' range. These results are crucial for the long-term management of Oregon white oak ecosystems and contribute to our understanding of vegetation dynamics.

Acknowledgements

I wish to sincerely thank some people without whom this project would not have been nearly as good. First and foremost, I acknowledge the contributions of my advisor, Dr. Ze'ev Gedalof, for direction, technical assistance, friendship, and fish tacos. Dr. Doug Larson gave me valuable advice, even though I did not always appreciate it at the time. Dr. Shelley Hunt provided valuable ecological insight.

Important to my research was the insight and support of my colleagues, and I need to acknowledge the members of the Department of Geography here at the University of Guelph. In particular, I thank my lab partners, Jennifer Franks, Lesley Davy, and Graham Clark, and my partner-in-cartographic-crime Adam Bonnycastle.

This research required the cooperation of numerous botanists and land managers, and so was conducted in part with the U.S. Department of Defense (Jeff Foster), the U.S. National Park Service, the U.S. Bureau of Land Management (Susan Carter, Melanie Roan, Julie Knurowski, Marcia Wineteer, Paul Hosten), the U.S.D.A. Forest Service (Brance Morefield, Marla Knight, Lauren Johnson, Allison Sanger), the U.S. Fish and Wildlife Service (Jock Beall), the Washington Department of Natural Resources (David Wilderman, Priya Shahani), and The Nature Conservancy (Jason Nuckols, Reese Lolley). I thank these organizations and their representatives for granting access to the oak trees, their effort in directing me to the sites, and their interest in understanding and preserving these beautiful ecosystems. Funding from the Washington Native Plant Society was much appreciated.

A few people provided accommodations, good food, and good conversation while we were in the field, especially Reese Lolley and his family, Jacob and Andrew Bond, and Liz and Lee Ann Maertens. My Dad was supportive as always. Nicole Maertens, my sister, provided a stylish truck.

Finally, I am deeply appreciative of the oak trees that we cored. With the above-mentioned in mind, I use the term 'we' throughout this manuscript.

Table of contents

List of tables

List of figures

Forward

"Climate is a dominant influence on the growth of a tree."
- Fritts Schweingruber 1996

"Every tree, on every site, in every climate zone, is unique."
- Fritts Schweingruber 1996

Introduction Chapter 1

A fundamental concern of biogeography is the mapping and explanation of forest interactions in space and through time (Lomolino et al. 2006a; Cox and Moore 2005; Loehle and LeBlanc 1996). Conventional biogeographical thought contends that climate is a dominant factor controlling the growth and distribution of plant species (Tivy 1993; Archibold 1995; Huntley 1995; Schweingruber 1996; Peterson and Peterson 2001; Gedalof and Smith 2001a; Kimmins 2004). Oregon white oak (*Quercus garryana* Dougl. ex. Hook.), also known as Garry oak, is part of a dynamic forest ecosystem type in which climatic variability is especially significant (Pellatt et al. 2007) and likely to become increasingly important (Fuchs 2001). This species is intimately related to climate in its morphology, phylogeny, and geography; climate defines the distribution, ecological position, and ecosystem characteristics that control the growth of these trees. This thesis is an assessment of the influence of climate on the growth of Oregon white oak and documents spatial variability in climatic controls among stands.

This next century is projected to be a time of extraordinarily rapid and unprecedented ecological change driven by climate (Allen and Breschears 1998; Eldridge 1998; Hansen et al. 2001; McCarty 2001; Reid et al. 2005). In particular, the impacts on the function, structure, composition, and distribution of forested ecosystems will be substantial (Cayan et al. 2001; Parmesan 2005; Shafer et al. 2001). Although forest productivity in North America is expected to increase over the coming decades due to changes in atmospheric gas concentrations and increased temperatures (Morgan et al. 2001; Bachelet et al. 2001; Field et al. 2007; but see Gedalof and Berg *in review*, Kurz et al. 2008), growth in moisture-limited Pacific North American forests is likely to decrease

(Field et al. 2007). This research has been directed by both conservation and resource needs and aims to identify species-specific processes and patterns crucial to the construction of accurate biogeographic projections and climatic reconstructions.

Oregon white oak ecosystems are important for conservation and land management efforts at local, regional, continental, and global scales. This tree is endemic to Pacific North America, a foundation species associated with diverse forest types that include many rare organisms. Oregon white oak is in decline, and so these ecosystems are considered among the most endangered in western North America (Erickson 2000; GOERT 2002; ODFW 2005; Scott et al. 2001). However, little dendroecological work has been applied to the species, especially not a long-term, high-resolution study covering the species' natural geographic range such as described here.

Many tree species produce annual rings that can be used to accurately date growth rates. Oaks, genus *Quercus*, have been successfully used in dendrochronology and climatology studies as temperate oak trees are sensitive to changes in climate (Fritts 2001; Kelly et al. 1989; Pedersen et al. 1998; Pilcher and Gray 1982; Abrams 2003; Du et al. 2007; Akkemik et al. 2006; Rozas 2005; Nowacki and Abrams 2008). Oak trees respond directly to temperature (Tardif et al. 2006; Pederson et al. 2004), rainfall (Gedalof et al. 2006), and soil moisture (Briffa and Wigley 1985).

The relative importance of climatic controls can vary spatially throughout a species' range (Brubaker 1980; Carrer et al. 2007). Biogeographical characteristics of Oregon white oak suggest that its response to climate may be mixed as well. For tree species like these oaks with distributions suggesting strong edaphic controls (e.g., soil drainage), long-lived tree species under strongly dynamic climatic controls (e.g., inter and intraannual variability), species near climatic-threshold values (e.g., moisture limited), tree species influenced by regular non-lethal disturbances (e.g., low-intensity fire), or for those tree species with poor dispersal abilities and whose distribution is likely to be in non-equilibrium with climate (e.g., by large zoodispersed acorns) an understanding of site and species-specific growth responses can improve both species and ecosystem modelling (Neilson et al. 2005; Araujo and Pearson 2005; Peterson et al. 2005).

This thesis describes Oregon white oak's relationship to its climate and details a dendroecological research project that examines the tree's climatic sensitivity, assesses its characteristic growth responses, and tests the hypothesis that climatic response varies among stands, all this on a previously underexplored species whose tree-ring dynamics are unknown. The relationship between climate and the growth of Oregon white oak is characterized by developing tree ring chronologies from a network of climatically sensitive stands representing much of the species geographical range and relating these chronologies to climatic variables to determine the direction, magnitude, and patterns of dendroclimatic response.

The emphasis of this thesis is on the biophysical geography of Oregon white oak and the species' relationship to climate, in particular by investigating the radial-growth of mature trees. A tree species occurs where sets of favourable complex environmental and ecological conditions intersect to allow establishment and growth. A growth-response to climate is the dominant control on stand structure and the distribution of species. These climatic influences may be altered by topography, soil characteristics, disturbance regimes, ecological interactions, anthropogenic intervention, and by historical legacy. However, the composition and distribution of any terrestrial ecosystem at a broad scale is primarily a function of climate, particularly interactions between temperature, precipitation, and sunlight.

The ecological and climatic influences on Oregon white oak's growth are complex, many aspects of which operate at multiple scales and can be difficult, impractical, or impossible to measure experimentally. The impact of climatic variability, however, can be explained by established dendroecological theory using a carefully selected set of tree-ring chronologies and high-resolution climatic data. Dendrochronological studies have demonstrated that empirical analyses of tree-rings can help determine the environmental limits on the growth of a species and aid in the understanding of controls on tree growth, stand structure, and forest distribution through time (Fritts 2001; Schweingruber 1996).

The scope of this thesis is the Pacific North American region over 111 years, from 1895 to 2005. Oregon white oak is represented by 18 stands, which in turn are represented by the annual radial-growth of individual trees. With the aim of quantifying the growth-climate relationship of this species, we collected increment cores from 382 Oregon white oak trees. At each of the 18 sites, we cored approximately 20 mature Oregon white oak trees, almost all were over 100 years old, and used statistical analyses to construct site chronologies. As a proxy for climate, we used four climatic variables with monthly resolution. We assembled 111 years of monthly-resolved climatic data for the region and extracted values corresponding to each site. These climatic values include monthly averages of maximum and monthly averages of minimum temperatures and total monthly precipitation amounts extracted from PRISM, a 4 km gridded dataset. The Palmer Drought Severity Index, an index of available soil moisture, integrates temperature, precipitation, sunlight, and soil texture. Monthly climatic indices spanning 18 months, from April in the year prior to growth through September of the growth year, plus seasonal values covering the same period, served as a link between the spatially and temporally inconsistent instrumental climatic data of the region and the tree-ring proxies.

We also assess the stands’ growth in relation to three quasi-periodic forcings, El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation.

We quantify the climatic niche of Oregon white oak by identifying unique correlation functions for each stand. Measuring the influence of temperature and precipitation on the species’ tree-ring structure allowed us to identify geographic patterns in dominant predictor climatic variables. Principal components analyses performed on both the ring-width indices and on the correlation functions facilitate further discrimination between the responses at each site.

This dendroecological study of Oregon white oak determined that climate exerts a strong regionally coherent influence on the radial-growth of Oregon white oak. This tree species is strongly sensitive to variability in climate and responds to spring conditions, both in the year of growth as well as in the year prior. The trees’ marked responses to temperature and precipitation during earlywood formation is most apparent in the strong correlations to moisture availability. In addition, a positive response to temperatures in the spring prior to the year of ring formation is a dominant influence on growth. Correlations between growth and climate are seen throughout the rest of the year, especially to fall temperatures and winter precipitation prior to growth. However, the relative importance of the climatic controls varies throughout the range of the species. Maps of the dendroclimatic response variables place these research findings in a spatial context, highlighting latitudinal, longitudinal, elevational, and ecological gradients in the direction and magnitude of the species' climatic response.

The chapters that follow are a discussion of the complex controls that climate exerts on the growth of Oregon white oak. The next chapter is a literature review exploring the biogeography of the species and its relationship to climate at multiple scales. The third chapter explains the design of the dendroecological research project undertaken here to quantify the tree's growth-response to climate and details the specific methods used. The fourth chapter presents these growth responses to climate in an ecophysiologically relevant context and assesses the geographic patterns of response that stands exhibit. The concluding chapter synthesizes the findings, facilitating the understanding of Oregon white oak's past growth as well as the species' likely response to future climatic change, and notes ways that this project can inform both biogeographic scholarship and the management of Oregon white oak ecosystems.

Background: Oregon white oak and climate Chapter 2

Knowledge of Oregon white oak's physical environment along with its biogeographical characteristics and ecological trajectory is crucial to understanding why this tree's growth-response to climate is both strongly synchronous and yet varies geographically. The biogeographic approach taken here highlights simple patterns and processes in response to varying geographies and discusses how this relationship creates complex relationships between the radial-growth of Oregon white oak trees and their climate.

Integral to this environmental systems approach is a consideration of scale in various dimensions. Climate is intimately connected with the tree’s role in its ecosystem and in the ecosystem’s role within its landscape. The spatial extent of analysis here spans the entire range of Oregon white oak, as the species' unique geography suggests a mixed response that cannot be documented at the stand level. The temporal extent of investigation is that relating to the lifespan of an oak tree, the timeframe of most human management actions, and reflects the rate of past climatic responses, but examining other temporal scales provides a deeper understanding of the tree’s growth-response to climate. Focusing on different levels of biological organization (e.g., organism, population, ecosystem) and levels of taxa (e.g., species, genus) can highlight the influence of various limiting factors. All this must be considered within the particular biophysical setting of the species.

Biophysical Geography of Pacific North America

Pacific North American topography is dominated by the Coastal and Cascade Mountain ranges which strongly influence its climate. The climate in turn drives the growth of and exerts complex controls on the productivity and distribution of the region's extensive forests.

Climate of Pacific North America

Western North America is strongly affected by Pacific air masses flowing onshore. In the winter, a low-pressure system centered over the Aleutian Islands is balanced by a weak high-pressure system off the California coast. Prevailing winds from the southwest in October through May bring warm air that cools over land and loses moisture. Winter, then, is a cool wet season. In spring, the high-pressure cell expands, migrating west and north throughout the summer. Relatively dry and cold air from the northwest during the summer warms over land resulting in very dry summer conditions. In autumn, the subtropical high weakens and the Aleutian low strengthens again. This regional pattern is classified as a Mediterranean summer dry climate (Koeppen 1923).

A characteristic feature of Pacific North American climate is its temporal and spatial variability (Zhang et al. 2000; Walther 2002). Oscillations of weather conditions occur at various temporal scales, not only diurnal and annual, but also decadal (Mantua et al. 1997; Graumlich and Brubaker 1986), centennial (Mann et al. 2002; D'Arrigo et al. 1999), and millennial (Pielou 1991). The spatial variability in temperature can be extreme, as latitudinal effects cause a north-south gradient in temperature. The mountain ranges interrupt the heat transport from the ocean and create an east-west gradient in temperature. These same mountain ranges also serve as topographic barriers triggering rainfall, and the same east-west gradient in precipitation results. Precipitation is greater west of the mountain ranges due to orographic uplift and the slowing of moisture-laden air masses. The amount of precipitation is lower in the rainshadow east of the mountains as the descending air dries.

Hemispheric scale climatic controls, or quasi-periodic forcings, strongly influence Pacific North America, affecting the climate in different ways, to different degrees, and at various frequencies (Cane 2004; Mantua and Hare). A few of the climatic teleconnections shown to influence Pacific North America are El Niño Southern Oscillation (Ropelewski and Halpert 1986; Barlow et al. 2001), the Pacific Decadal Oscillation (Nigam et al. 1999; Mantua and Hare 2002), and the Atlantic Multidecadal Oscillation (Gray et al. 2003, 2004).

The tropical Pacific Ocean is characterized by strong westward surface winds driving currents that cause the accumulation of warm water near Indonesia. El Niño Southern Oscillation (ENSO) is a disruption of that coupled ocean-atmosphere system: every two to seven years the tradewinds weaken and warm water moves eastward in what is termed El Niño event, or the warm phase of ENSO (Rasmussen and Wallace 1983; Cane 2004; Schoennagel et al. 2005). La Niña, or cold phase of ENSO occurs after 6 to 18 months when westward winds strengthen, cold water returns to the equator, and warm water contracts to the west. This quasi-periodic forcing is strongly correlated with climatic variability in Pacific North America (Yarnal and Diaz 1986; Gershunov and Barnett 1998), especially with the redistribution of rainfall (Zhang et al. 1997; Barlow et al. 2001). El Niño events bring slightly warmer winter temperatures and less precipitation, while La Niña years are colder and associated with greater precipitation throughout much of the region during the winter (Gershunov and Barnett 1998; Glantz 1998; Dettinger et al. 1998; Castello and Shelton 2004).

The Pacific Decadal Oscillation (PDO) is a basin wide shift in temperature with two periods of roughly 23 years each (Mantua et al. 1997; Minobe 1997; Gedalof and Smith 2001b; Biondi et al. 2001; D’Arrigo et al. 2001; Gedalof et al. 2002; Trenberth and Hurrell 1994; Bond and Harrison 2000), although the strength and periodicity of this oscillation is not temporally stable (Gedalof et al. 2002). In western North America, the Pacific Decadal Oscillation is most closely associated with long periods of winter precipitation anomalies (Cayan 1998; Dettinger et al. 1998; Nigam et al. 1999). Warm phases of the PDO are associated with warmer winters and less precipitation in Pacific North America (Minobe 1997). Cool phases are associated with decreased temperatures and increased rainfall (Trenberth and Hurrell 1994; Latif and Barnett 1996), as well as changes in tree growth, seedling establishment, and overall forest productivity, at least at lower elevations (Zhang et al. 1997; Mantua and Hare 2002).

The Atlantic Multidecadal Oscillation (AMO) is a 20 to 40 year cycle of sea surface temperatures over the entire North Atlantic (Gray et al. 2004). Alternating between warm and cool phases, only a 0.5º C difference between extremes occurs, but this quasi-periodic forcing is associated with climatic variability throughout the northern hemisphere (Enfield et al. 2001). In particular, in Pacific North America, warm phases of the AMO correspond with low rainfall (Enfield et al. 2001; Gray et al. 2004).

The climate of Pacific North America is not static at any scale (Barry and Carleton 2001; Petit et al., 1998; Mitchell 1976); unprecedented changes in climate are projected for this century (Christopherson 1997; Field et al. 2007). The extended hot and dry summers combined with earlier snowmelt will alter moisture balances in the region (Field et al. 2007; Raper and Giorgi 2005). The temperatures in 2040 are projected to be 3° C higher in Pacific North America than in 2007, a larger increase than the global average and annual average precipitation is projected to increase by 20%, with a concurrent increase in the number and magnitude of extreme events (Christensen et al. 2007; Field et al. 2007). The greater interannual variability in precipitation will affect the hydrological regime and likely increase the frequency and intensity of future drought conditions (Mote 2003; Christensen et al. 2007; Field et al. 2007). The increasing seasonal difference in precipitation, wetter winters and drier summers, combined with the year round warming, will result in decreased soil moisture levels (Mote et al. 2005; Barnett et al. 2005).

Forests of Pacific North America

The forests of Pacific North America are distributed at a broad scale according to regional and elevational patterns in climate (Franklin and Dyrness 1988). Local patterns of biodiversity can change abruptly and dramatically in this region, but broad-scale biogeographic patterns exist. Forests in the region are sensitive to climatic variation in part because the warm dry summers cause physical stress of mature trees and limit seedling establishment. Indirectly, the climate drives disturbance regimes that are essential for functioning ecosystems (Whitlock et al. 2003b; Gedalof et al. 2005). At local scales, the distribution and structure of forests are influenced not only by climate but by physiography (Peterson and Peterson 2001; Peterson et al. 2002; Villalba et al. 1994), edaphic factors (Nowacki et al. 1990; van Breeman et al. 1997; Ricklefs 1997; Fritts 2001), disturbance regimes, including their type, magnitude, intensity, frequency, and timing (Johnson 1992; Wimberly and Spies 2001), and by both positive and negative biological interactions (Lortie et al. 2004).

Pacific North America is dominated by very productive conifers in the mountains and along the coast, while more dry-adapted coniferous tree species occur east of the Cascade Mountains. Further south and in the valleys less cold-tolerant hardwoods and grasses are supported. In between these ecosystem types are Oregon white oaks.

Biogeography of Oregon white oak

Oregon white oak is distributed from southern British Columbia through northern California, from 50° to 34° north latitude, extending over 1500 km from north to south (Figure 2.1). Stretching along the west coast of North America in a longitudinally narrow strip of land situated in the rainshadows of the Coastal, Olympic, Cascade, and Sierra Nevada Mountains, the tree's natural range rarely exceeds 100 km in width. At its southernmost limit, disjunct populations of two shrubby varieties of Oregon white oak grow in the Sierra Nevadas.

Endemic to Pacific North America, Oregon white oak is the only oak tree naturally occurring in the northern half of its range. Stands with this species exist along the eastern edge of southern Vancouver Island and on some Gulf Islands, and at least three natural discontinuous populations exist on mainland British Columbia. Scattered populations also grow east of the Cascade Mountains. Some occupied habitats remain in Washington's Puget Sound and the trees are common in Oregon's Willamette Valley. The hills of southern Oregon are the historic center of the species and the trees are abundant in northern California as well (Stein 1990; McShea and Healy 2002).

Figure 2.1. Global distribution of Oregon white oak (modified from Little 1971).

This tree species is commonly regarded as having a wide ecological amplitude, but often inhabits drier sites (Pellatt et al. 2007; Niemiec et al. 1995). Oregon white oak stands are often fragmented by extreme topography or land-use and are in decline due in large part to fire exclusion, encroachment of conifers, invasive species, and anthropogenic expansion (Agee 1993; Fuchs 2001). This species is Oregon's most important oak (Burns and Honkala 1990; Niemiec et al. 1995). Oregon white oak trees are established near sea level in the north and at elevations up to 2300 metres above sea level in California (Stein 1990; Anderson et al. 1999; McShea and Healy 2002).

The Oregon white oak tree and climate

Currently, the near-Mediterranean climate that predominates throughout the range of Oregon white oak is characterized by warm, dry summers and cool, wet winters. Oregon white oak occurs in a variety of climatic regimes ranging from cool and moderate along the coast to the greater temperature and precipitation extremes east of the Cascade Mountains (Thilenius 1968; Stein 1990; Anderson et al. 1999; Fuchs 2001). Average annual temperatures associated with this species range from 8° to 18° C with monthly averages as low as -10° C in January, and local precipitation amounts range from about 17 to 260 cm yr^{-1} (Stein 1990; Niemiec et al. 1995; Anderson et al. 1999). Although wind is the third most dominant climatic influence on the growth of most tree species (Schweingruber 1996), it has little effect on the growth of Oregon white oak trees (Niemiec et al. 1995).

Oregon white oak is a broadleaved deciduous tree that regularly grows 10 to 20 metres tall and may reach 150 cm or more in diameter (Hitchcock and Cronquist 1973; Farrar 2006). The trees display characteristic growth forms in response to their environment (Peter and Harrington 2002; Niemiec et al. 1995). When grown in the open, the tree produces a dense, rounded crown. When the stand is crowded and the canopy closed, its crown is narrow and irregular and the entire tree is strongly directed toward available sunlight. Oregon white oak trees often grow asymmetrically and produce gnarly branches. The species' environment, and particularly its climate, has also affected the species on evolutionary time scales, including but certainly not limited to shaping its wood, bark, roots, leaves, flowers, and fruits.

Oak wood is straight-grained, strong, hard, and stiff. Oregon white oak is one of the heaviest oaks in North America; its specific gravity is above 0.7, an index of its density and reflecting its ability to hold relatively large amounts of water (USDA 2007; Farrar 2006). Oregon white oak heartwood is 100,000 times less permeable to water than most red oaks (Siau 1971), due in part to the plugging up of earlywood vessels by tyloses (Niemiec et al. 1995; Abrams 2003; USDA 2007).

The bark (Figure 2.2) is thick, corky, and resistant to fire (Niemiec et al. 1995; Fuchs et al. 2000; Peterson and Reich 2001). The root system of an Oregon white oak is laterally extensive; an adaptation to dry conditions (Farrar 2006). The deep taproot has long been recognized as an overwinter storage organ (Lewis 1911) and allows access to water deeper than its associates can access (Brown and Archer 1990; Weltzin and McPherson 1999).

Oregon white oak is deciduous due to the relatively cold winter temperatures it experiences (Farrar 2006). Its lobed leaf is adapted for sunlight-intensive conditions (Koike 1988; Abrams et al. 1994; Kimmins 2004) (Figure 2.2). The tree has a variable leaf shape (Hitchcock and Cronquist 1973), a trait that in other species has been shown to correlate to climate (Abrams et al. 1994; Cole et al. 2008). The leaf is leathery on its upper side and hairy below to prevent moisture loss (Gilkey and Dennis 2001).

Figure 2.2. Photographs of Oregon white oak’s bark and leaf.

The small, green, male flowers of Oregon white oak are in catkins and facilitate the dispersal of pollen by wind in spring (Gilkey and Dennis 2001). The acorn, an annual fruit with a hard pericarp and a large endosperm is adapted in part to avoid desiccation (Daubenmire 1968; Niemiec et al. 1995). Oregon white oak's acorns are zoodispersed and are produced in large, locally synchronized masting events (Peter and Harrington 2002), the frequency and magnitude of which is influenced by climatic variability (Koenig and Knops 2000), especially moisture availability in spring and summer (Sork et al. 1993; Peter and Harrington 2002).

Heliophytic and drought-tolerant, Oregon white oak trees can withstand and make use of higher light intensities and less available water than neighboring species (Hibbs and Yoder 1993; Niemiec et al. 1995; Pellatt et al. 2007). Its water impermeability also allows the tree to tolerate periodic flooding (Stein 1990; Howard 2002). Adapted to a low intensity, high frequency fire regime, this tree species often exists where other tree species cannot (Stein 1990; Niemiec et al. 1995; Pellatt et al. 2007). The wood of white oak decays slowly and burns hot, so fuels are stockpiled, fire is encouraged, and in this way oak ecosystems are able to maintain themselves in fire-dominated ecosystems (Gedalof et al. 2006; Nowacki and Abrams 2008). Even though Oregon white oaks are slow growing, shade-intolerant, have relatively limited seed dispersal, and are generally considered poor competitors (Hitchcock and Cronquist 1973; Franklin and Dyrness 1988; Foster and Tilman 2003; Brudvig and Asbjornsen 2005; Farrar 2006; Pellatt et al. 2007), these long-lived trees endure a wide range of environmental conditions and so can persist by tolerating stress until able to re-establish during more favourable times (Fuchs 2001; Agee 1993).

Climatic factors limiting to growth exist in all tree species, especially during the growing season (Laroque and Smith 1999), but also due to influences during the previous growing season (Fritts 2001; Adler and Levine 2007), or while the tree is dormant (Gedalof et al. 2004; Pederson et al. 2004). Therefore, understanding the phenology and underlying ecophysiology of Oregon white oak aids in interpreting its dendroclimatic response (Figure 2.3). However, because little research has been directed specifically at Oregon white oak's radial growth, here we reference other white oaks with similar life histories.

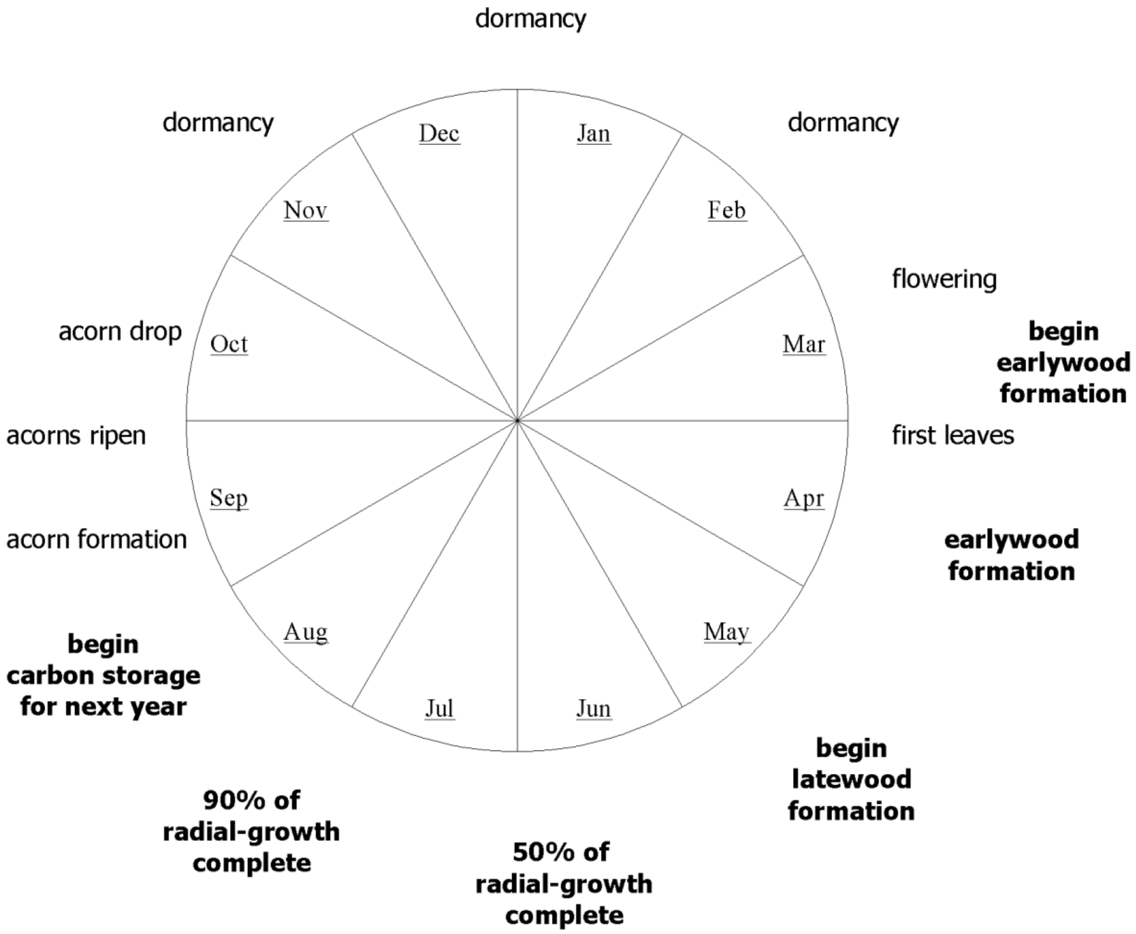

Figure 2.3. Idealized annual cycle of phenology and growth in Oregon white oak.

Oak and other ring-porous species display flush-type growth in which bud burst and leaf emergence is approximately coincident with radial-growth (Kikuzawa 1983; Abrams 1996; Tardif 1996; Gonzalez and Eckstein 2003). Thus, conditions during the formation of earlywood are important, especially soil moisture (Akkemik et al. 2007), but much of the spring cambial growth is dependent on the previous year's carbohydrate storage.

The emergence of oak flowers and the beginning of twig growth precede leaf-out, in Oregon white oak occurring anytime between March and early June (Stein 2002; Peter and Harrington 2002). Flowering lasts only a week or two on any single tree (Stein 1990) and is immediately followed by leaf expansion. In other white oaks, cambial growth was initiated in March or April (Fritts 2001; Du et al. 2007; Akkemik et al. 2007). The majority of radial growth occurs in May and June (Du et al. 2007; Akkemik et al. 2007). By the end of July, 90 percent of growth has occurred, and the remainder is completed by September (Foster and LeBlanc 1993; Fritts 2001; Akkemik et al. 2007; Du et al. 2007). When radial growth is finished in any year, storage of carbohydrates within roots takes priority. Importantly, Oregon white oak has high root allocation priority and low radial growth priority, so ring-widths vary greatly in response to environmental changes (Waring and Pitman 1985).

Masting every two to six years is a conspicuous component of oak reproduction (Farrar 2006). Acorns form, ripen, and drop throughout August, September, October, and November (Stein 1990; Peter and Harrington 2002). A stand's masting pattern likely complicates the climate signal. Some carbon reallocation certainly takes place, even though little effect on radial-growth of masting oaks has been documented (Speer 2001). This signal interacts with the annual phenology of the species and has an important influence on the oak's ecosystem.

The Oregon white oak ecosystem and climate

Placing the tree within the context of its ecosystem can help us understand the species’ climatic tolerances. For instance, these trees occur both in pure and mixed stands (Figure 2.4) which can alter the influence of various climatic factors on radial growth.

Figure 2.4. Pure (upper panel) and mixed (lower panel) Oregon white oak stands.

Oregon white oak ecosystems are species-rich (Thysell and Carey 2001; Niemiec et al. 1995) and are important at landscape and regional scales for the abundance and diversity of wildlife in the region (Howard 2002). They support at least 454 native species of plants in British Columbia (MacDougall and Turkington 2005) and eight rare plant communities occur only within their range, including 20% of the total number of rare plants in the province (Fuchs 2001). The ecosystem type in Canada contains at least 129 species at risk including plants, insects, reptiles, and mammals, of which 23 are considered threatened or endangered at a global scale (GOERT 2002; COSEWIC 2003). In the United States, these ecosystems are also considered highly endangered (Noss et al. 1995). Generally, more species of birds occur in these stands than in the regions' other forests (Anderson 1972; Niemiec et al. 1995; Hagar and Stearn 2001). Additionally, oaks in western North America have the longest mushroom season of any forest type there (Arora 1986) plus a 'remarkable' diversity of ectomycorrhizal symbionts (Southworth et al. 2001). Lastly, oak trees are extremely resistant to decay (Nowacki and Abrams 2008), can survive heart rot (Figure 2.5), and so are certainly important for wildlife as long-standing snags and as long-lasting often-hollow logs.

Figure 2.5. Hollow, rotten-centered Oregon white oak tree at White Salmon Oaks.

Soils typically associated with Oregon white oak vary in their depth, texture, and nutrient content (Fuchs et al. 2000), but are often shallow, rocky, and extremely well drained (McPherson 1997; Fuchs 2001). These trees also occur on shallow clay soils that dry during the summer months and have little available moisture (Erickson 2002; Fuchs 2001). Soil characteristics interact with climate, strongly influence the growth of trees, and add complexity to Oregon white oak's dendroclimatic response.

Oregon white oak has a mosaic distribution within its’ mapped range, interspersed among other forest and grassland ecosystems. The sites inhabited by this tree are diverse, including coastal bluffs, rocky outcrops, valley floors, and foothills (Gilkey and Dennis 2001; Erickson 2002), occurring in both woodlands and savannas (Hitchcock and Cronquist 1973; Stein 1990; Agee 1993; Niemiec et al. 1995). However, some characteristics of sites with Oregon white oak are common and these drier areas tend to limit competition: soils are either shallow or extremely well drained (Stein 1990; Roemer 1993; Erickson 2002) and the climate throughout its range is characterized by several consecutive months of a semiarid moisture regime (Franklin and Dyrness 1988; Fuchs 2001). Drought tolerant species such as oaks regularly outcompete more mesophytic species on soils with low moisture holding capacity (Nowacki and Abrams 2008; Roemer 1993; Abrams 1990).

Oregon white oak’s habitat, the ecological role of the tree within its stand, the tree’s position in the landscape, and its recent and rapid decline are all intimately connected to climate. Several distinct ecotypes of Oregon white oak exist, namely woodland and savanna types. Each has characteristic growth forms and are associated with highly diverse sets of species (Roemer 1993, Erickson 2002), both of which add to the complexity of the tree's growth-climate relationship.

Oak woodland is a common habitat type on valley floors, valley margins, and on ridge tops (Thilenius 1968; Kimmins 2004; Niemiec et al. 1995). Douglas-fir (*Pseudotsuga menziesii*), hazelnut (*Corylus cornuta*), and snowberry (*Symphoricarpos alba*) are common associates here, as are Nootka rose (*Rosa nutkana*) and honeysuckle (*Lonicera ciliosa*) (Thilenius 1968; Franklin and Dyrness 1988; Fuchs 2001). In seasonally inundated sites, Oregon ash trees (*Fraxinus latifolia*) and willow (*Salix spp.*) can coexist with the species.

The oak savanna habitat type, however, is quite different, characterized by widely spaced trees and clumps of shrubs alternating with areas of grasses and herbs. The coexistence of grasses and trees are the distinguishing feature of this rare habitat (Cole 1986). A temperate savanna will include some organisms from both of its adjacent ecosystems, the forest and the grassland, but will also support organisms that have adapted to its unique conditions. This results in a highly productive ecotonal system containing large amounts of biodiversity (Scholes and Archer 1997). Conspicuous associates include camas (*Camas quamash*), long-stolon sedge (*Carex inops*), and Roemer's fescue (*Festuca roemerii*). Like the woodland, an oak savanna is a transitional zone: both in space, occurring between forest and grassland; and in time, as tree-grass interactions move the geographic boundary between the two habitats reflecting the current dominance. Some areas and habitats are more stable than others, depending on their specific controls (Jackson and Bartolome 2002). Fire, soil, grazing, and climate can all limit the distribution of these forest types (Stein 1990; Fuchs 2001; Pellatt et al. 2007).

The fire cycle in any forest type is in large part determined by climate (Swetnam and Betancourt 1990; Millspaugh 2000; McKenzie et al. 2004; Heyerdahl et al. 2002; Hessl et al. 2004; Gedalof et al. 2005). High frequency, low-intensity fires help maintain oak ecosystems (Regan and Agee 2004; Pellatt et al. 2007; Nowacki and Abrams 2008), as these small disturbances are mostly confined to the ground layer and do little damage to mature trees, especially these fire-adapted oaks. Fire selectively eliminates grasses and tree seedlings that might encroach into sites inhabited by Oregon white oak (Agee 1993; Pellatt et al. 2007). This is thought to be the case with the maintenance of the oak savanna by indigenous peoples, who set fires regularly in Pacific North America over thousands of years (Agee 1993, 1996; Turner 1999; Fuchs 2001; Pellatt et al. 2007).

At broad scales, climate is the dominant factor in the creation of soil from bedrock. In turn, soil characteristics relating to nutrients and water permeability certainly influence the growth and distribution of Oregon white oak. For the limited purposes of this monograph, soil is considered a confounding variable and is further discussed only where it interacts with more direct climatic influences.

Climate also plays a more direct role in maintaining woodland and savanna conditions. The rainfall is often temporally distinct at an annual scale, with most of the precipitation restricted to just eight months of the year, and so several consecutive months of drought occur. This limits the moisture available for tree growth and allows fires to occur, both of which reduce competition from more mesophytic and fire-intolerant species and causes Oregon white oaks to establish in pulses (Gedalof et al. 2006; Pellatt et al. 2007). These fluctuations in recruitment may be due to the slow expansion of either the trees during wetter periods, or the grasses during consecutive years of dry conditions (Chesson and Warner 1981; Grime 1973), or by stand-altering disturbances such as fire (Gedalof et al. 2006; Pellatt et al. 2007).

Oregon white oak trees are stress-tolerators (Abrams 1990; Niemiec et al. 1995; Fuchs 2001): they establish and persist when moisture is limited or after fire and so maintain local dominance (Stein 1990; Niemiec et al. 1995; Kimmins 2004; Pellatt et al. 2007). These trees often form pure stands and successfully reproduce under their own canopy (Fuchs et al. 2000), thus Oregon white oak is considered a climax species (Pellatt et al. 2007). Furthermore, they grow slowly, delay maturity, produce large seeds, and live for long periods, all of which are common characteristics of other climax species (MacArthur and Wilson 1967; Grime 1979; Stearns and Crandall 1981).

However, Oregon white oak can also be considered a seral, or late-successional species, as it is overtopped by other tree species in lieu of disturbance (Franklin and Dyrness 1988; Stein 1990; Fuchs 2001) which then limits its radial-growth (Pellatt et al. 2007). Oregon white oak is also correctly labeled a pioneer species, establishing rapidly after fire by sprouting (Sugihara and Reed 1987; Hibbs and Yoder 1993; Niemiec et al. 1995; Regan and Agee 2004). For these oak ecosystem types, succession may not be an appropriate model for describing vegetation change in that progression towards a climax state is not unidirectional and is certainly not stable (Johnson and Miyanishi 2008). These ecosystem types follow an ever-moving climatic target, and so the endpoint is not deterministic (Nowacki and Abrams 2008).

The concept of an integrated community stresses both individualistic responses to the environment and the interconnectedness of components and processes within ecosystems (Lortie et al. 2004). Assemblages seem to persist through time to some degree, due in large part to their similar environmental tolerances and co-evolved or ecologically usurped associations. The number and strength of biophysical linkages will vary between species, and those with many strong non-redundant connections like Oregon white oak will likely exert a large influence on their ecosystem (Smith 2007; Lortie et al. 2004).

Dominant species influence the associated understory and the fire regime (Gavin et al. 2007; Nowacki and Abrams 2008), which in turn influence radial-growth. A foundation species is one that defines the structure of its ecosystem and has disproportionate effects upon it, providing resources, creating habitat, altering microclimate, and influencing ecosystem functions (Hamburg and Cogbill 1988; Ellison et al. 2005). Temperate oak trees are commonly considered keystone species (Fralish 2004; Speer 2001). Ellison et al. (2005) labeled oaks in similar habitats in other regions of North America foundation species, and this concept has direct bearing on the biogeography of Oregon white oak forest ecosystems and their relation to climate.

Foundation species like Oregon white oak stabilize the system because at the stand level, long-lived trees with high seed production can persist even when conditions favor other species (Ellison et al. 2005). However, the presence of a single foundation species can result in a more fragile system, because with little functional redundancy ecological processes are more easily disrupted (Liebold et al. 2004; Ellison et al. 2005). The extirpation of a foundation species will result in a cascade of altered ecological linkages and may have large effects on the biota (McCann 2000; Ellison et al. 2005), even altering the successional trajectory of the site (Ebenman and Jonsson 2005; Nowacki and Abrams 2008) which will in turn affect the climate-growth relationship of individual trees.

Thysell and Carey (2001) described the dependence of many organisms on the conspicuous architectural presence of Oregon white oak. In addition, the oak's acorns are critical for wildlife throughout the species' range (Wolff 1996; McShea and Healy 2002). Just as producers often control the range of consumers (Cox and Moore 2005), oaks influence the population structure and so the distribution of western gray squirrels (Ryan and Carey 1995; Thysell and Carey 2001), acorn woodpeckers (Niemiec et al. 1995), streaked horned larks (Stinson 2005), the western bluebird (GOERT 2008), plus insects such as weevils, aphids, and butterflies (Stinson 2005). If oak trees are lost, then those animal species that are strongly associated with them will at a minimum shift their ecological impact (e.g., switching food sources or nesting sites) and may possibly be extirpated (Brudvig and Asbjornsen 2005; Pellatt et al. 2007).

Upscaling of processes and patterns, from organism to stand to landscape, is used for prediction, and in order to fully understand Oregon white oak's relationship to climate one need take a landscape-scale perspective and place this oak ecosystem in the context of its regional vegetation. The ongoing transformations between savanna and woodland and the decline of the ecosystem need to be examined at various scales.

Oregon white oak has long been recognized as an ecotonal species (McCulloch 1940; Pellatt et al. 2007). An ecotone is a transition zone, or discontinuity, between biological communities in space or time, whether that boundary is gradual or abrupt (Kimmins 2004; Hansen and di Castri 1992). Ecotones are dynamic spatial-temporal biophysical systems with processes interacting at various scales (McMenamin 1992; Delcourt and Delcourt 1992; Gosz 1993; Neilson 1993; Kolasa and Zalewski 1995). The plants within an ecotone grow under stressful conditions where environmental and ecological impacts can be extreme (Holland et al. 1991; Pitelka 1997).

What biogeography has taught us about ecotones and characteristics of their inhabitants can help us better understand the mechanisms that control the growth and distribution of other ecotonal species (Tivy 1993; Risser 1993; Kolasa and Zalewski 1995; Lamb and Mallik 2003). Ecotonal species are general indicators of change (Loehle 2000). Species that inhabit these areas tend to be especially sensitive to climatic changes and climatic variability (Rizzo and Wiken 1992; Neilson 1993; Gosz 1993; Churkina and

Suirezhev 1995; Cox and Moore 2005; Adler and Levine 2007), and the response of trees to climate tends to occur sooner and is larger at an ecotone (Risser 1995; di Castri et al. 1988; MacArthur 1972; Kronberg et al. 1996; Allen and Breschears 1998; Loehle 2000). Semiarid ecotones are among the most sensitive to changes in climate (Field et al. 2007), and rapid contractions of some of these systems are projected (Allen and Breschears 1998; IPCC 2007). Therefore, the ecotonal nature of Oregon white oak highlights the fact that the species is particularly sensitive to changes in climate. This is important, for the increasing climatically driven habitat fragmentation of ecotonal species at their range limits is predicted (Gosz 1993; Neilson 1993; Kolasa and Zalewski 1995; Shafer et al. 2001).

Oregon white oak occurs between forested and non-forested ecosystems (Stein 1990; Ryan and Carey 1995; Thysell and Carey 2001; Thilenius 1968; Farrar 2006; Gedalof et al. 2006) which grade into each other both spatially and temporally (Stein 1990; Regan and Agee 2004; Pellatt et al. 2007). Temporally, these systems act as ecotones as the geographic boundaries between the ecosystems adjust in response to changing environmental conditions (Cole 1986; Weltzin and McPherson 1997; Thysell and Carey 2001; Devine and Harrington 2006). For instance, many of the oak woodlands existing today developed over time from oak savanna (Thilenius 1968) and one can see evidence of this in the occasional areas of open-grown trees (Gedalof et al. 2006). Furthermore, many scientific articles state that oak woodlands and savannas are in a transitional phase (Thilenius 1968; Barnhart et al. 1987; Stein 1990; Thysell and Carey 2001; Koole et al. 2004; Gedalof et al. 2006; Nowacki and Abrams 2008). This transitory nature is the manifestation of the temporal nature of an ecotone and reflects the dominance of particular species or ecosystem types at a specific time (Risser 1995).

Additional evidence for this transitional nature comes from eastern North America where similar oak savannas turned to woodland (Curtis 1959; McPherson et al 2000; Nowacki and Abrams 2008). Oregon white oak ecosystems, like many ecotones, are important for regional biodiversity (Terbrough 1985; Niemiec et al. 1995; Anderson et al. 1999; Fuchs 2001).

Oregon white oak is a flagship species (Thysell and Carey 2001) in an ecosystem that is already undergoing changes in its composition, structure, and overall pattern on the landscape due to a complex suite of interacting anthropogenic, ecological and environmental influences (Erickson 2002; Harrington 2002; Smith 2007). For instance, less than 15% of historical Oregon white oak populations still exist in the United States (PNW Ecosystem Consortium 1998). Oregon white oak habitat is also among the three most threatened ecosystems in Canada, and less than five percent of historical Oregon white oak ecosystems remain intact there (Lea 2002; GOERT 2002; Erickson 2002; Macdougall 2004). The extant stands throughout its range are in decline and becoming increasingly fragmented (Agee 1993; Fuchs 2001; Riitters et al. 2003; ODFW 2005), and so this ecosystem type is considered one of the most endangered habitat types in North America (GOERT 2002; Scott et al. 2001). Oak savannas in general are among the rarest ecosystems in the world (Nuzzo 1986; Nowacki and Abrams 2008). As Oregon white oak is a declining foundation species (Thysell and Carey 2001; McShea and Healy 2002; Smith 2007) in one of the most diverse ecosystems in North America (Fuchs 2001; Hansen et al. 2001), it is a conservation priority both in the United States (Larsen and Morgan 1998; Lorimer 2003) and in Canada (GOERT 2002; COSEWIC 2003).

As oak woodland and savanna are lost, diversity is expected to decrease (Cole 1977), in part because the adjacent ecotypes contain both fewer total species as well as fewer rare species (Thysell and Carey 2001). To highlight the immediacy of the threat, note that several species associated with the Oregon white oak ecosystem have already been locally extirpated, and 129 are considered at risk in British Columbia alone (GOERT 2008). A naturally diverse and structurally complex community is thought to be both more stable in terms of its resistance to stress and its resilience after disturbance, as well as being more productive by lengthening energy and nutrient cycling pathways and contributing to their efficiency (Tilman et al. 1997; Chapin et al. 1997; McCann 2000).

Much of the land once inhabited by Oregon white oak has been converted to agriculture or anthropogenic development (GOERT 2002; Thilenius 1968; Scholes and Archer 1997; Lea 2002). Habitat degradation is common in this forest type, and many possible drivers of Oregon white oak's decline have been proposed. Habitat loss, invasion by exotic species, encroachment by conifers, changes in herbivory, and altered fire regimes all interact to threaten Oregon white oak ecosystems in site-specific ways (Fuchs 2001; Brudvig and Asbjornsen 2005).

Due to their proximity to human communities and their characteristic open canopies, oak woodlands and savannas in the Pacific Northwest are extremely vulnerable to invasive species (Fuchs 2001). In fact, much of the Oregon white oak habitat that remains is often dominated by invasive shrubs, herbs, and grasses (Thysell and Carey 2000; Macdougall 2004) which can alter local soil moisture levels (Davy 2008).

Encroachment by Douglas-fir can overtop the shade-intolerant oaks by limiting air movement, increasing relative humidity, and creating wind and light limited conditions unsuitable for oak establishment (Ryan and Carey 1995; Agee 1996; Barnhart et al. 1996; Tveten and Fonda 1999; Thysell and Carey 2001; Gedalof et al. 2006). The formerly-open ecosystems then assume increasingly woodland-like conditions before transforming into forest. Fire, extended periods of drought, and insect outbreaks on conifer species are thought to be important mechanisms in slowing this encroachment (Roemer, unpublished; Pellatt et al. 2007).

Insect defoliation can be an important process in the Oregon white oak ecosystem (Stein 1990; Roemer unpublished; Fuchs 2001). Selective browsing by deer or introduced livestock can result in the decline of an oak tree stand, for saplings are browsed, seedlings are trampled, and the ground is compacted by these animals (Jackson et al. 1998; Fuchs 2000). Insect outbreaks or grazing pressure cause an increase in amounts of non-native vegetation and a decrease in fire frequency (Fuchs 2000), highlighting the interconnectedness of these influences on Oregon white oak.

For thousands of years, North American indigenous people regularly burned Oregon white oak ecosystems to encourage camas, onion, deer, turkey, and other edge and open-habitat adapted organisms (Roemer 1972; Agee 1996, White 1999; Turner 1999). Without fire, many species are able to out-compete these slow-growing oaks (Tveten and Fonda 1999; Dunwiddie 2002; Pellatt et al. 2007). The diversity in some Oregon white oak ecosystem types is explained by the Intermediate Disturbance Hypothesis, where fire or periods of drought prevent competitive exclusion in continually changing ecosystems (Grime 1973; Connell 1978; Roxbrough et al., 2004).

Now however, a new threat to the species is looming: short-term influences can be swamped by relatively weak but persistent forces such as climate (Parmesan and Yohe 2003). Rapid climate change is especially significant to species like Oregon white oak with narrow environmental tolerances, poor dispersal abilities, or poor competitive abilities (Fuchs 2000; Araujo and Pearson 2005). The influences of these characteristics are compounded by the fragmentation of Oregon white oak habitat (Erickson 2002; Foley et al. 2005; Pellatt et al. 2007). Ecological interactions, once disrupted, can result in long-term changes in ecological processes (Janzen 1988; Nowacki and Abrams 2008). Should this species continue to decline, the size of the ecological ripple is likely to be substantial (Franklin et al. 1991; Fuchs 2001; Brudvig and Asbjornsen 2005).

Biogeographic-Dendroecological Approach

Biogeography is the scientific study of the spatial and temporal distribution of organisms, the explanation of those patterns, and the ways in which organisms interact with their physical landscape (Lomolino et al. 2006a; Cox and Moore 2005). Examining the biogeography and the ecological role of the species at multiple scales is essential to its understanding because climate acts at multiple scales and is undoubtedly one of the mechanisms that determine the growth of the trees, the structure of its ecosystem, and the species' overall distribution on the landscape (Fritts 2001; Gaston 2003). This environmental systems perspective allows us to recognize patterns of controls on Oregon white oak's radial-growth. Paleogeography and ecogeography both contribute to our understanding of climate's influence on Oregon white oak and direct this research.

Paleogeography, Oregon white oak, and climate

Understanding the relative roles of past forces in shaping current patterns of growth and distribution can offer a valuable perspective on present and future controls: low-frequency trends become evident and natural variability can be more accurately characterized (Myers and Giller 1988; Avise 2001). Phylogeography and palynology are two disciplines that have evaluated the distribution of Oregon white oak in the context of its past.

Phylogeography, a branch of biogeography, concerns itself with the study of the spatial and temporal distribution of species' evolutionary lineages, the processes that control them, and the effect of landscape on evolution. In particular, the geographical and evolutionary relationships of the oaks, genus *Quercus*, have been investigated (Nixon 1997; Manos et al. 1999; Grivet et al. 2006). Their ancestral home was in the mountains of Mexico and 140 species of oak are currently known to exist there today, mostly evergreen in habit (Nixon 2002). Oaks are now one of the world’s most diverse groups of tree species (Nixon 2002). The white oaks (*Lepidobalanus*) are the most widespread group in this genus and have established around the world in no small part due to their drought tolerance (Abrams 1990; Aranda et al. 2005).

In the late Tertiary, a species of shrubby oaks existed in the Rocky Mountains that were particularly adapted to xeric conditions, the *Quercus gambelii-garryana* complex. This once-widespread species split vicariously into two during a long-term drying event (Nixon 2002). Oregon white oak remains, then, as the member of its genus that reaches the furthest north in western North America.

Palynology, the study of fossil pollen, has been conducted within the range of Oregon white oak, and understanding the trajectory of the tree during the Holocene helps identify its environmental tolerances. A mosaic of habitat patches today characterizes the distribution of Oregon white oak, but these were more extensive and less fragmented in the region over the last 8500 years, especially during warmer climates (Whitlock 1992; Pellatt et al. 2001; Thysell and Carey 2001; Brown and Hebda 2002a; Abrams 2003; Ritland et al. 2005). Oak pollen, increased amounts of charcoal, and relatively warm and dry climates have coincided throughout most of the Holocene (Hebda et al. 2000; Brown and Hebda 2002; Whitlock 2003a; Allen et al. 1999; Pellatt et al. 2001).

The distribution of Oregon white oak on Vancouver Island, for instance, expanded westward from 8800 - 8300 ybp during a warm, dry climate characterized by frequent fire (Pellatt et al. 2001). A large, long-lasting decrease in oak pollen abundance began around 6800 ybp as conditions cooled. However, oak pollen increased again around 3800 ybp in spite of continued cooling and maintained a strong presence until just this century (Brown and Hebda 2002b) (Figure 2.3). For at least the last two thousand years, anthropogenic burning influenced the landscape, and it is this disturbance that is thought to have maintained some of these oak landscapes in non-equilibrium with the more direct effects of climate by limiting competition from less fire-adapted species (Agee 1996; Turner 1999; Brown and Hebda 2002a).

Ecogeography, Oregon white oak, and climate

Ecogeography is the branch of biogeography concerned with identifying the spatial and temporal distributions of ecosystems and the processes that differentiate them, and in particular, the roles of climate and landscape in shaping ecological patterns. The unique ecology, geography, and physiology of Oregon white oak suggest that both its radial-growth and its distribution may be particularly sensitive to both climatic variability and to projected climatic change.

A fundamental tenet of biology holds each species unique, yet still, strong ecogeographical tendencies are apparent on the landscape (i.e., macroecological rules) (Lomolino et al., 2006b; Gaston et al., 2007). In particular, biogeographic characteristics are associated with the climatic-response of an organism and ecological, biological, and geographic qualities of the organism and the stand influence the climatic sensitivity of that organism (Table 2.1).

The ecological condition of the stand will in part determine to what degree climate controls the growth of a tree. For instance, dominant species are more sensitive to climatic variability (Phipps 1982, Fritts and Swetnam 1989; Laroque and Smith 2005), while subordinate and understory species tend to be more sensitive to slight variations in habitat such as soil (Tivy 1993; Kimmins 2004; but see Orwig and Abrams 1997). For example, overstory oaks are more sensitive than understory oaks (Nowacki and Abrams 1997). Shaded individuals tend to be more drought-stressed than those in the sun due to greater declines in leaf water potential (Vallardes and Pearcy 2002). The amount of arboreal dominance, or the degree of canopy closure, decreases the sensitivity of individual trees to climatic variability (Fritts 2001), and similarly, high tree density and greater competition can increase a tree's sensitivity to temperature and winter precipitation (Franks 2007).

Biological characteristics of individual trees can also affect the growth-climate relationship of the species. Older and larger trees have shown decreased sensitivity to climate (Larson et al. 2000; Rozas 2005). Faster-growing ring-porous hardwoods, those trees in which latewood contributes more to total radial-growth, can be more sensitive to conditions in the year of growth than slower-growing, earlywood dominated trees (Douglas Larson, personal communication).

Furthermore, geographic factors influence growth and the so response of trees to climatic variability varies with site conditions (Graumlich 1993; Villalba et al. 1994; Peterson and Peterson 1994; Ettl and Peterson 1995; Laroque and Smith 1999; Peterson and Peterson 2001; Gedalof and Smith 2001a). For instance, lower elevation trees tend to be more sensitive to climate (Peterson et al. 2002), and in particular, the growth response to drought in lower-elevation trees is greater than in high-elevation tree species (Peterson and Peterson 2001; Peterson et al. 2002; Adams and Kolb 2004). Slope aspect interacts with temperature and drought stress increases on warm-aspect slopes (Graumlich 1991; Peterson 1998; Villalba et al. 1994). Steep or convex slopes and those closer to the ridgetop are associated with a decrease in moisture availability and tree growth (Cox and Moore 2005; Du et al. 2007). Savanna systems are especially sensitive to climate, particularly rainfall (Rizzo and Wiken 1992; Gedalof et al. 2004; Cox and Moore 2005), and in general, trees on xeric sites are affected more by drought than those on more mesic sites (Tardif and Bergeron 1997; Rubino and McCarthy 2000). Impacts of climatic change are projected to be more severe and immediate on well-drained soils (Graumlich 1991).

Biogeographic characteristics are also associated with variability in tree growth. Due to the longitudinally narrow distribution of Oregon white oak, many of the populations exist near the limits of their environmental tolerances, a trait which has been shown to be a characteristic associated with sensitivity to climatic variability and a geographically mixed response among stands. That is, sites closer to the edge of a species' distribution tend to have more extreme growing conditions than interior sites and so marginal populations tend to be more sensitive to climatic variability (Brubaker 1986; Rizzo and Wiken 1992; Kullman 1993; Cullen et al. 2001; Fritts 2001; Chhin 2004). Tree species commonly associated with ecotones, like these oaks, have been shown to be especially sensitive to climatic variability (Neilson 1993; Gosz 1993; Churkina and Suirezhev 1995): the dendroclimatic response tends to occur sooner and to be larger within an ecotone (Kronberg et al. 1996; Allen and Breshears 1998; Loehle 2000). In other woodland-grassland ecotones, trees were shown to directly respond to precipitation patterns (Weltzin and McPherson et al 2000; Adler and Levine 2007). Organisms in stressful environments, where growth is limited by only a few factors, are excellent study organisms for dendroecological analyses (Schweingruber 1996).

Table 2.1. The influence of biogeographic characteristics on dendroclimatic response.

biogeographic characteristic	**associated response to climate**
Ecological	
a dominant species	increased sensitivity
an overstory species	increased sensitivity
total arboreal dominance	decreased sensitivity
more shaded conditions	increased drought stress
more interspecific competition	increased sensitivity to temperature
higher tree density	increased sensitivity to winter precipitation
Biological	
older and larger hardwoods	decreased sensitivity
slower growing hardwoods	decreased sensitivity to prior year's climate
Geographical	
low elevation sites	increased drought stress
warm aspect sites	increased drought stress
steep slope angle	increased drought stress
convex slope	increased drought stress
higher slope position	increased drought stress
xeric sites	increased drought stress
Biogeographical	
marginal populations	increased sensitivity
ecotonal species	increased sensitivity

The spatial variability in the region’s climate, soils, and botanical associates (Franklin and Dyrness 1977; Stein 1990) suggests that the species’ relationship to climate may be mixed: that the relative importance of climatic controls varies throughout the range of the species (Brubaker 1980; Kienast et al. 1987; Gedalof and Smith 2001a; Nakatawase and Peterson 2006; Carrer et al. 2007). Climate in large part determines the biotic potential of an area (Tivy 1993; Kimmins 2004), the climate of Pacific North America is variable (Stein 1990), and Oregon white oak is sensitive to that parameter (Erickson 2002; Gedalof et al. 2006; Pellatt et al. 2007). Consequently, these ecosystems are also dynamic which suggests a research approach that assesses the temporal component as well as the spatial. Dendrochronology is an effective approach to better understand the controls on tree growth, stand structure, and forest distribution through time (Schweingruber 1996; Jacoby and D’Arrigo 1995; Fritts 2001).

Dendroecology, Oregon white oak, and climate

Dendroecology has proven an effective tool for understanding controls on forest growth (Fritts and Swetnam 1989; Gedalof et al. 2006), and in particular, a tree species’ response to climatic variability and change (Graumlich and Brubaker 1986; Villalba et al. 1992; Cook and Peters 1997; Orwig and Abrams 1997; Peterson and Peterson 2001; Gedalof and Smith 2001a; Oberhuber 2004).

The rate of tree growth is an integrated response to both past and current stresses (Kozlowski et al. 1991). External conditions that affect tree growth include the amounts of light, heat, atmospheric gas concentrations, water, and the types and amounts of available soil minerals (Fritts 2001). The amount of daylight and soil conditions change very little from year to year, although the amount of shade experienced by the tree might.

External variables interact to determine internal conditions such as amounts of photosynthate, vital minerals, growth regulators, enzymes, and water within the tree (Fritts 2001). Influences are complex, as limiting factors vary at diurnal and annual scales, with the life-history stage, and with the age of the individual tree (Fritts 2001; Carrer and Urbinati 2003; Buckley et al. 2004). Other stochastic events, disturbances such as fire, insect outbreaks, or disease, can also affect growth rates. The result is the formation of growth structures that are then preserved as tree rings.

A tree-ring is a layer of wood cells that is produced in one year and results from differential seasonal growth patterns (Figure 2.6). Oregon white oak's earlywood is the lighter color of a ring due to larger diameter thin-walled cells associated with rapid growth during spring. This makes the wood ring-porous. The darker color of the ring that follows is latewood, a zone of denser cells that reflects slower rates of growth in summer. Wood rays form perpendicular to the tree bole. The width of these tree-rings is the average of climatic conditions experienced and serves as an ecophysiological record that can be correlated to the climatic or ecological factors that influenced them (Cook and Kairiukstis 1990; Cook and Briffa 1990; Stokes and Smiley 1996; Schweingruber, 1996). This technique allows the assessment of both climatic and ecological trends (Fritts 2001; Fritts and Swetnam 1989).

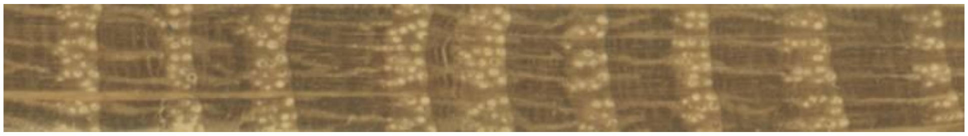

Figure 2.6: Surface image of Oregon white oak tree-core scan.

Strengths of dendrochronology include its annual resolution extending hundreds of years with precise spatial resolution. Ring-widths are a direct measurement of growth, not a proxy, and have been strongly correlated to climate (Douglass 1920; Schweingruber 1996; Fritts 2001). The weaknesses of dendrochronology when investigating growth-climate relationships are also important to mention. The genetics of the organism affect its growth rate and adds to the variability of growth in any individual tree and so the interpretation of its record. Associating growth to climate is further complicated by variability in site conditions. Only the radial growth of the tree is actually being measured; however, radial-growth is positively and strongly correlated to tree height, leaf area (Kimmins 2004), and to other biological functions as well, such as acorn production (Peter and Harrington 2002) and the growth of oak seedlings (Guyette et al. 2004; Goldblum and Rigg 2005).

Adopting a biogeographical approach and considering the paleogeography and ecogeographical characteristics of Oregon white oak in relation to its climate allows a more thorough understanding of this valuable tree species and its decline. Placing the growth-climate relationship in biogeographic context provides insight into the dendroclimatic response described in the following chapters. Individual trees, the species, and the ecosystems are all influenced by climate, and this chapter shows that scale-dependent properties emerge which alter the tree's relationship to climate. Assessing this relationship has little meaning outside of the tree’s role in its ecosystem, which defines the structure of the system, and in the ecosystem’s role within the landscape, which is why society is concerned about this species' decline. By taking a dendroecological approach and focusing on different scales of biological organization and levels of taxa, the influence of climatic factors limiting to growth can be more readily interpreted.

Aim, objectives, and hypothesis

We took a biogeographical approach and used dendroecological techniques to characterize the relationship between climate and the radial growth of Oregon white oak. We designed this research project to quantify climatic limits to growth in the dominant life-history stage of the species by comparing ring-width indices to climatic variables and so develop a characteristic growth response. Here, we aim to test the hypothesis that the relative importance of climatic controls varies throughout the range of this tree species.

We minimized confounding variables by selecting sites and trees likely to maximize the climate signal over those associated with other environmental influences on growth. We sampled trees at 18 sites representing much of the species' geographical range and cored at least 20 Oregon white oak trees in each stand. We then developed standardized tree-ring chronologies for each site (RWIs) by measuring and cross-dating the tree ring-widths, statistically removing biological trends, and averaging the measurement series for the trees at each site.

Employing a 4 km gridded climate dataset extending from 1895 through 2005 allowed a spatially precise and temporally extensive analysis. For each of the 18 sites, we acquired 111 years of monthly climatic variables (CVs), namely average monthly maximum temperature (Tmx), average monthly minimum temperature (Tmn), and total monthly precipitation (Ppt). The Palmer Drought Severity Index, an index of available moisture (Mix), integrates temperature, precipitation, sunlight, and soil properties at a coarser scale. These four climatic variables served as the link between meteorological instrumental data and the tree-rings.

We assessed the growth-climate relationship of the 18 stands using the trees' characteristic responses to the four climatic variables and to indices of three quasi-periodic forcings (QPFs). The dendrochronological record was compared to climatic variables and correlation functions (CFs) for each stand. This strategy identifies significant associations between radial-growth and climatic variables, allowing an assessment of both climatic and ecological influences (Fritts and Swetnam 1989; Fritts 2001). Principal components analyses identified important associations between Oregon white oak's growth-response and climatic variability.

We tested the hypothesis that radial-growth of Oregon white oak trees is strongly correlated to climate yet shows a geographically mixed growth-response. This hypothesis is supported if stands show either significant but very different correlation functions or if they display very different signs or magnitudes of the most important principal component loadings. Specific methods follow.

Tree-Ring Chronologies

Study sites and trees

The tree-ring chronologies form a network of climatically sensitive sites spanning much of the geographical distribution of Oregon white oak. This was not a random sample; rather, we maximized the expected climatic signal by selecting stands that consisted of at least 20 Oregon white oak trees likely to be over 100 years old and of similar age, arrangement, and condition. Targeted criteria included characteristics associated with sensitivity to climate: well-drained soil, minimal anthropogenic influence, not irrigated, not overtopped by other tree species, and including locations both in the interior of and near the margins of the species' current range. Choosing stands extending over most of the geographical range of the species is likely to capture more of the variability in climate and in climatic response.

Furthermore, we strove to choose those sites representative of common habitat types and so sites with both woodland (WSO, BTB) and savanna (OKK, BDH) characteristics were included, as were sites with harsh (JNC, ONG, TRR) and more moderate (NYP, BTB, NHB) growing conditions (Table 3.1). Extremely unproductive sites were avoided to minimize false or absent rings caused by inconsistent growing conditions. Sites spatially distributed to be representative of the species' entire natural range were prioritized. Importantly, an effort was made to include those sites that were culturally (MAM, BDH), biogeographically (SKC, TRR), or ecologically (PNB, NHB) distinctive and of high conservation (NYP, TOC, CGR) or scientific (BTB, ONG, TRR) value. Individual sites were selected with the guidance of local and regional biologists.

We visited 17 sites between southern Vancouver Island and northern California throughout May and in early June 2007. An existing tree-ring chronology was used from Rocky Point on southern Vancouver Island, which was sampled in 2003 and described elsewhere (Gedalof et al. 2006). These 18 sites met the above selection criteria well, but to varying degrees. For instance, the oaks at WSO are growing among other tree species, MAM is a seasonally inundated site, BRG is located next to a creek, TOC apparently had two large fire events within the time span of analysis, and OKK is infested with mistletoe, each of which may confound a strict interpretation of the climate signal, but is indicative of how stands such as these actually respond. At each site, we determined the geographic position of each stand and its elevation using a handheld Global Positioning System. We collected descriptive data (Table 3.1) including slope gradient (slope), topographic orientation (aspect), and percent canopy coverage (canopy).

Table 3.1: Site geography and descriptive data including site names, site codes, geographic coordinates, and approximate elevations, slopes, and aspects.

study site	**site code**	**latitude ºN**	**longitude ºW**	**elevation m a.s.l.**	**slope º**	**aspect º**
Rocky Point	RYP	48.3249	123.5467	15	2	50
Nisqually Plain	NYP	47.0699	122.5059	107	2	310
Mima Mounds	MAM	46.9039	123.0466	86	2	200
White Salmon Oaks	WSO	45.8047	121.4658	237	35	270
Swauk Creek	SKC	47.1298	120.7446	546	2	205
Tieton Oaks Creek	TOC	46.7179	120.8314	543	2	345
Badger Gulch	BRG	45.8409	120.5335	340	20	200
Jordan Creek	JNC	45.3441	121.3413	795	10	165
Baskett Butte	BTB	44.9672	123.2572	115	20	90
Pigeon Butte	PNB	44.3980	123.3172	168	15	240
Coburg Ridge	CGR	44.0976	123.0123	232	20	245
North Bank	NHB	43.3226	123.2490	281	35	250
Sam's Valley	SVY	42.5141	122.9379	424	4	160
Oregon Gulch	ONG	42.0563	122.3527	965	20	160
Oak Knoll	OKK	41.8399	122.8543	629	15	150
Clark Creek	CCR	41.0418	121.6562	940	3	195
Twin Rocks Ridge	TRR	39.7888	123.0063	1044	10	200
Bald Hills	BDH	41.1474	123.8843	837	20	180

Spatially locating these sites allows comparisons of selected stands to the species overall range (Figure 3.1). The common phytogeographic pattern of decreasing altitude with increasing latitude reflects regional climatic conditions (Brown 1999; Gaston 2003) and is also true of the sampled Oregon white oak stands (Figure 3.2, upper panel). The climatic location of the sites facilitates understanding of their dendroclimatic response (Figure 3.2, lower panel). Every stand of Oregon white oak sampled here is on a south-facing aspect.

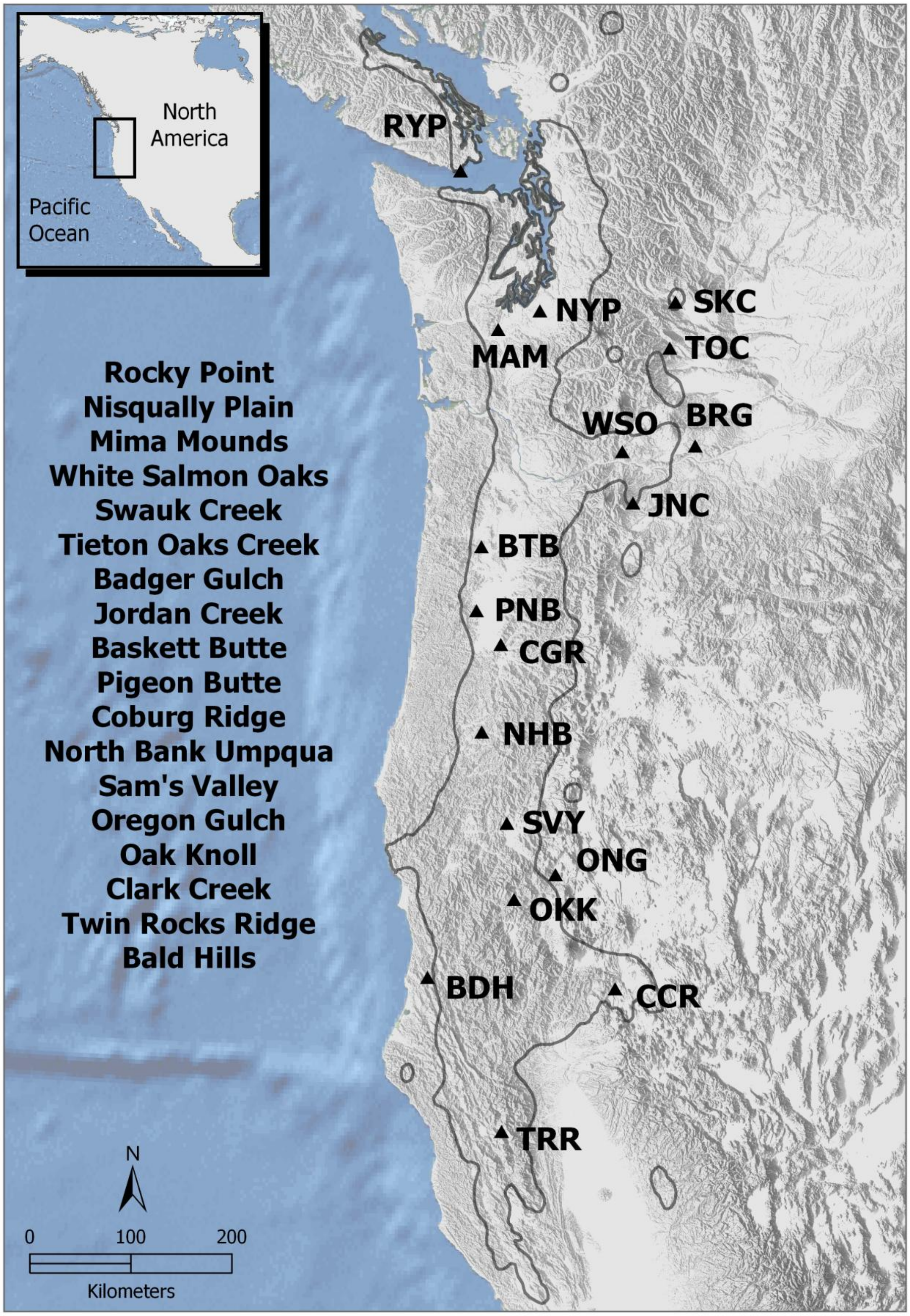

Figure 3.1. Locations of study sites are shown with triangles, site codes follow table 3.1, and the current distribution of Oregon white oak is outlined in black (Little 1971).

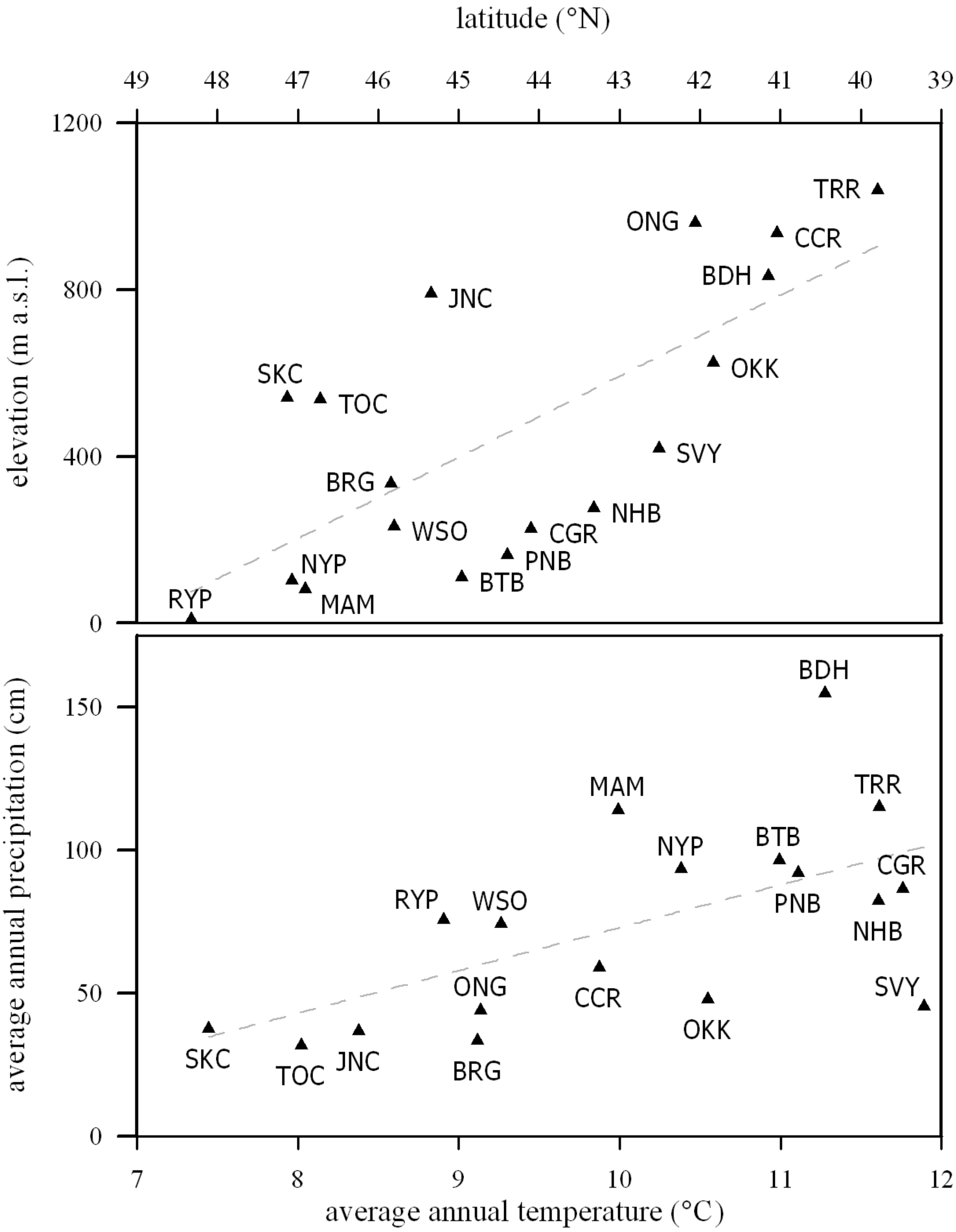

Figure 3.2. Biogeographic profile of Oregon white oak study sites. The upper panel shows the relationship between latitude and elevation and the lower panel compares the average annual temperatures to the average annual precipitation. Site codes follow table 3.1.

We further minimized variables that might obscure the climate signal by choosing dominant trees representative of their stand, not crowded nor overtopped by other tree species, and with long-lived healthy individuals being preferred. Where possible, we avoided uncommon or extreme microtopography as well as trees with multiple stems, low-branches, disfigured boles, strongly asymmetric radial-growth, or damaged crowns.

We cored 20 to 22 (mean = 21) trees at each site, all within approximately 50 metres of each other. To assure an adequate sample size and length of record at Clark Creek, we cored an additional 10 trees with similar stand conditions located about 750 metres west of the others. We extracted from each tree a single 4 mm diameter core using a 40 cm-long two-thread increment-borer, this from a cross-slope side of the tree, approximately 135 centimetres above the ground (i.e., breast height). Sampling more trees rather than taking additional cores from the same trees reduces the standard error (Fritts 2001). This method identifies any climate signal and facilitates comparison with other forestry studies (Fritts 2001). We avoided coring areas on the tree bole near branches or with obvious structural damage. Despite asymmetries in growth, most cores revealed the pith or very near to it. The extracted tree-ring increment cores were stored in plastic straws and bundled with others from the same site.

Chronology development

We used standard dendroecological techniques to prepare the tree-cores and develop the 18 tree-ring site chronologies. Tree-ring increment cores air-dried naturally, were permanently glued into slotted plywood boards transverse side up, and sanded with progressively finer paper to clarify the tree ring structure. The cores were scanned at a resolution of 1200 dots per inch and each of the more than 40,000 tree rings measured to within 0.01 mm using WinDendro (Version 2004; Sheppard and Graumlich 1996). Six to nine rings/cm are considered to be normal for this species (Stein 1990; Niemiec et al. 1995), and the trees measured here were similar, averaging less than 10 rings/cm.

Visual matching of distinctive ring patterns (Douglass 1920; Fritts 2001; Stokes and Smiley 1996; Yamaguchi 1991) enabled us to accurately crossdate the majority of these tree-cores. Crossdating was verified with statistical analyses of ring-width measurements using COFECHA (Holmes 1983; Grissino-Mayer 2001) which detects errors by calculating correlations between multiple series of ring-width measurements.

In these Oregon white oak tree cores, narrow bands of large earlywood cells alternated with a wider band of smaller latewood cells. Annual tree-ring boundaries, the transitions from latewood to earlywood, were distinct: false rings (i.e., intraannual bands) were rare and absent rings were absent. Even though ring-width measurement was complicated by ecological signals and deviations in rings near the wide rays, nearly all tree-cores examined successfully crossdated (346 out of 382 cored, 15 to 26 at each site, mean is 19). The other 36 tree-ring measurement series were removed from the analysis because of questionable crossdating or extremely poor correlations with other trees at the same site. Only those 346 ring-width indices that verifiably crossdate and are significantly positively correlated with other ring-width series at the same site are included in subsequent analyses.

One to three years of tree-ring measurements were truncated from the oldest part of each tree's ring-width record as these were often poorly correlated to other trees' ring-width measurements at the same site (Fritts 2001). These relatively weak correlations are likely due to problems inherent in our sampling and measuring techniques and the less-predictable growth dynamics associated with young age. We eliminated a few additional older segments due to the lack of overlap with other trees at the same site. The 346 ring-width measurement series included 39,922 tree-rings and show mostly positive intrasite and intersite correlations, although in some decades at some sites the tree-ring patterns showed weak or even negative correlations to other sites, this likely due to stand-wide ecological disturbances. These chronologies will be deposited in the International Tree-Ring Data Bank (Grissino-Mayer and Fritts 1997). The mounted increment-cores are archived in Dr. Ze'ev Gedalof's Climate and Ecosystem Dynamics Research Laboratory in the Department of Geography at the University of Guelph.

The ring-width measurements from the trees at Rocky Point (RYP) consisting of 20 crossdated tree cores were added to the analysis at this point. These trees were initially chosen to characterize stand dynamics, so a random subset of trees was selected, similar to the number of cross-dated trees at the other 17 sites to maintain statistical rigor in this analysis and facilitate comparison with other research.

Then, in order to clarify the climate signal, individual ring-width measurement series were transformed into stationary dimensionless indices using ARSTAN (Cook and Holmes 1986; Cook and Krusic 2005). This analysis removes trends in each individual tree's growth related to its increasing circumference, changes in physiological processes due to age, and changes in growth conditions owing to stand dynamics (Guiot 1986; Cook and Briffa 1990; Cook and Holmes 1996; Fritts 2001).

First, a negative exponential curve was fitted to each series to remove long-term low-frequency trends inherent in the growth of mature trees. Then, because the first curve is not flexible enough to remove effects of stand dynamics (e.g., overtopping, release events), each series was detrended a second time by fitting a cubic smoothing spline with a 50% frequency cutoff of 50 years (Cook and Peters 1981; Cook and Briffa 1990). The relatively low cutoff value was necessary to minimize the effects of disturbances common at these sites. After each detrending, every ring-width measurement was divided by the value predicted by the respective curve (Cook and Briffa 1990; Cook and Kairiukstis 1990).

Prewhitening the ring-width indices using autoregressive and moving average analysis (ARMA) removed autocorrelation effects, or the amount of ring-width variation that is correlated to previous ring-width values (Guiot 1986; Biondi and Swetnam 1987; Cook and Briffa 1990). Individual indices from the trees at each site were then combined into overall tree-ring site chronologies by averaging each year's growth value using a biweight robust mean (Mosteller and Tukey 1977; Cook and Briffa 1990; Goldblum and Rigg 2005). Chronologies were then rewhitened, which returns the common pooled persistence to the residual chronologies, minimizing the noise but retaining the climate signal (Cook and Holmes 1986; Cook and Krusic 2005). After detrending, tree-ring records were further truncated to exclude values outside the years of analysis, 1895-2005.

We statistically described the variability of trees within and between site chronologies. The average growth rate of the trees in each stand was estimated by calculating the average width (Wav) of the tree-rings for the years 1970 through 2005 (through 2003 at RYP). We used just the measurements of the most recent 36 years (34 years at RYP) to minimize age-related differences in ring-widths. Rewhitened statistics include standard deviation (SD), mean autocorrelation (AC), and mean sensitivity (MS). The mean interseries correlation (IC), signal to noise ratio (SNR), and expressed population signal (EPS) were calculated for the series in ARSTAN using prewhitened statistics. The SNR and EPS values varied little throughout the majority of each chronology, so these values were interpolated for 1950.

Climatic Data

In an attempt to associate the radial-growth of Oregon white oak to those climatic factors that most strongly influence it, climatic variables were selected based on what other oak trees in similar temperate conditions respond to (Rozas 2005; Du et al. 2007; Akkemik et al. 2006) and what other trees in the region have been shown to be influenced by (Fritts 2001). Climatic variability and extremes rather than mean conditions have a greater influence on tree-growth (Easterling et al. 2000; Tardif and Stevenson 2002; Oberhuber 2004) and on ecosystem function (Field et al. 2007), so we chose to use maximum and minimum temperatures rather than estimate average values. Studies of white oaks in other areas suggest that the growth response to temperature is not independent of its effect on the hydrologic balance of the site (Briffa and Wigley 1985; Foster and LeBlanc 1993), so we also employed an ecophysiologically relevant moisture index (Mix), the Palmer Drought Severity Index (Palmer 1965): positive values indicate abnormal wetness and an increase in moisture available to the trees. The use of readily available climate proxies facilitate comparison with other studies, so surface air temperatures (Tmx, Tmn), amounts of precipitation (Ppt), and the moisture index (Mix) are the basis of this dataset.

Divisional climatic datasets have been used for similar projects as they may best represent the regional climate (Fritts 2001), are often the best datsdets available, and the region is often the spatial scale of analysis. However, trees do not respond to an average regional climate, but rather directly to their local conditions (Easterling 2000). Individual meteorological station instrumental data have also been commonly used, but these stations often provide short records and may be inconsistent in time or space. Individual stations, then, may not adequately represent the actual climate experienced by the trees either, as local variability in climate is significant in areas of complex topography (Luckman and Kavanagh 1998). Climatic variables as close as possible to what the oak trees actually experience assist in more precisely modeling their growth response.

With this need for precision in mind, we trained our growth-climate model with PRISM (Parameter-elevation Regressions on Independent Slopes Model) (Daly et al. 1994, 1997; PRISM 2007), which interpolates monthly 4 km gridded climatic values from instrumental point data and a digital elevation model. Thus, spatial precision is within 2 km, but the accuracy is still affected by the complexity of the terrain within and around the grid and proximity of station data used to train the model. We estimated the climatic values for the site in British Columbia (RYP) by simply using the values from the PRISM grid cell in the United States closest to it. This grid cell is at 48.1137º N latitude and 123.1859º W longitude, only 35 km from Rocky Point, and likely to have a similar climatic history. This integrated interpolation is an excellent method for simulating climates of complex terrains where Oregon white oaks occur, where meteorological records are incomplete, and suitable for multivariate analyses like those employed here and which demand extensive spatial and temporally consistent climatic data. We obtained average monthly maximum and average monthly minimum temperatures (Tmx and Tmn) and total monthly precipitation amounts (Ppt) from the PRISM grid cell corresponding to that site's location for each month for 111 years, 1895-2005.

The PDSI is a normalized index of soil moisture conditions, integrating temperature, precipitation, evapotranspiration, runoff, soil quality, and light availability into a single value (Palmer 1965; Heim 2002). This moisture index reflects abnormal wetness or dryness and is widely used as a predictor of the moisture available to plants even though it has been criticized for displaying strong persistence from month to month

(Heim 2002). This index is available at a gridded 2.5º scale (Dai et al. 2004). Average annual values of these climatic variables as well as extreme values found in January and July facilitate comparisons between sites (Table 3.2).

Table 3.2. Average climatic variables for each site. The January, annual, and July averages of average monthly maximum temperatures, average monthly minimum temperatures, and total monthly precipitation amounts for the years 1895-2005.

	Tmx (ºC)			**Tmn (ºC)**			**Ppt (cm)**		
site code	**Jan**	**year**	**Jul**	**Jan**	**year**	**Jul**	**Jan**	**year**	**Jul**
RYP	5.6	8.9	20.9	0.2	4.5	9.7	142	76	17
NYP	6.9	10.4	24.6	0.1	5.1	10.7	165	94	20
MAM	6.6	10.0	25.2	-0.3	4.2	9.6	211	114	17
WSO	2.6	9.3	26.7	-3.3	3.7	11.4	158	75	7
SKC	1.2	7.4	25.8	-7.1	1.1	10.2	75	38	8
TOC	1.2	8.0	26.9	-6.3	2.1	11.0	65	32	8
BRG	2.6	9.1	29.1	-5.3	2.4	10.8	69	34	5
JNC	2.9	8.4	27.4	-5.2	2.0	9.6	75	37	5
BTB	7.3	11.0	28.0	0.2	4.6	9.5	193	97	9
PNB	7.2	11.1	27.3	0.5	5.2	10.6	186	93	6
CGR	8.3	11.8	27.3	1.4	6.0	11.3	154	87	9
NHB	8.8	11.6	28.3	0.8	5.1	10.5	134	83	12
SVY	7.9	11.9	31.4	-0.5	4.7	11.7	89	46	7
ONG	4.5	9.1	28.7	-4.2	2.1	10.5	84	45	9
OKK	6.4	10.5	31.2	-3.4	2.6	10.3	110	49	6
CCR	6.3	9.9	30.6	-5.0	1.4	8.5	120	60	3
TRR	9.1	11.6	30.1	-0.2	4.5	11.8	288	116	1
BDH	8.9	11.3	26.4	1.5	5.5	10.9	331	156	5
max	9.1	11.9	31.4	1.5	6.0	11.8	331	156	20
mean	**5.8**	**10.1**	**27.5**	**-2.0**	**3.7**	**10.5**	**147**	**74**	**8**
min	1.2	7.4	20.9	-7.1	1.1	8.5	65	32	1

Trees respond to their environment differentially during their climatic growth window (Fritts, 2001), so the temporal extent of the selected climatic variables must also be ecophysiologically relevant. As a proxy for climate, we employed four monthly variables (Tmx, Tmn, Ppt, Mix) and assessed their relationship to the growth of Oregon white oak over an 18 month climatic window in which the trees were most likely to respond, from April of the year preceding growth through September of the year of growth (A-M-J-J-A-S-O-N-D-J F M A M J J A S). This period encompasses the current growing season, the rainy dormant season that precedes it, and the previous year's growing season, all of which have been shown to influence the growth of other trees in the region (Fritts 2001; Gedalof et al. 2004). Studies in other temperate regions found that up to 90% of oak growth occurs between March and September, almost all before July (Du et al. 2007; Akkemik et al. 2007; Fritts 2001; Foster and LeBlanc 1993). Additionally, we aggregated these variables into six seasons: spring (A-M-J-), summer (J-A-S-), and fall (O-N-D-) of the year prior to growth (Spr-, Sum-, Fal-) and winter (JFM), spring (AMJ), and summer (JAS) of the growth year (Win, Spr, Sum), in total spanning the same 18 months. We also performed correlation analyses between the ring-width indices and these seasonal values.

All results of the correlation analyses need to be considered in relation to the specific climatic location in which they occur, so climographs derived from the PRISM data show the average climates in which the trees grew from 1895-2005 (Figure 3.3). Time series of the detrended ring-width indices show trends and anomalies for the 111 years of analysis, 1895-2005 (Figure 3.4). The datasets represented by these two figures are the basis of this dendroecological assessment. The same ring-width data for the 108 years of overlap presented as a contour diagram illustrates the coherence, and lack thereof, among site chronologies (Figure 3.5).

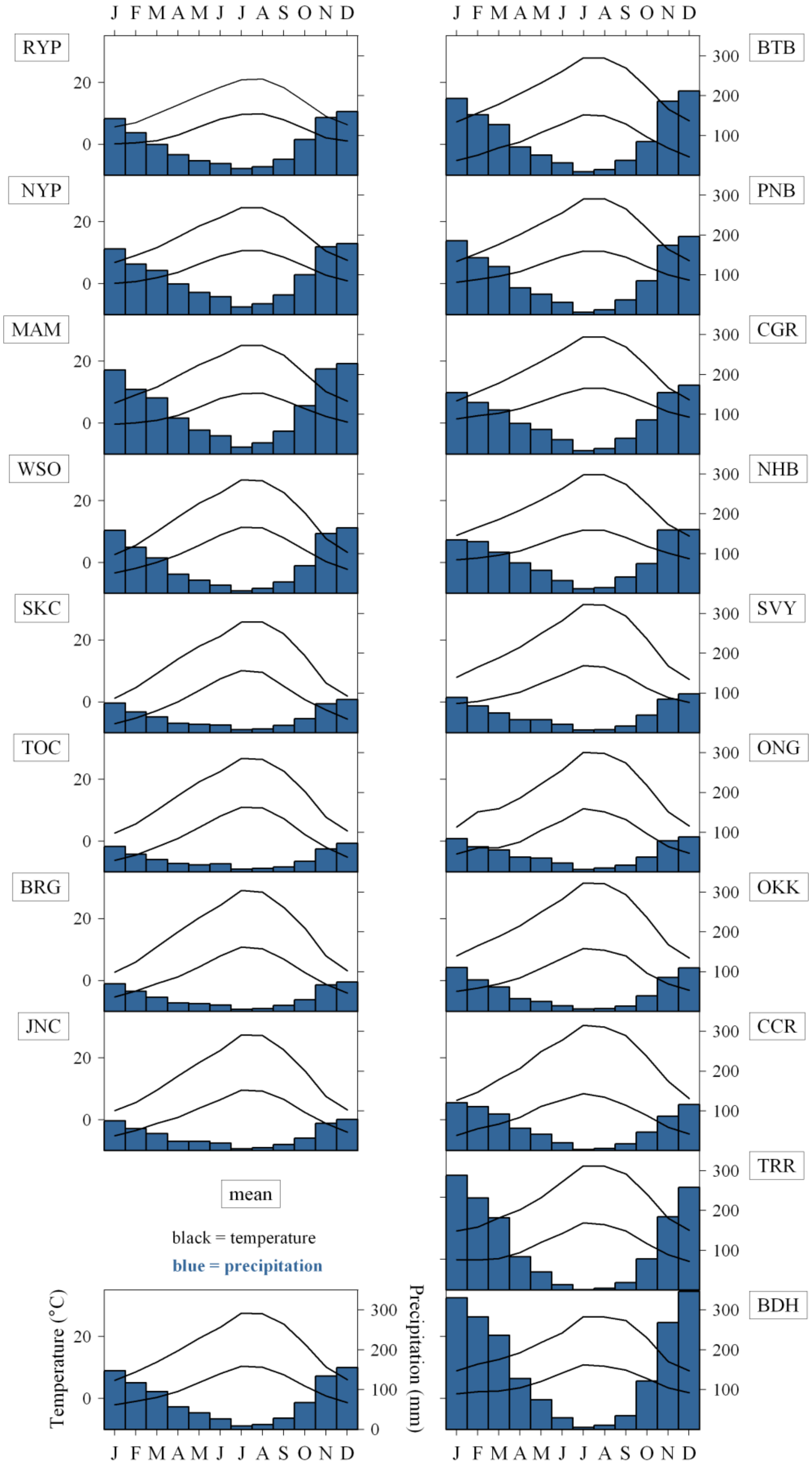

Figure 3.3. Average monthly maximum and minimum temperatures and amounts of precipitation between 1895 and 2005 from PRISM 4km grids at each of the 18 sampled sites.

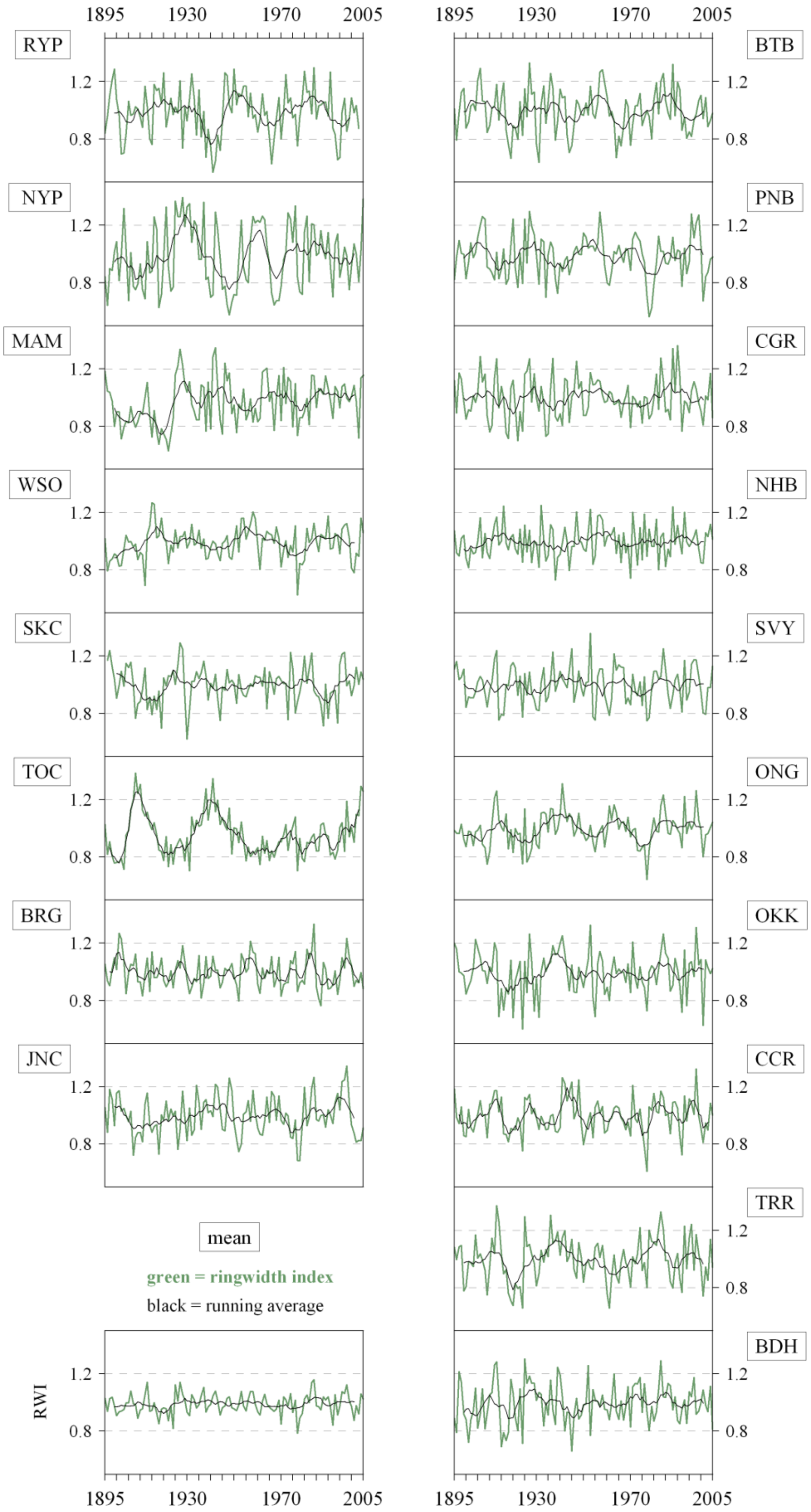

Figure 3.4. Time series of detrended ring-width indices are in green. Black lines show 9 year running averages.

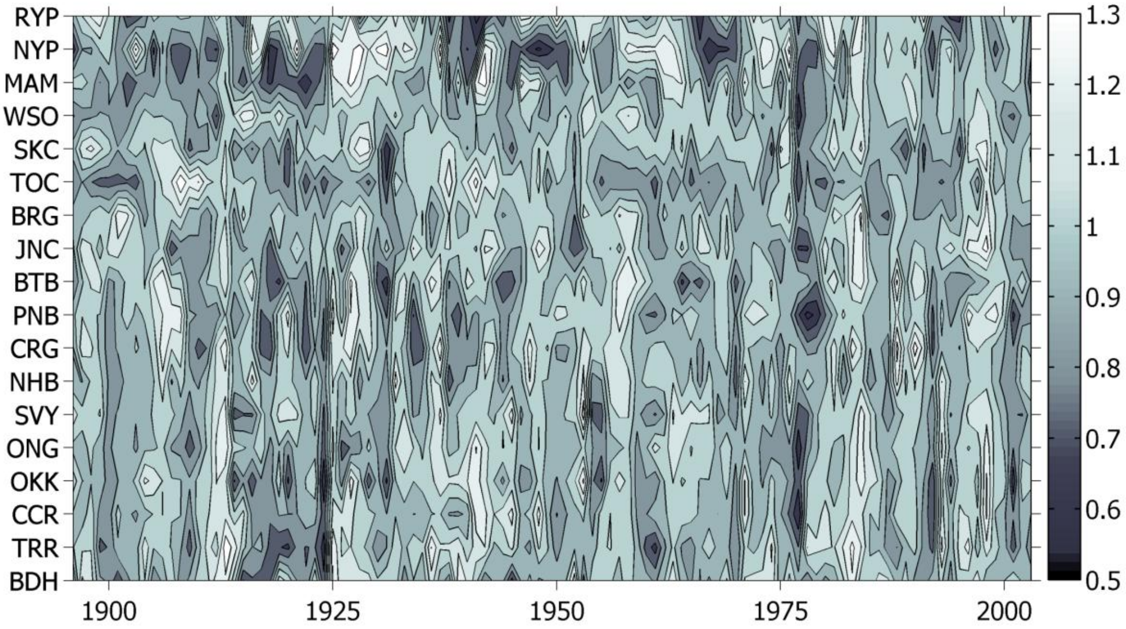

Figure 3.5. Contour diagram of the 108 years of overlapping detrended ring-width indices.

Additionally, we compared three quasi-periodic forcings shown to impact the Pacific North American biosphere, ENSO, PDO, and AMO described in the previous section, to the 18 site chronologies in order to assess their influence on the growth of Oregon white oak. Overlapping monthly standardized values for these three quasi-periodic forcing indices extend 105 years (1901-2005). We built six seasonal indices for each of the three quasi-periodic forcings, 18 in total. Each index represents climatically similar timeframes in which the expression of the synoptic signal likely affects the growth of the trees in a consistent manner, as done for the other climatic variables.

Associations between radial-growth and the indices of El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation were assessed (Figure 3.6). A measurement of El Niño Southern Oscillation (ENSO) is the Southern Oscillation Index (SOI), monthly sea surface temperature anomalies between 5° north and 5° south latitude, 170° to 120° west longitude (Kaplan et al. 1998). The index for the Pacific Decadal Oscillation (PDO) is taken from the leading principal component of monthly sea surface temperature anomalies north of 20º latitude (Mantua et al. 1997). The Atlantic Multidecadal Oscillation (AMO) is represented by monthly values of North Atlantic sea surface temperatures between 0º and 70º N (Enfield et al. 2001).

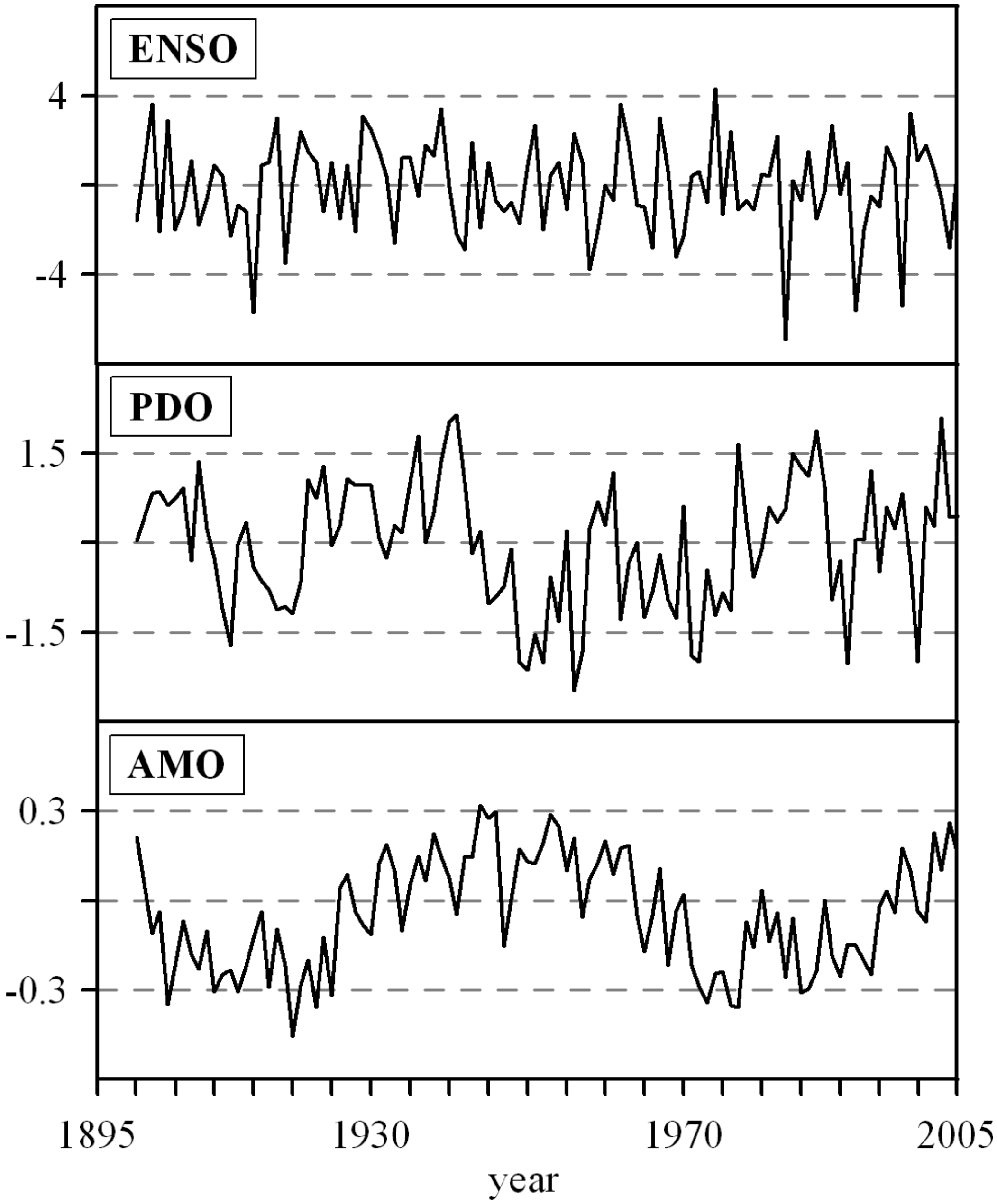

Figure 3.6. Time series of three quasi-periodic forcings extending from 1901-2005: El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Atlantic Multidecadal Oscillation (AMO).

Statistical and pattern recognition analyses

Climatic influences are complex, as limiting factors vary in their influence over diurnal, seasonal, and annual cycles (Fritts 2001; Carrer and Urbinati 2003; Buckley et al. 2004), and so attributing growth to a causal factor requires complex calculations. Correlation analyses identify those climatic variables most important in predicting radial growth. Specifically, we applied correlation analyses to average monthly maximum temperature, average monthly minimum temperature, total monthly precipitation, and the values of the monthly moisture index for each site spanning an 18-month climatic growth window for each of the 110 years of analysis to the detrended ring-width indices from the same site.

Some strengths of correlation analyses are that they are easy to replicate, easy to understand, and objective. For the purposes of this thesis, correlations refer to Pearson product-moment correlation coefficients and only those correlations associated with a p-value less than 0.05 are considered significant, those showing a confidence level of 95%.

We also evaluated the growth response using principal components analyses, a statistical tool that has been widely used in ecological and environmental studies (McGarigal et al. 2000). Principal components analyses discard little information, but reduce complex datasets to a few meaningful variables (empirical orthogonal functions) that explain the maximum amount of variation in that dataset (McGarigal et al. 2000). Dominant patterns are identified, extracted, and organized along gradients. The relative amount of variance explained in the original data cloud is represented by eigenvalues, and those empirical orthogonal functions and principal components associated with the more important eigenvalues explain more of the variance. These pattern recognition analyses broadly follow methods outlined in Carrer et al. 2007.

In order to place the growth response at each site along continua, we conducted two separate principal components analyses. The first analysis was conducted on the site chronologies (RWIs): the 108 years of overlapping detrended ring-width indices extending from 1896 through 2003. The second principal components analysis was performed on the correlation functions (CFs) identified above.

In the first principal components analysis, eigenvectors were derived from the correlation coefficient matrix of the ring-width indices and then ranked according to the amount of variance explained. As the ordination values do not of themselves associate with particular environmental variables, the most important principal component scores were correlated to the climatic variables in order to determine which physical forces are most associated with these empirical orthogonal functions. The associations made between climatic variables and the principal component scores assigned variability in response to real world phenomena, and in particular, to the monthly and seasonal values of temperature, precipitation, and moisture availability. We used a similar technique in the second principal components analysis, that conducted on the correlation coefficient matrix of the correlation functions.

Additionally, the RWIs were compared to the seasonal values of three quasi-periodic forcings: El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation. We correlated these indices to the ring-width indices from each of the 18 stands, identified those that are statistically significant, and spatially assessed their correlation coefficients.

To determine if Oregon white oak exhibits a mixed response to climate, we identified geographic patterns in stands’ dendroclimatic responses by spatially locating correlation functions and assessing them in relation to the stands' particular physical characteristics (e.g., latitude, longitude, elevation, percent of canopy cover). These associations illuminate various aspects of Oregon white oak's climatic response, placing the correlation functions in ecogeographic context. We further assessed the coherence of Oregon white oak’s response to climate across the region by spatially plotting the loadings of each significant empirical orthogonal function. This strategy resulted in the identification of important but less obvious patterns of dendroclimatic responses. The following chapter presents the findings of the statistical analyses in a geographic context along with an interpretation of their suspected ecophysiological basis.

The growth-climate relationship Chapter 4

The radial-growth of Oregon white oak is significantly correlated to climatic variables including monthly and seasonal averages of temperature, amounts of precipitation, and soil moisture availability. We determined that although the growth of Oregon white oak is sensitive to climate throughout the year, a spring growth window exists in which climate plays a more substantial role. A dominant characteristic pattern of growth occurs as most stands respond in the same direction to most climatic forcings, but the relative importance of these controls varies throughout the range of the species.

This chapter identifies Oregon white oak's characteristic response to climatic variability and assesses geographic patterns of dendroclimatic response among the 18 stands. First, we present and then discuss the chronology statistics as they relate to climate. Then, the results of the correlation analyses comparing the detrended ring-width indices to monthly averages of climatic variables are assessed, as is Oregon white oak's response to quasi-periodic forcings. Two principal components analyses also identify Oregon white oak's dominant characteristic response and highlight other important relationships. The findings of these three analyses are considered in a geographic context and attributed to species-specific ecophysiological behaviors and stand characteristics.

Tree-ring chronology statistics

We built and statistically described the 18 tree-ring chronologies using ARSTAN. The nine statistical analyses performed on the ring-width series and associated detrended chronologies characterize variability of growth within and between stands (Table 4.1).

Table 4.1. Tree-ring chronology descriptive statistics for each stand include the number of crossdated series included in the analyses over the total number of trees cored (xdated / cored), the timeframe that the tree-ring site chronology covers (extent), that chronology's length (length), the average length of the series that contributed to the site chronology (mean length), the average ring-width measurement at the site (Wav), mean interseries correlation (IC), mean sensitivity (MS), standard deviation (SD), mean autocorrelation (AC), signal to noise ratio (SNR), and the expressed population signal (EPS).

site code	**xdated /cored**	**series extent**	**series length**	**mean length**	**Wav mm**	**IC**	**MS**	**SD**	**AC**	**SNR**	**EPS**
RYP	20 / 20	1861-2003	143	119	1.14	.330	.182	.253	.417	20.0	.936
NYP	19 / 20	1855-2006	152	134	1.16	.536	.230	.253	.386	19.0	.966
MAM	22 / 22	1860-2006	147	99	1.27	.367	.172	.213	.479	19.1	.940
WSO	20 / 22	1850-2006	157	108	0.63	.326	.120	.146	.404	19.7	.918
SKC	20 / 20	1896-2006	111	84	0.96	.344	.125	.129	.289	16.4	.834
TOC	19 / 20	1742-2006	265	111	0.68	.354	.186	.317	.339	18.3	.921
BRG	17 / 22	1836-2006	171	122	0.81	.349	.109	.113	.187	16.2	.872
JNC	20 / 22	1872-2006	135	118	0.63	.356	.130	.139	.344	18.8	.925
BTB	18 / 20	1872-2006	135	119	0.94	.387	.146	.152	.319	18.0	.923
PNB	16 / 21	1865-2006	142	121	1.37	.373	.137	.222	.440	15.0	.899
CGR	18 / 20	1867-2006	140	129	0.74	.415	.147	.149	.153	18.0	.931
NHB	15 / 20	1768-2006	239	135	0.97	.303	.164	.155	.091	13.3	.852
SVY	20 / 20	1852-2006	155	118	0.79	.415	.137	.141	.171	18.8	.938
ONG	20 / 22	1866-2006	141	114	0.68	.323	.108	.121	.363	17.9	.882
OKK	20 / 21	1840-2006	167	113	0.74	.531	.169	.181	.239	19.7	.947
CCR	26 / 30	1801-2006	206	118	0.84	.430	.117	.126	.259	23.1	.944
TRR	17 / 20	1860-2006	147	109	0.72	.426	.136	.163	.164	16.1	.915
BDH	19 / 20	1875-2006	132	123	0.90	.445	.154	.155	.199	18.0	.953
min	15 / 20	1742	111	84	0.63	.303	.108	.113	.091	13.3	.834
mean	**19 / 21**	**1847-2006**	**160**	**116**	**.89**	**.389**	**.148**	**.174**	**.292**	**18.1**	**.916**
max	26 / 30	2006	265	135	1.37	.536	.230	.317	.479	23.1	.966

These statistics include the number of trees successfully crossdated in relation to the total number cored at each site, the extent and length of the chronologies, and the mean length of the measurement series that contributed to those chronologies. The average width of the tree-rings for the years 1970 through 2005 (through 2003 at RYP) is presented, as is the mean series correlation, mean sensitivity, standard deviation, mean first-order autocorrelation, signal to noise ratio, and the expressed population signal.

Mean widths for the tree-rings at each site were estimated by averaging raw ring-width measurements for the years 1970-2005. Only values for these 36 years were included in order to minimize age and size-related differences in ring-widths. These values reflect the interaction of site characteristics and local climate and indicate overall growth rate at the site.

The average width of the trees in these 18 stands varied greatly, ranging from 0.63 mm to 1.37 mm (Figure 4.1). As Oregon white oak's earlywood formation is dependent on the previous year's conditions and seems to vary less than its latewood, faster-growing trees (i.e., those with larger average ring-widths) tend to be more positively influenced by current growing season conditions and have wider latewood widths. Thus, average widths of these 18 stands are correlated to the ring width indices' mean autocorrelation, although these are weak and not statistically significant (Wav, AC, $r = 0.44$, $p < .07$).

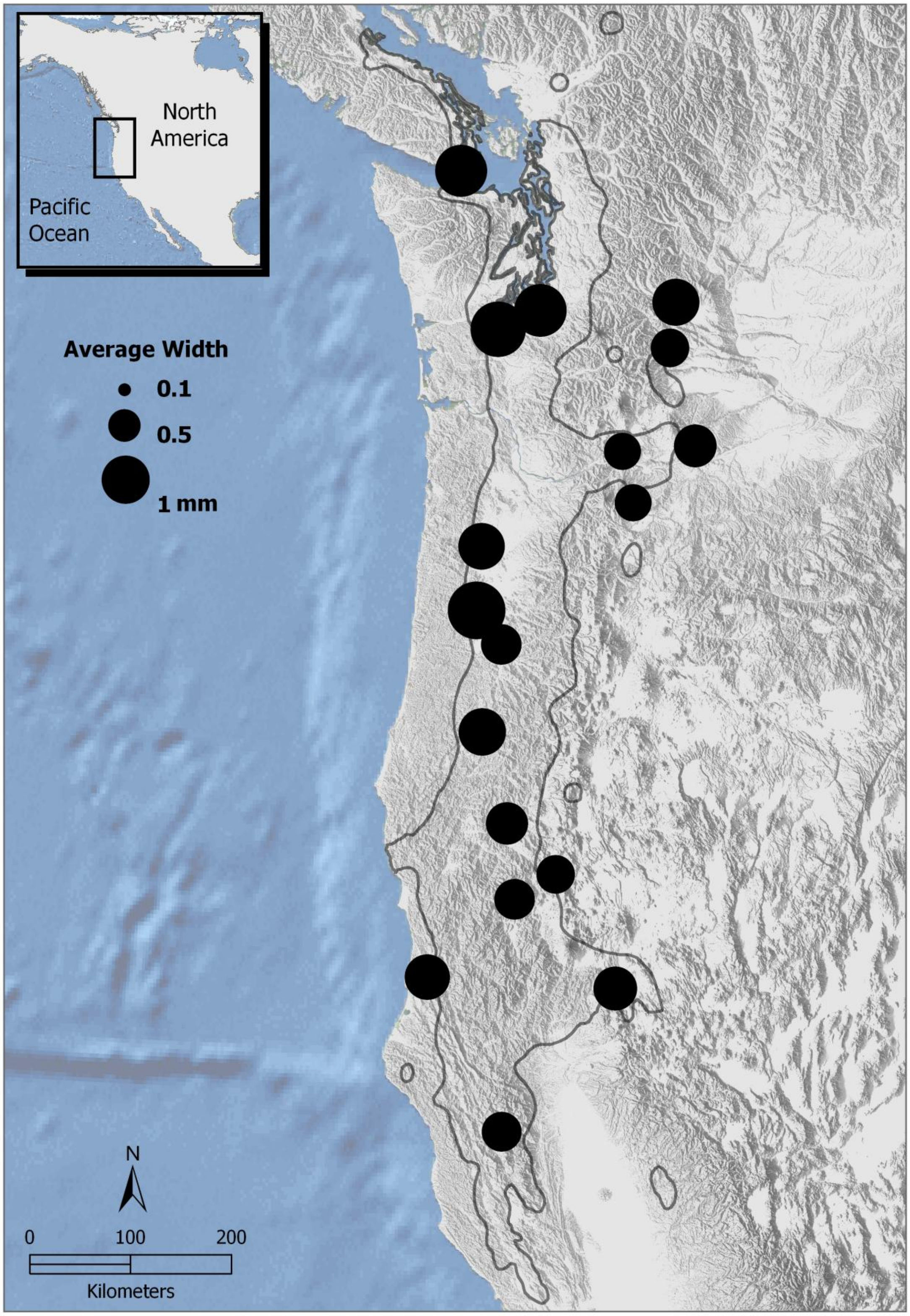

Figure 4.1. Average width of tree-rings in each stand for the period 1970-2005. The size of each circle is proportional to the average width of the ring. The distribution of Oregon white oak is outlined in black.

Mean interseries correlation is a measure of the strength of a tree-ring site chronology as it measures the degree of commonality in the individual contributing series. Specifically, we calculated the mean correlation coefficient between each ring-width series that contributed to the mean site chronology. High values correspond to greater similarity of ring-width indices among trees at the site. The interseries correlation in oaks is thought to increase when climatic limitations increase (Jacobi and Tainter 1988). If so, then Nisqually Plain and the most southerly stands are more climatically controlled than the other stands assessed here. But in this study, at least in some cases, it seems more likely that these sites are just those with the most homogenous stand conditions or where non-climatic exogenous disturbances influence the growth of many of the trees in the same direction.

Mean sensitivity is a measure of the relative difference in width between adjacent rings. This statistic quantifies the average influence of the environment on the growth of the trees at that site. A high value may indicate that the trees are climatically responsive, and so possess dendroclimatological utility (Fritts 2001; Oberhuber 2004). Lower mean sensitivity values can be due to suppression and release events (Rozas 2005). However, in this study, stands with higher mean sensitivity values showed low correlations to climatic values (see below) while those stands with the most obvious release events showed the greatest differences between adjacent rings (e.g., RYP, NYP, and TOC in Figure 3.2).

Similarly, the standard deviations of the detrended ring-widths represent the variability among all ring-widths at the site. Again, higher values are often associated with trees that show greater responsiveness to climate. A population may not be strongly limited by climate if the values for mean sensitivity and standard deviation are similar to those of interior populations (Tardif and Stevenson 2001), and this seems to hold true for stands such as WSO and BDH. Low values of mean sensitivity and standard deviation indicate that a stand responds complacently: WSO, SKC, BRG, ONG, and CCR respond to climatic variability to a lesser degree (see Appendix A).

The mean autocorrelation is a measure of the degree to which a year's growth is correlated with the preceding year's growth rather than external factors. Positive values indicate that the previous years' growth influences the current years' growth. Thus, a high autocorrelation value is indicative of a persistent lag effect (Rozas 2005), while a low autocorrelation indicates that growth is only weakly pre-conditioned by climate, stand dynamics, or growth in the previous year. A low standard deviation and high autocorrelation may mean that the stand is less effective for assessing climate. These stands with low standard deviation, MAM, WSO, and JNC in particular, are some of those stands with the highest percentage of arboreal canopy coverage.

The signal to noise ratio is calculated by multiplying the number of trees included in the chronology by their average correlation and then dividing that number by the difference between one and the average correlation. A number above 15 is considered acceptable and indicative of a strong climatic signal (Dewitt and Ames 1978). The expressed population signal is an estimate of the degree to which a tree-ring expresses the true population signal and can be an indicator of dendroclimatological utility, with values higher than 0.850 considered acceptable (Cropper 1982). The signal to noise ratio and the expressed population signal show the degree to which the chronology signal is expressed after averaging. Both the signal to noise ratio and the expressed population signal were interpolated for 1950 to facilitate comparison between stands. All stands display high values of both these two statistics relative to other dendroclimatic studies of oaks, implying that the selected trees adequately captured a common growth signal.

All descriptive statistics presented here readily compare with those in many other tree-ring studies of temperate hardwoods. The mean, minimum, and maximum values are shown to provide a standard with which to assess the values at the sampled sites and should not be considered an accurate representation of the species as a whole.

Correlation functions

Correlation function analyses are a statistical model of a tree’s growth-response to climate (Blasing et al. 1984). The values generated in these analyses indicate the extent of agreement between the annual radial-growth of Oregon white oak trees and climatic variables over 18 months at each stand (Figure 4.2).

Diagrams of the correlation functions graphically present the absolute and relative importance of these monthly and seasonal correlation coefficients in a pattern roughly reflecting their latitudinal position (Figures 4.3 and 4.4). The number of sites showing significant correlations to each of the monthly and seasonal climatic variables shows the coherence of response among stands (Figure 4.5). The strongest and most synchronous dendroclimatic responses are associated with conditions in the spring.

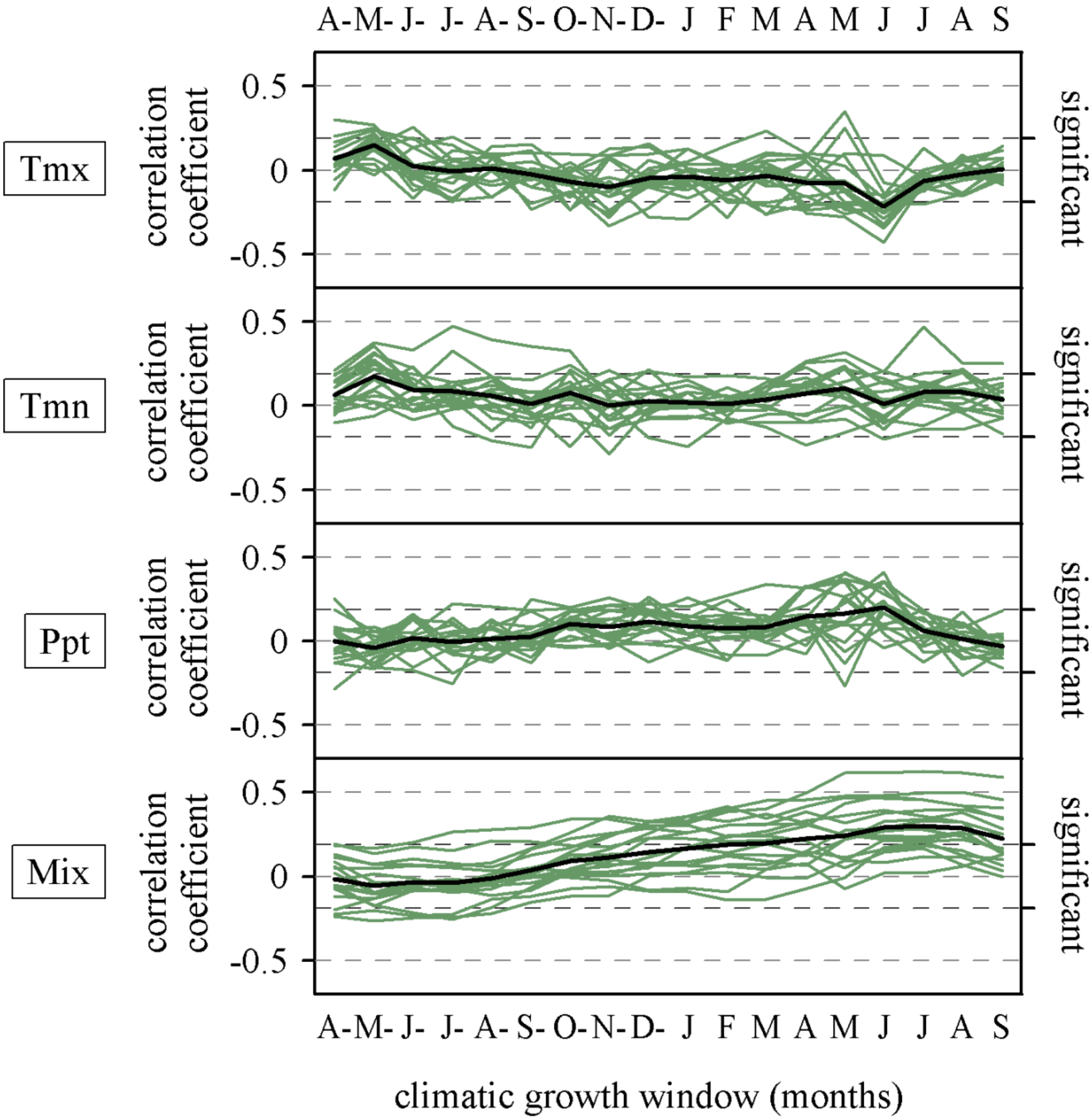

Figure 4.2. Correlation functions for all 18 sites for each of the four climatic variables. The black line represents the average response for each climatic variable.

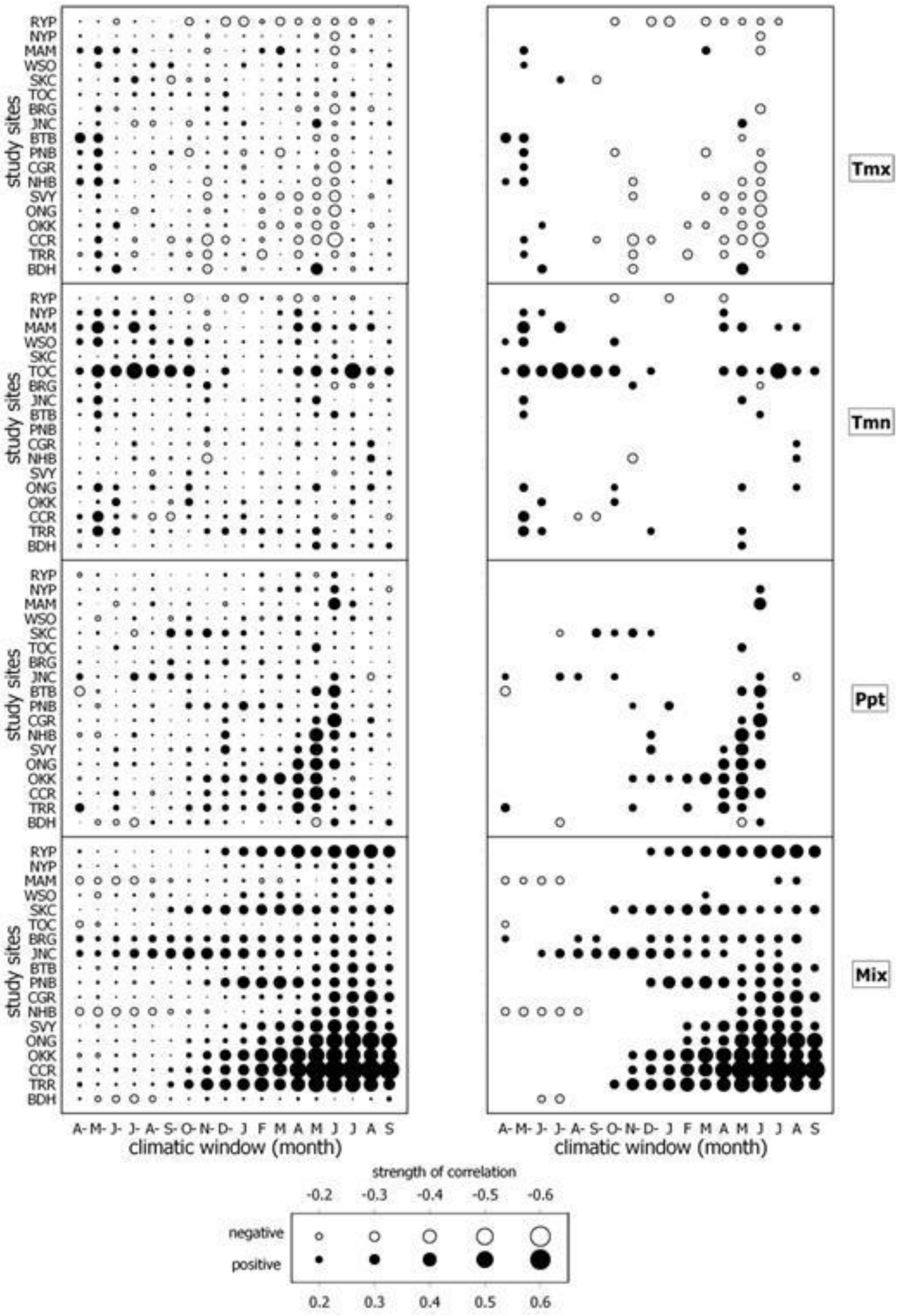

Figure 4.3. Relationships between growth and monthly climatic variables. All correlations are presented in the left panel, only those correlation coefficients deemed significant are presented on the right. Black circles represent positive correlations coefficients and white circles represent negative correlations, while the size of the circle is proportional to the strength of the relationship.

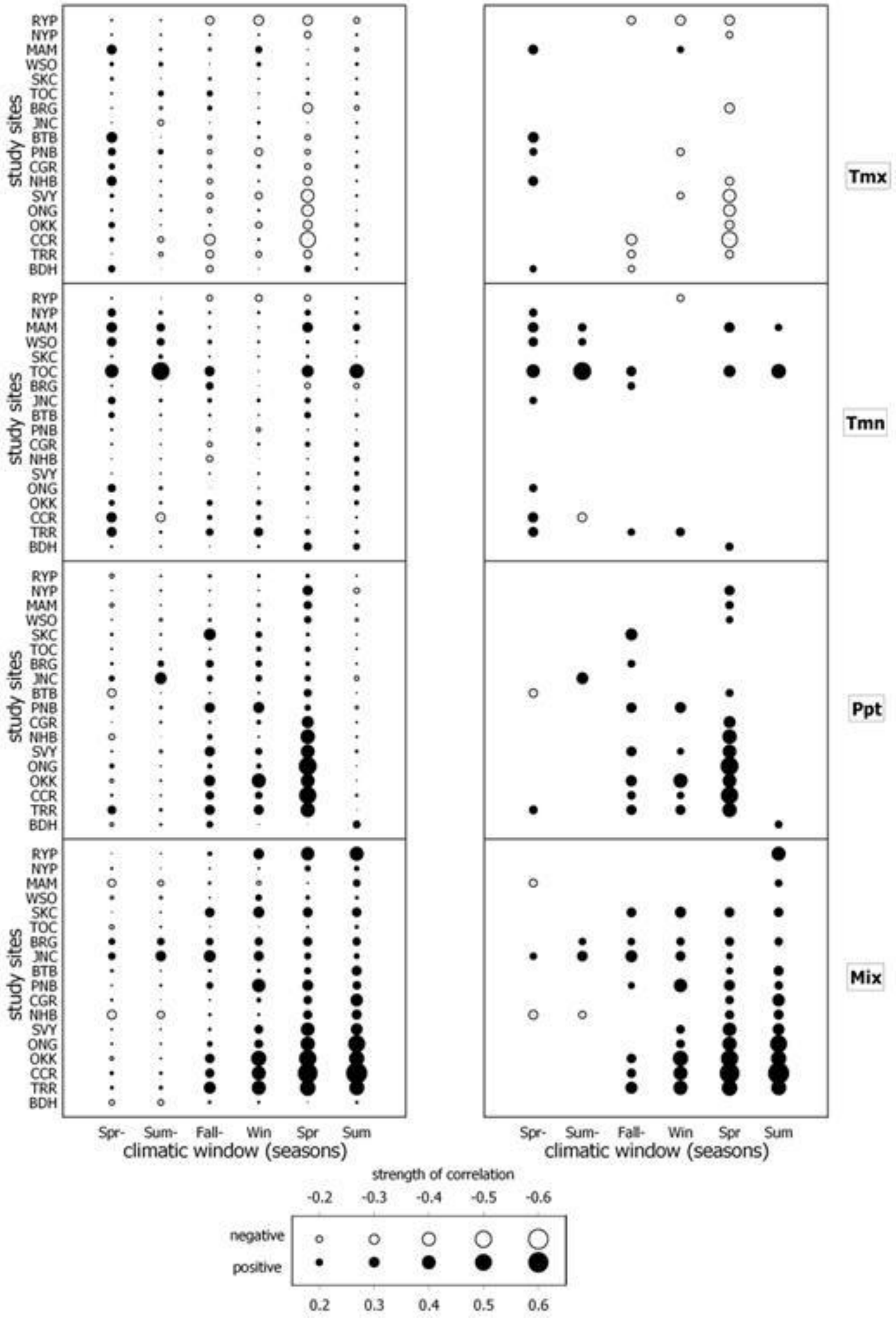

Figure 4.4. Relationships between growth and seasonal climatic variables. All correlations are presented in the left panel, only those correlation coefficients deemed significant are presented on the right. Symbols as in Figure 4.3.

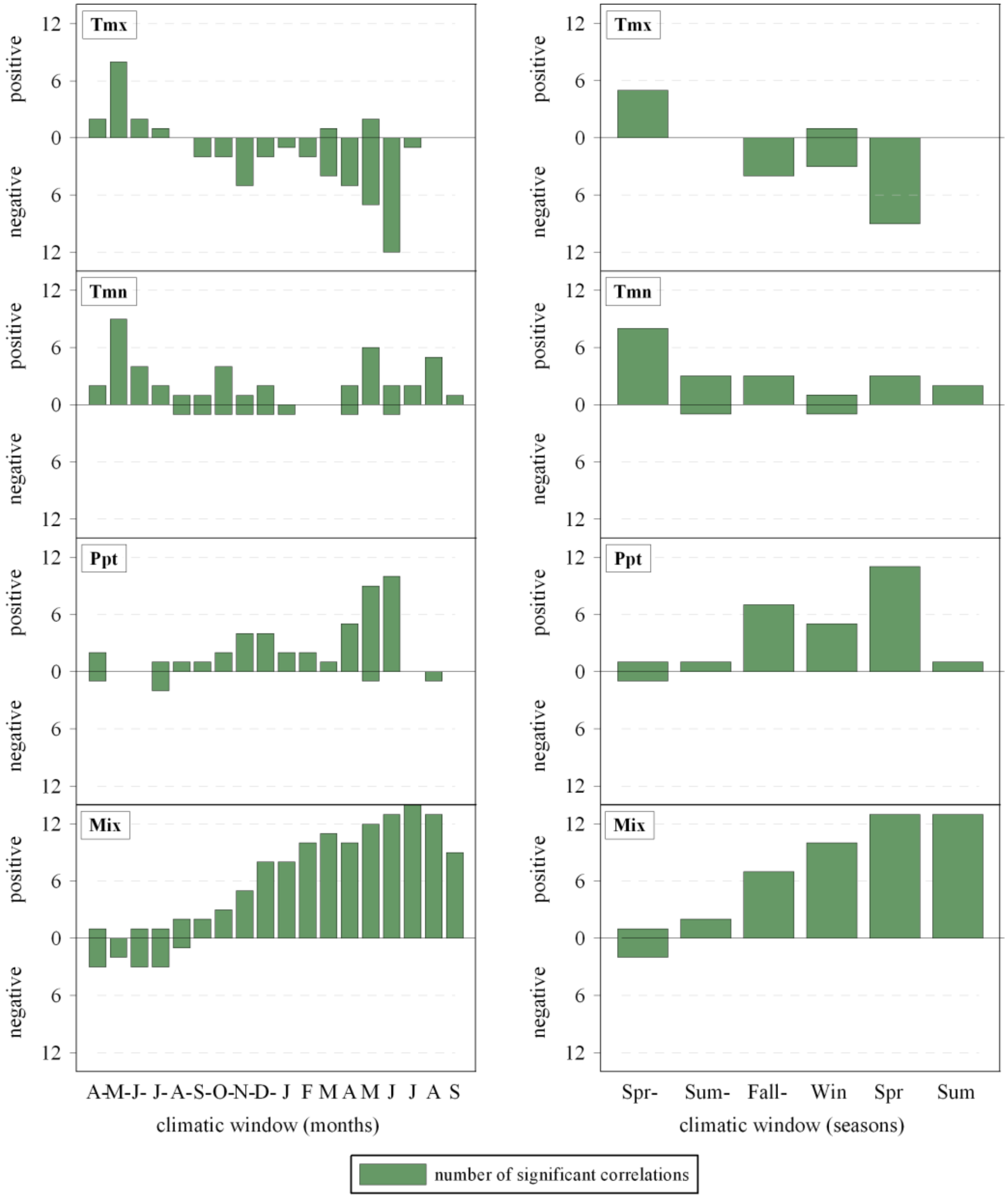

Figure 4.5. Number of sites significantly correlated to their local climatic variables for each month (left panels) and season (right panels).

We attribute growth to climatic variables because this is an obviously coupled system: climate controls growth. So, these correlation functions show the characteristic ways in which the 18 stands of Oregon white oak respond to climate. The dominant regional response of Oregon white oak is one in which its growth is negatively correlated with maximum temperatures in June, positively correlated with precipitation in May, and strongly positively correlated to the moisture index throughout the year of growth, but especially in spring. Furthermore, the growth of the trees correlates positively to both maximum and minimum temperatures in May prior to the year of growth.

Temperature and growth

Strong correlations between the growth of Oregon white oak and local temperatures highlight the value of this predictor variable. Temperature has a characteristic effect on oak tree growth throughout the 18-month climatic growth window and throughout the range of the species. That is, responses to maximum temperatures are usually negative, while responses to minimum temperatures are often positive.

However, the relative importance and even the direction of temperature controls varies throughout the year. Therefore, for instance, in fall, winter, and spring, higher average maximum temperatures tend to limit growth, but during spring in the year before the growing season, higher temperatures are associated with increased growth. This temporal complexity in the growth response has been documented in other tree species in Pacific North America (e.g., Laroque and Smith 1999; Holman and Peterson 2006) as well as in oaks in other areas (e.g., D'Arrigo et al. 1997; Tardif et al. 2006; Cedro 2007).

The spatial variability among the stands in the importance of temperature during any particular month indicates a geographically mixed response to climate (Brubaker

1980; Gedalof and Smith 2001a; Carrer et al. 2007). An understanding of this spatial pattern is essential for long-term management of these ecosystems as well as facilitating more accurate biogeographic projections and climatic reconstructions. The following paragraphs unpack the results of the correlation analyses, identify probable mechanisms controlling growth, and describe spatial patterns in the stands' responses.

The positive correlations to temperature in the spring prior to the year of growth are very coherent throughout the range of the species (Figures 4.6 and 4.9). All but two of the stands respond positively to maximum temperatures in May (RWI, CF Tmx May, maximum r = 0.271), but these same two stands are positively correlated instead to maximum temperatures in April. A similar but stronger pattern occurs in the response to minimum temperatures in those months (RWI, CF Tmn May and April, maximum r = 0.374). This positive response to temperature is likely attributable to a warmer and longer growing season. Warmer soils produce conditions favourable to mycorrhyzae and tend to increase root and shoot growth. Consequent increases in leaf area may limit radial growth in the current year but facilitate greater storage later in the year for use in earlywood formation the following spring. This is a climatic response common to determinate-growth species like these oaks.

Although the stands of Oregon white oak show mostly synchronous responses to temperature, the relative strength of this climatic control varies throughout the range of the species. Significant longitudinal gradients in the response to both maximum and minimum temperatures are evident (longitude, CFs Tmx and Tmn Spr-, r = -0.426 and 0.404, respectively), with the stands east of the Cascade Mountains being the largest contributor to this pattern. These more continental stands respond less positively to maximum temperatures in spring prior to the year of growth, suggesting that these trees are approaching their temperature optimum in this season. The opposite gradient in response to minimum temperatures may indicate that the extreme diurnal variability east of the Cascades, especially low night-time temperatures, may limit growth.

The 18 stands of Oregon white oak show a mixed response to summer temperatures in the year prior to growth, especially July. A weak negative relationship between growth and July temperatures is characteristic of the most southerly stands, which is likely due to the tendency of higher summer temperatures to cause moisture stress and an associated growth decrease the following year (LeBlanc and Foster 1992; Pan et al. 1997). Positive correlations between growth and July temperatures in the more northerly stands may reflect that these stands exist below their summer optimum temperature. This latitudinal gradient in the species' characteristic response to July temperatures (latitude, CF Tmx July, r = 0.513; latitude, CF Tmn July, r = 0.508), although less important than some other controls, is notable in that the stands at the southern end of the species' range respond negatively to this control while stands at the northern end respond positively, suggesting an ecoclimatic boundary in southern Oregon (Peterson and Peterson 2001). D'Arrigo et al. (1997) noted a similar mixed dendroclimatic response in a northern white oak species in Japan.

The growth-response to maximum temperatures in fall prior to the year of growth follows a latitudinal gradient (latitude, CF Tmx Fal-, r = 0.613). Thirteen stands show a negative relationship to maximum temperatures in November (RWI, CF Tmx Nov-, minimum r = -0.333); the five strong enough to be significant are among the most southerly sites. Stands at higher latitudes tend to respond less negatively and those stands east of the Cascade Mountains respond positively to these fall temperatures (Figure 4.7). A negative correlation to maximum temperatures in the fall prior to the year of growth occurs in other northern white oak species (D'Arrigo et al. 1997; Du et al. 2007). Conversely, five stands show weak positive responses to fall temperatures prior to the growing season (RWI, CFs Tmx and Tmn Fal-, maximum r = 0.164) which may be due to the lengthening of the season and an increase in root growth and carbon storage. The increased temperatures may also aid in the recovery of nutrients from leaves after senescence. Fall temperatures east of the Cascade Mountains may be lower than Oregon white oak's optimum at this phenological stage. This pattern of response has been documented in other white oaks (e.g., Hughes et al. 1978; LeBlanc and Foster 1992; LeBourgeois et al. 2004; Pederson et al. 2004).

Overall, Oregon white oak is one of the hardwoods most resistant to cold in Oregon and Washington (Niemiec et al. 1995). Still, the position of ecotones is often controlled by winter temperatures (Neilson 1993) and Oregon white oak's distribution is thought to be sensitive to minimum temperatures in winter (Pellatt et al 2001). We found that temperatures in winter over the last 110 years only weakly affect the growth of these oak trees, but the response is synchronous: most stands show negative correlations to maximum temperatures and positive correlations to minimum temperatures during this season. The negative correlation between radial-growth and winter temperatures has been documented in several other white oak species (e.g., Hughes et al. 1978; Pilcher and Gray 1982; Rozas 2005). This is a geographically mixed growth-response in that a correlation between the latitude of the stand and its response to maximum temperatures in February is positive (latitude, CF Tmx Feb, r = 0.628) and the correlation between a stand's latitude and its responses to minimum temperatures in January and February are negative (latitude, CF Tmn Jan and Feb, r = -0.572, -0.476). That is, more southerly stands tend to respond more negatively to maximum temperatures in winter and most of these also respond positively to minimum winter temperatures. A few stands in the northern half of the species' distribution show positive correlations to winter temperature, which has also been noted in other oak species, especially in those trees growing at higher latitudes (e.g., Eckstein and Frisse 1982; D'Arrigo et al. 1997; Kelly et al. 1989; Pederson et al. 2004). This geographic trend suggests that the winter temperatures exert some control, albeit weak, in the northern stands of Oregon white oak. Root and shoot damage is possible in extreme weather, but a more common effect of low temperatures in oaks is xylem embolism, which reduces water movement during next spring's growing season (Cochard and Tyree 1990; Tyree and Cochard 1996; Hacke and Sauter 1996). This blocking of the xylem is one reason that oak's exhibit a strong response to prior season's conditions (Hacke and Sauter 1996), and likely influences the species' distribution (Tyree and Sperry 1988), limiting the species' establishment at northern latitudes and high elevations.

The amount of irradiance positively influences growth up to a point, so increased growth in late spring and early summer is to be expected. However, this increased daylight coincides with the times of highest temperature, so any increase in growth can be limited by heat stress. Foster and LeBlanc (1993) found the relationship between growth and spring temperature to be the single most important predictor of growth in the oaks that they studied. Research on the growth-climate relationship of other white oaks has found a negative relationship to spring temperatures during the growing season (Jacobi and Tainter 1988; D'Arrigo et al. 1997; LeBourgeouis et al. 2004; Rozas 2005; Cedro 2007; Akkemik et al. 2006; Du et al. 2007).

A characteristic response of Oregon white oak stands is the negative relationship to temperatures in late spring during the season of growth (Figure 4.8). Of the 18 stands sampled, 15 are negatively correlated with average maximum temperatures in spring; nine of these correlations are strong enough to be considered significant (RWI, CF Tmx Spr, minimum r = -0.475). The correlations to maximum temperatures in June in particular are very strong, with 17 stands showing a negative response, 12 of which are significant (RWI, CF Tmx Jun, minimum r = -0.430). Less strongly expressed is the relationship between growth and maximum temperature in May, but still 13 of the sites respond negatively, 7 of which are strong enough to be considered significant (RWI, CF Tmx May, minimum r = -0.279). The growth response to minimum temperatures in spring is the opposite in most cases. Even though the annual radial-growth of 14 stands is positively correlated to minimum temperatures in spring, only three of these are significant (RWI, CF Tmn Spr, maximum r = 0.345) (Figure 4.11). High temperatures in spring may limit earlywood formation and stress new latewood development by increasing evaporation and decreasing soil moisture availability. In this moderate climate, negative correlations to maximum temperature are likely associated with moisture deficit (Fritts 2001; Foster and LeBlanc 1993; Kozlowski et al. 1991).

A strong latitudinal gradient in growth-response to maximum spring temperatures occurs (latitude, CF Tmx Spr = 0.444): sites at lowe latitudes tend to be more adversely affected by high temperatures during this season. This certainly has to do with regional climatic conditions, as those southernmost sites also have some of the higher temperatures and lower amounts of rainfall in spring relative to the other stands sampled here. The inverse relationship between temperature and soil moisture is likely important and should not be discounted. Those stands east of the Cascades respond more strongly positively to minimum temperatures during spring relative to other Oregon white oak stands, indicating that these trees tend to be more adversely affected by low temperatures during this season. The extreme diurnal variability in temperature associated with these sites results in lower night-time temperatures, which may inhibit physiological processes. An alternative but not mutually exclusive mechanism behind this pattern is that positive responses to minimum temperatures during spring at some sites may be due to a warmer soils and a longer growing season, as the initiation of cambial activity in oak trees is controlled by accumulated heat (Kozlowski et al. 1991; USDA 2007). This relationship to minimum temperatures in spring also suggests that an increase in damage to oak trees from insects has not played a significant role in these stands during the last 110 years, although higher minimum temperatures and consequent increases in insect populations may negatively influence associated species, thus limiting competition and positively influencing the growth of Oregon white oak trees (Roemer unpublished).

Warm summers in Pacific North America can increase drought stress on some trees. However, as most of Oregon white oak's radial growth is complete before the onset of limiting temperatures, only very weak associations between summer temperatures and radial-growth occur in these white oak stands (similar to Rubino and McCarthy 2000; Cedro 2007). Oaks respond to heat stress by closing stomates and increasing water-use efficiency (Kozlowski et al. 1991). The growth at 13 out of 18 stands are insignificantly negatively correlated to maximum summer temperatures and 14 stands show positive correlations to minimum summer temperatures. These weak dendroclimatic trends in summer suggest that temperatures in these seasons may not exert strong controls independent of their inverse relationship to moisture availability.

The characteristic response of Oregon white oak to average maximum temperatures, then, is temporally complex in that Oregon white oak's ring-widths are positively associated to maximum temperatures in spring prior to growth, but radial-growth at most sites is negatively correlated to maximum temperatures in most other seasons. In contrast, the growth of most Oregon white oak stands is positively associated with average minimum temperatures throughout the 18-month climatic window.

Not every stand, however, responds equally strong to this climatic forcing. In summary, stands at higher latitudes tend to respond positively to temperatures both in the summer and in the winter prior to the growing season. Those stands east of the Cascade Mountains respond less positively to maximum temperatures in the spring in the year before growth and more positively to average minimum temperatures during this season. Unlike the other Oregon white oak stands assessed here, these more continental stands also tend to respond positively to temperatures in the fall prior to growth and to minimum temperatures in spring during the growing season. The lower latitude a stand of Oregon white oak is located, the more negatively the stand tends to respond to temperatures in the summer before the year of growth. Similarly, these more southern stands respond more negatively to maximum temperatures in the fall and winter prior to growth, especially in November and February, and more negatively to maximum temperatures in spring during the growing season. The temporally complex and spatially mixed response to temperature described in this section is seen in the following six maps (Figures 4.6 through 4.11).

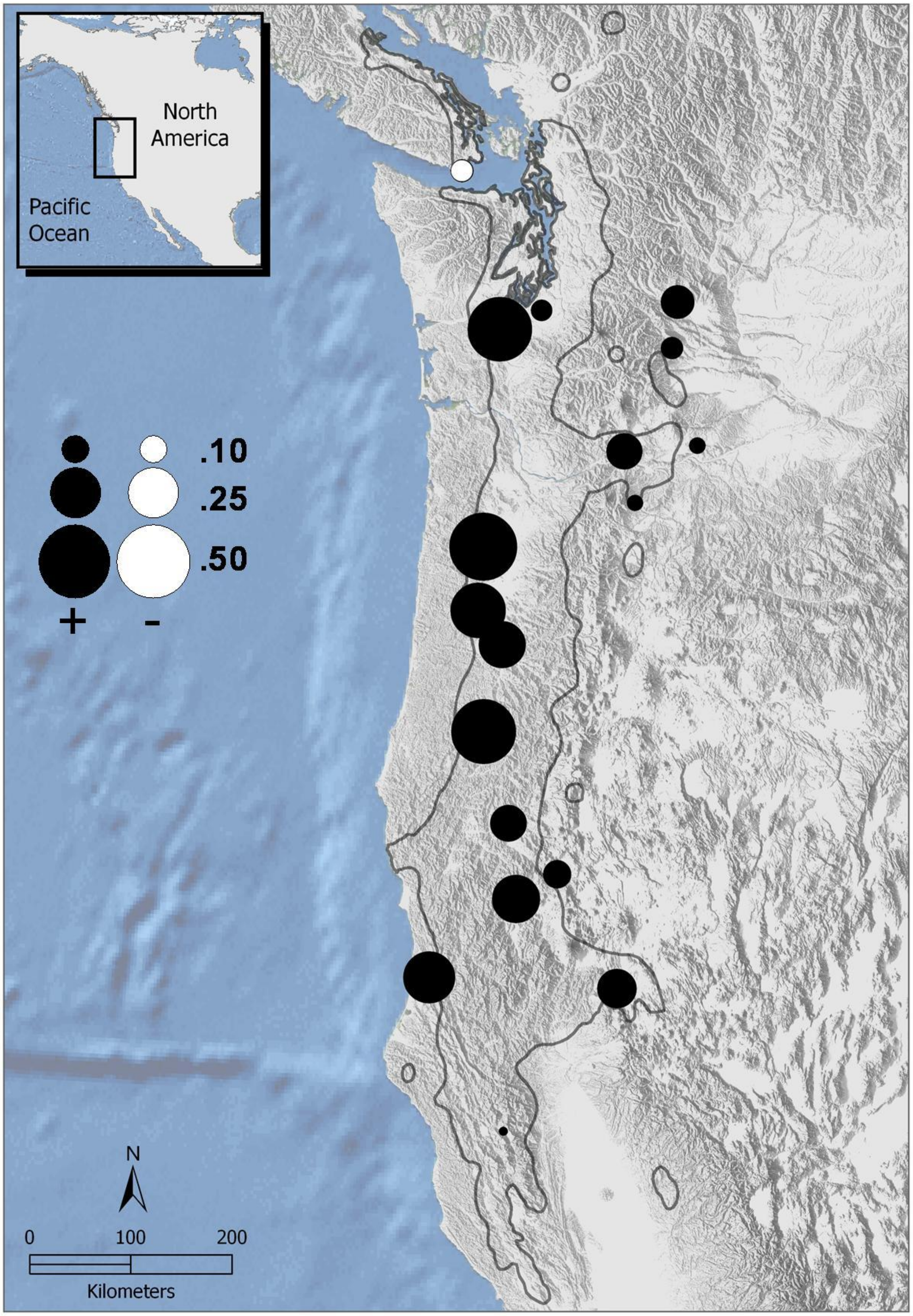

Figure 4.6. Correlation coefficients between maximum temperatures in the spring prior to growth and radial-growth of Oregon white oak. Black circles represent positive and white circles represent negative correlations. The sizes of the circles are proportional to the strength of the correlation. The distribution of Oregon white oak is outlined in black.

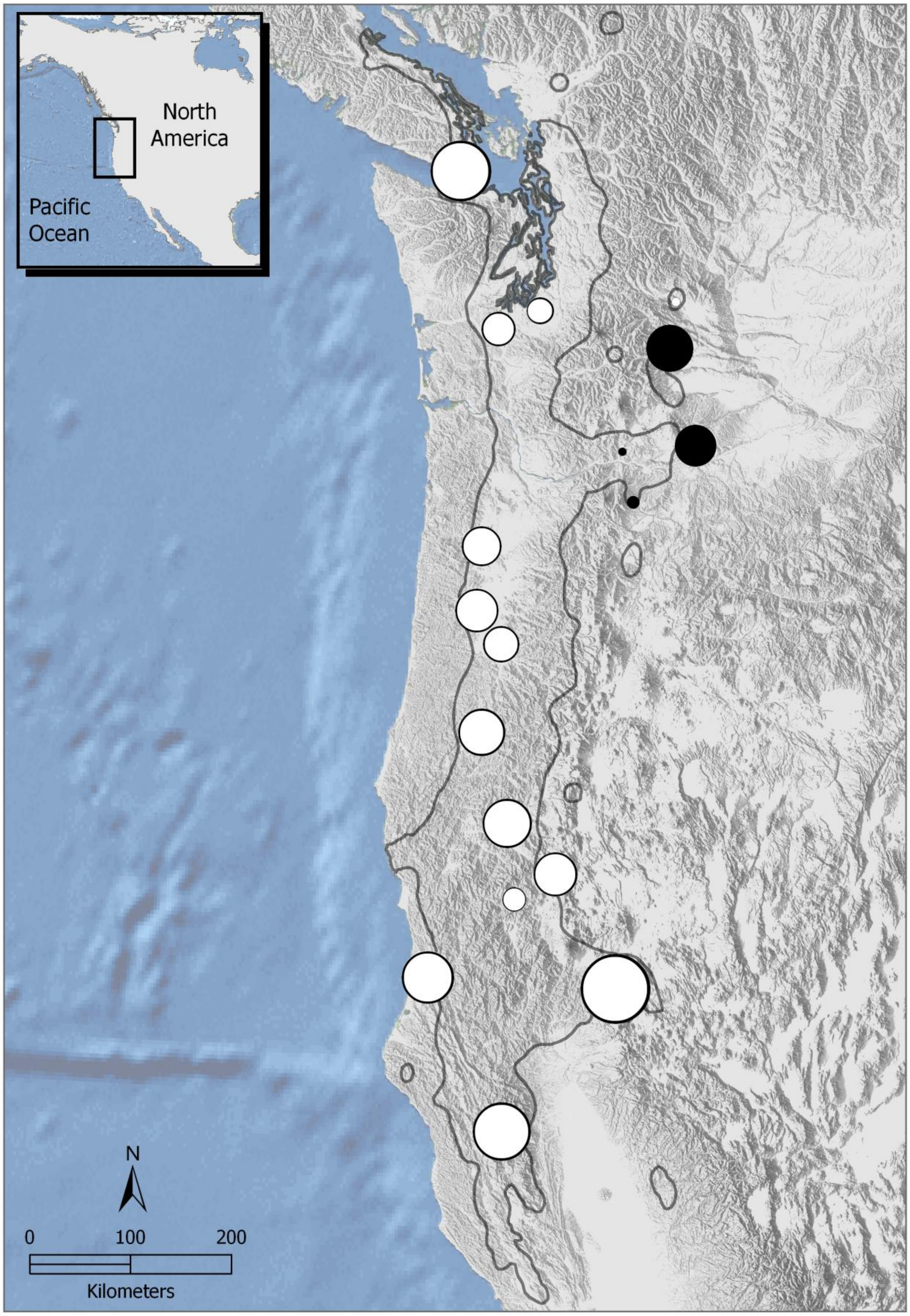

Figure 4.7. Correlation coefficients between average monthly maximum temperatures in the fall prior to growth and the annual radial-growth of Oregon white. Symbols as in Figure 4.6.

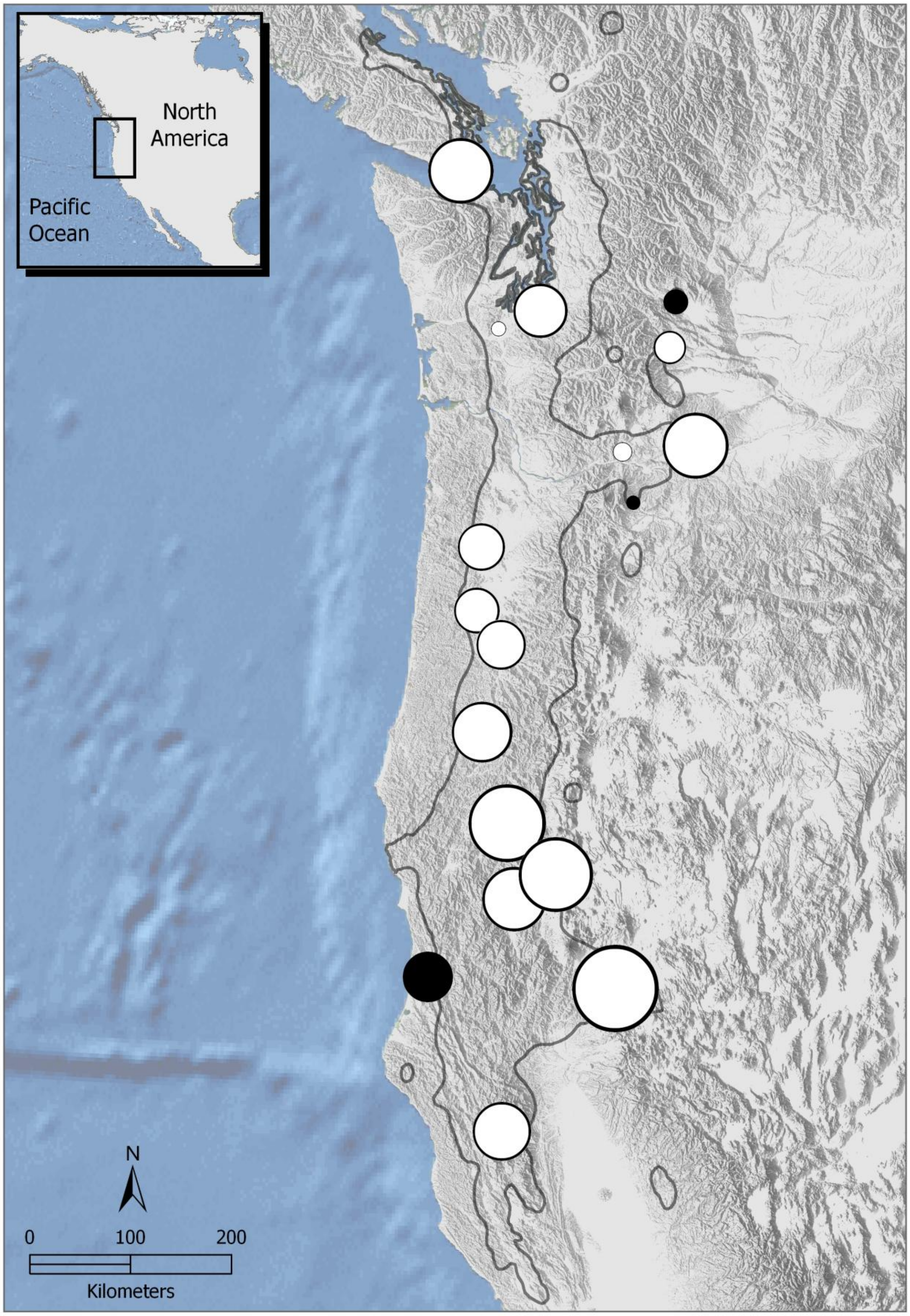

Figure 4.8. Correlation coefficients between average monthly maximum temperatures in the spring and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

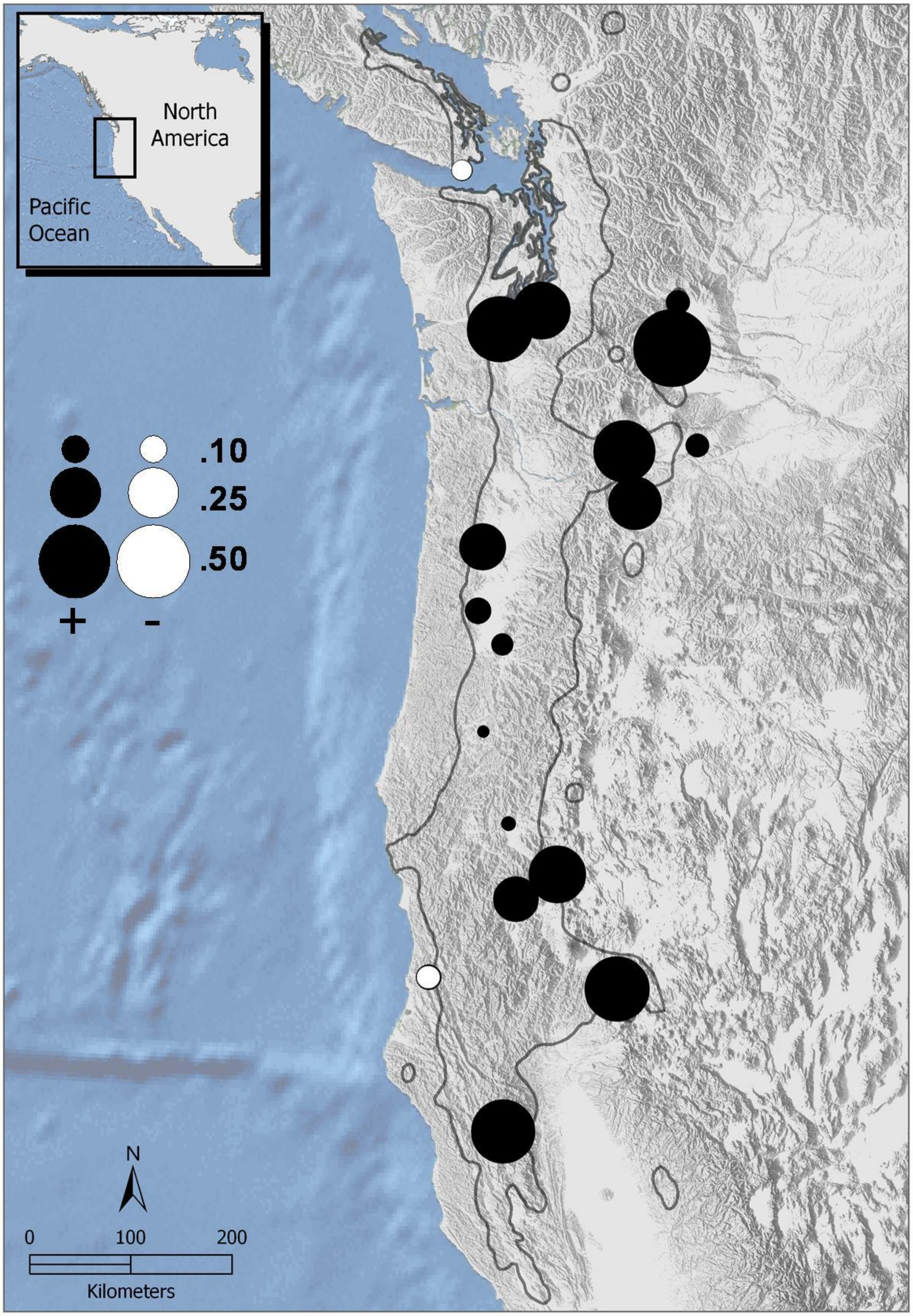

Figure 4.9. Correlation coefficients between average monthly minimum temperatures in the spring prior to growth and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

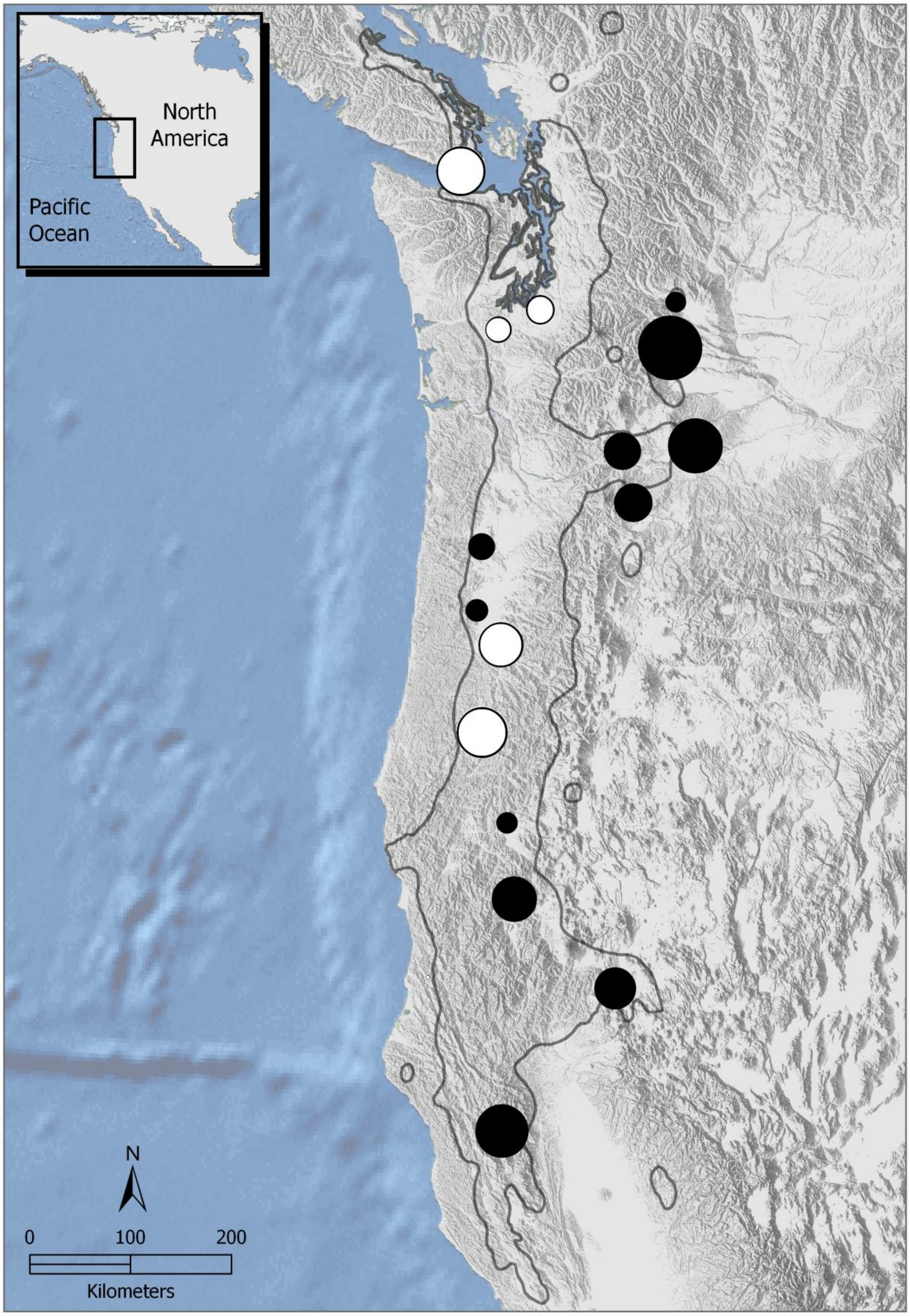

Figure 4.10. Correlation coefficients between average monthly minimum temperatures in the fall prior to growth and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

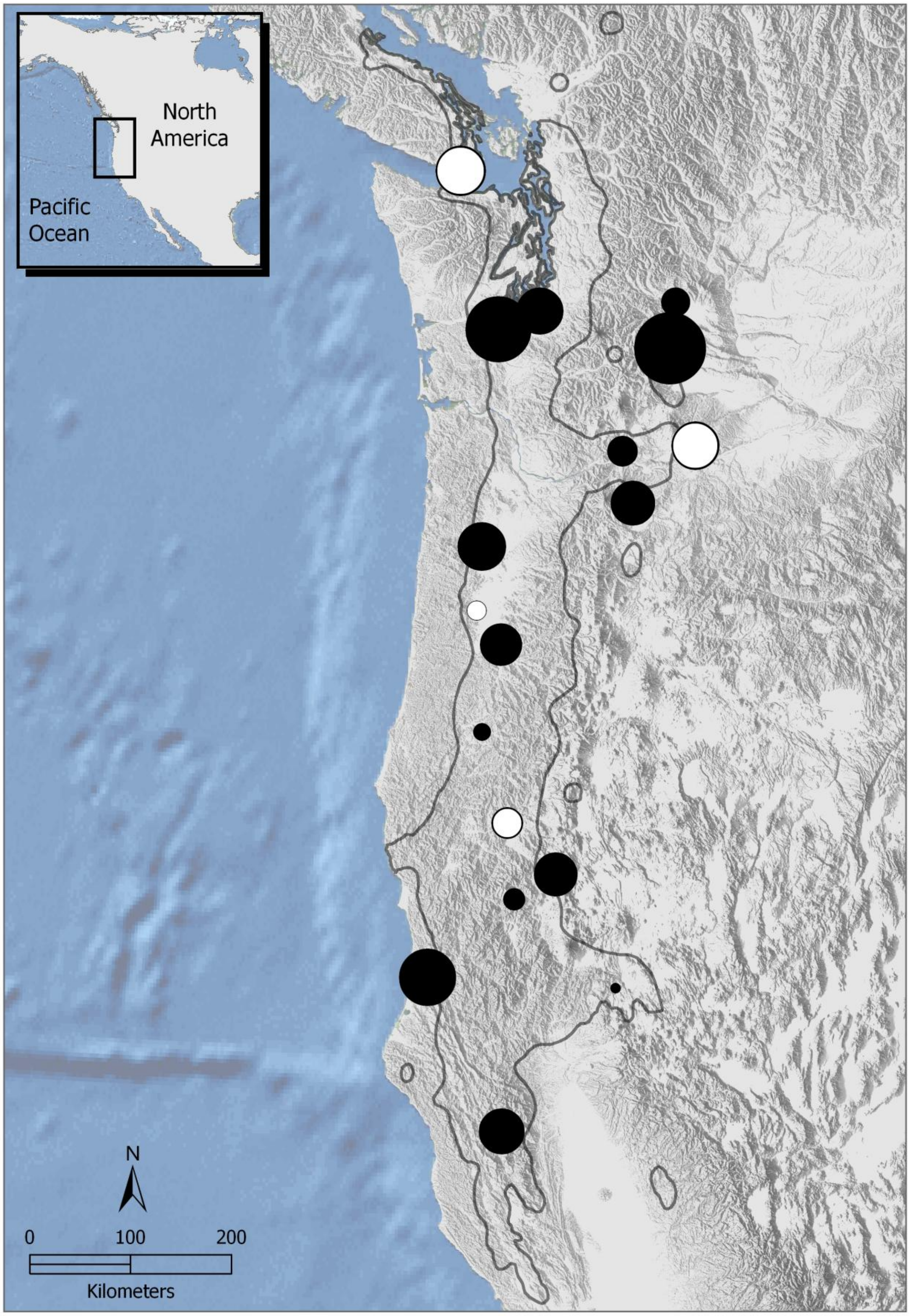

Figure 4.11. Correlation coefficients between average monthly minimum temperatures in the spring and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

Precipitation and growth

Precipitation is a dominant factor influencing tree growth as it provides nutrients and water to a tree's root system (Schweingruber 1996). Furthermore, species commonly associated with Oregon white oak habitat types are known to be sensitive to precipitation patterns (Roemer 1972; Reigel et al. 1992) suggesting that some life-history stage of Oregon white oak may be as well. In this study, responses to precipitation in spring and summer prior to the growing season are weak and not spatially synchronous. However, almost all of the sampled Oregon white oak stands respond positively to precipitation in the fall and winter prior to the growing season, and even stronger and more spatially synchronously during spring earlywood formation. The following paragraphs identify Oregon white oak's characteristic response to precipitation and attribute these to ecophysiological characteristics of the species. The geographic position of the stands can influence the dendroclimatic response, and so spatial patterns in response are described.

Rainfall in spring in the year prior to growth can significantly increase the growth of Oregon white oak by recharging soil moisture at a crucial phenological stage, and eight stands respond positively to this variable (RWI, CF Ppt Spr-, maximum r = 0.156). However, as the species is highly dependent on growth and climatic conditions in the seasons prior to ring formation, a year of increased growth may inhibit the next, possibly due to carbon reallocation towards reproductive behavior (e.g., acorn development). Rainfall and cloud cover are certainly associated, so decreased irradiance may also play a role in this negative relationship between growth and rainfall. Ten of the Oregon white oak stands respond negatively to precipitation in the spring prior to growth (RWI, CF Ppt Spr-, minimum r = -0.253) (Figure 4.12). Correlations between radial-growth and amounts of precipitation in the summer prior to growth are also weak and similarly mixed.

Ring-width indices at 16 of the 18 sites correlate positively to precipitation amounts in fall prior to the year of growth (Figure 4.13), seven of which are strong enough to be considered significant (RWI, CF Ppt Spr-, maximum r = 0.340). Other studies have shown this same relationship in other white oak species (e.g., LeBourgeouis et al. 2004; Cedro 2007; Du et al. 2007). A positive response to fall precipitation is likely related to the end of the stressful summer and the consequent contribution to soil moisture for use by the trees later in the spring growing season.

As spring and summer rainfall is often inadequate to sink below the root zone of grasses to where mature oaks uptake water from, winter precipitation is an important influence on the radial-growth of Oregon white oak as a source of soil moisture recharge (Gedalof et al. 2004; Devine and Harrington 2005; Pellatt et al. 2007). The effects of winter precipitation, even though occurring out of the growing season, have been shown to affect the growth of other tree species in the region (Laroque and Smith 2003; Nakatawase and Peterson 2006) and in species of white oak elsewhere (Rozas 2001; Du et al. 1997; Muzika and Guyette 2004; Cedro 2007).

A classic response to moisture-stress in the early growing season is reduced growth. Many other studies on the growth-climate relationships of white oaks have documented positive correlations to precipitation in spring, especially in June (e.g., Fritts 1962; Pilcher and Gray 1982; Jacobi and Tainter 1988; LeBlanc and Foster 1992; Rubino and McCarthy 2000; Muzika and Guyette 2004; Rozas 2005; Tardif et al. 2006; Akkemik 2006; Du et al. 2007). Strong correlations to spring precipitation are expected during foliage emergence and cambial activation, both of which require water, or when temperatures increase coincident with the dry season: rainfall at this crucial growth stage can lengthen the time of rapid early growth and may even provide water for use during the more stressful summer. The response of Oregon white oak trees to rainfall in spring over the last 110 years is pronounced, with 17 sites showing a positive response, 11 of which are significant (RWI, CF Ppt Spr, maximum r = 0.532) (Figure 4.14). The radial-growth of Oregon white oak tends to be greater in years when more rainfall precedes or accompanies the growing season. This response to precipitation is strongest earlier in the more southern stands, occurring in April and May, and later in stands at the northern end, where the strongest positive responses to precipitation occur in June. Rainfall contributes to the available soil moisture necessary in maintaining leaf turgor pressure and for continued photosynthesis.

In general, then, Oregon white oak trees respond positively to precipitation during most seasons, especially during fall and winter where increased rainfall recharges the supply of groundwater and during spring early in the growing season. These stands show a mixed response however in that the relative importance of precipitation in controlling growth is inconsistent throughout the range of the species. In particular, a longitudinal gradient in the response to precipitation occurs in both spring and summer prior to growth. These correlations are weak, but spatial differences in response are significant in summer (longitude, CF Ppt Sum-, r = 0.411). More easterly stands tend to respond positively to rainfall in the spring and summer in the year prior to growth, but those more westerly stands respond negatively (Figure 4.12). This mixed response is possibly due to the drier conditions and more limited understory associated with the more continental stands, so any rainfall at these sites during these months is likely to contribute to available soil moisture. Also, a negative relationship between latitude and the magnitude of response to precipitation occurs in fall, winter, and spring (latitude, CF Ppt Fal- Win Spr, r = -0.475, -0.558 and -0.607 respectively): stands at lower latitudes respond more positively to precipitation during these seasons (RWI, CF Ppt Fal- Win Spr, maximum r = 0.318, 0.417, 0.532), while stands east of the Cascade Mountains respond less strongly (RWI, CF Ppt Fal- Win Spr, maximum r = 0.340, 0.178, 0.164) (Figures 4.13 and 4.14). Site differences in elevation and the amount of arboreal canopy coverage certainly play a role in these geographic patterns and are discussed below.

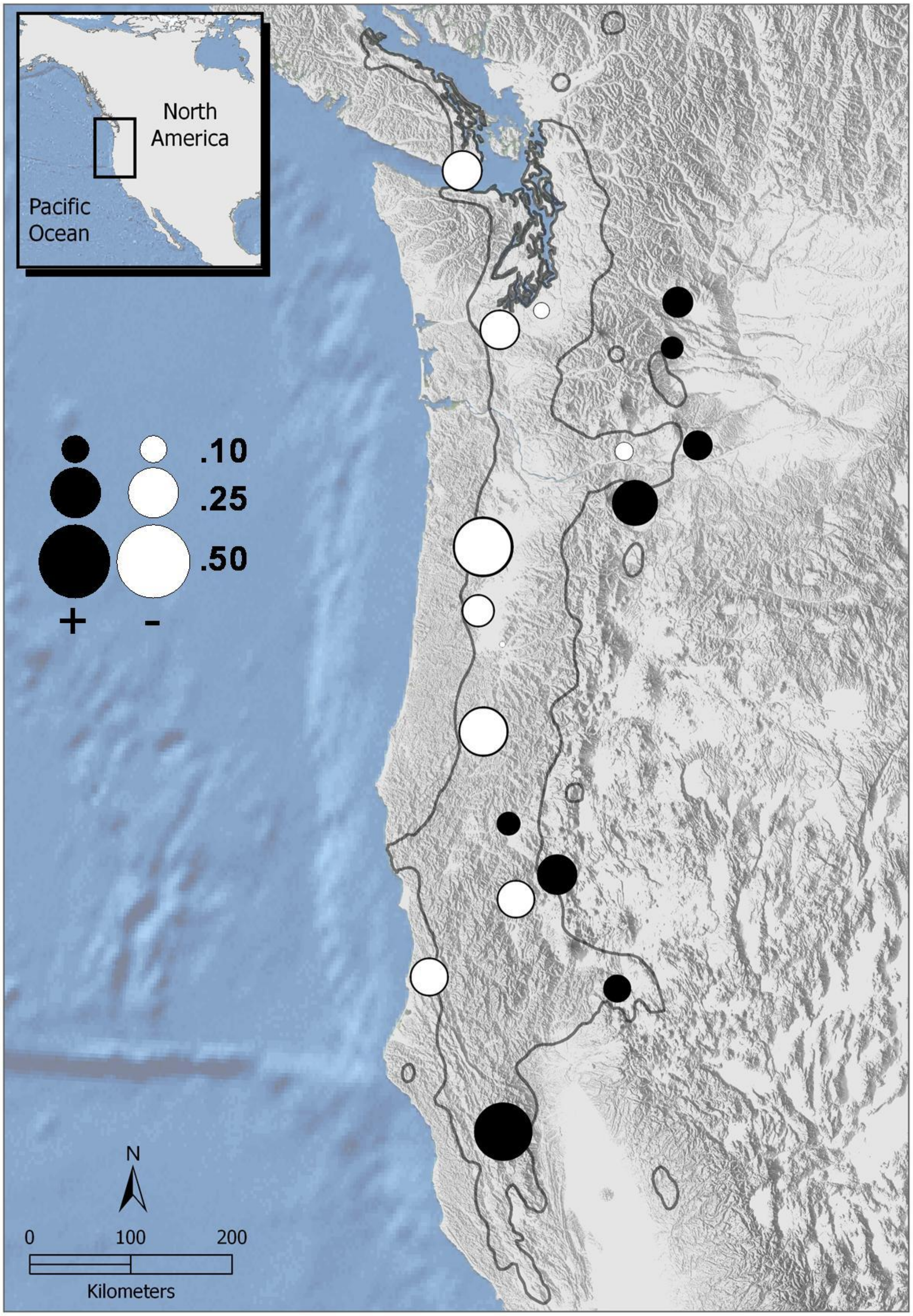

Figure 4.12. Correlation coefficients between monthly precipitation in the spring prior to growth and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

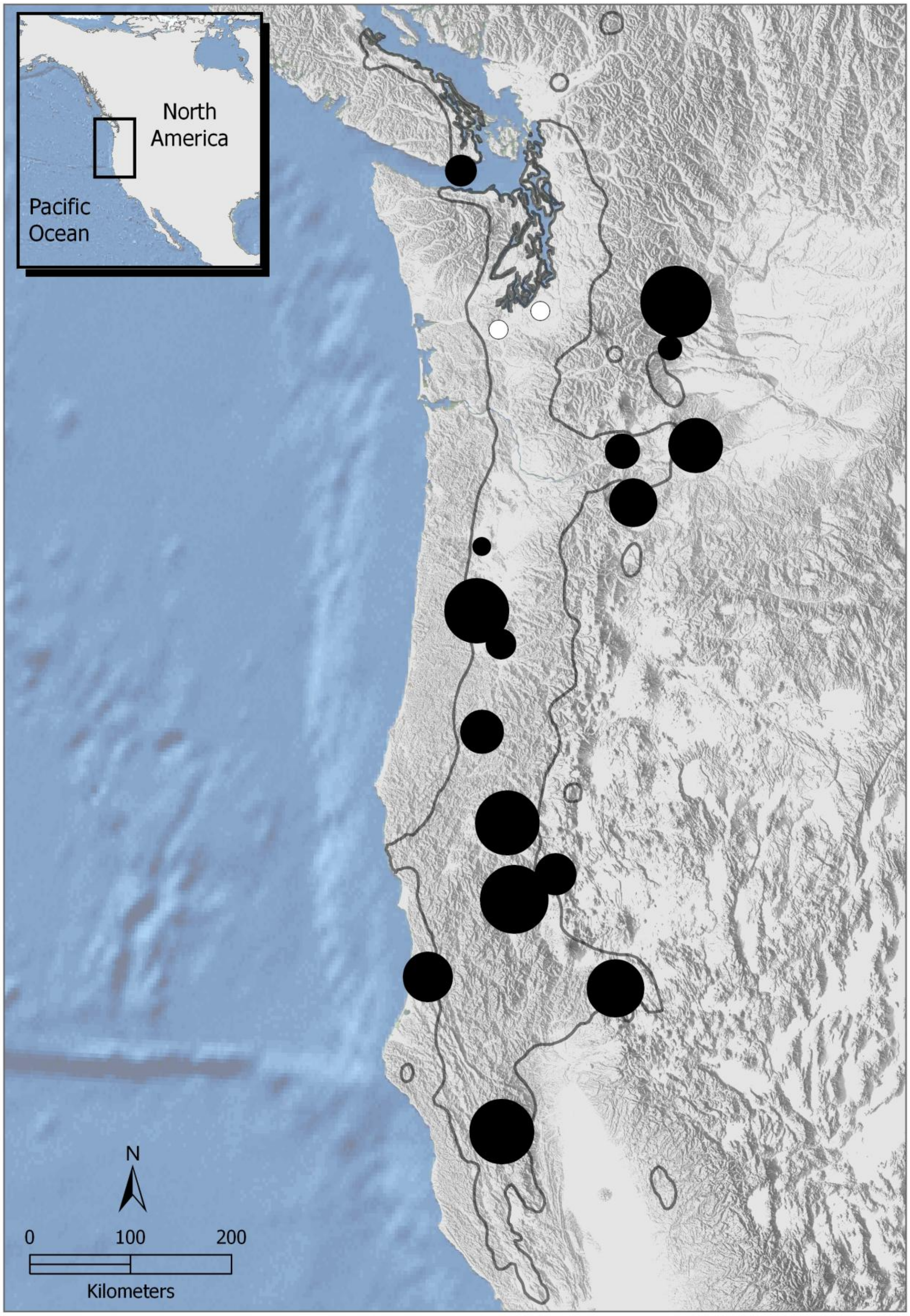

Figure 4.13. Correlation coefficients between monthly precipitation in the fall prior to growth and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

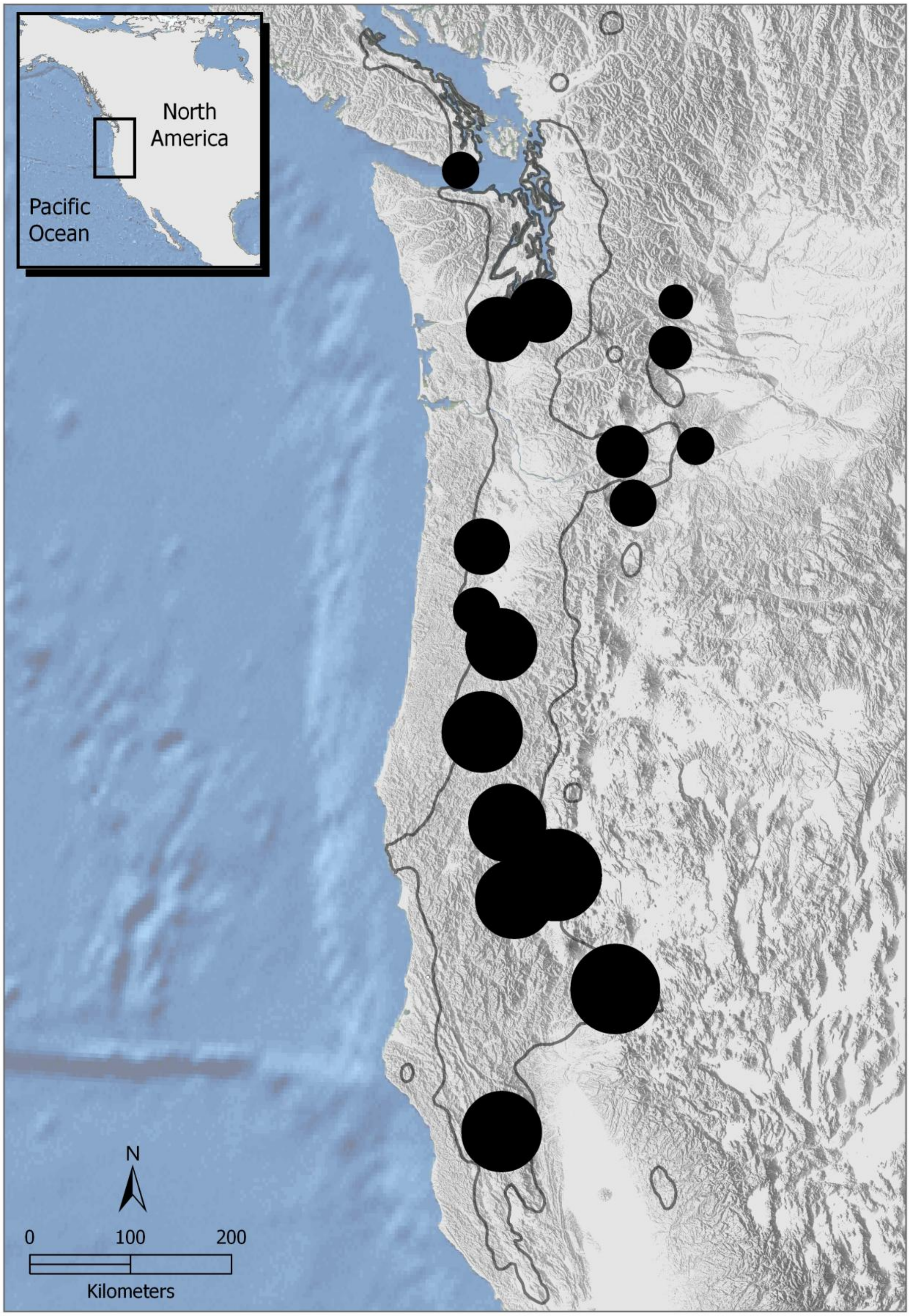

Figure 4.14. Correlation coefficients between monthly precipitation in the spring and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

Moisture availability and growth

Temperature and precipitation interact with soil characteristics to determine the moisture available to plants. Lack of available moisture can limit tree growth by interrupting the flow of nutrients and water crucial to biochemical pathways (Douglass 1920; Tivy 1993; Schweingruber 1996; Pederson 1998; Allen and Breshears 1998; LeBlanc and Terrell 2001; Vallardes and Pearcy 2002; Larcher 2003; Baldocchi and Valentini 2004; Akkemik et al. 2007). Positive associations between the radial-growth of Oregon white oak and the amount of available soil moisture occur at nearly every site throughout most of the climatic growth window.

Five of the 18 stands show negative relationships to soil moisture availability in spring prior to the year of growth. These correlations are likely related to the strong positive responses to temperatures at these stands during this season, which are then reflected in the moisture index, but more complex relationships related to reproductive behaviour are possible as well. That is, good growing conditions may induce the tree to reallocate its carbohydrate reserves toward completion of acorn formation instead of into storage for use in later years.

Nearly every stand of Oregon white oak in this study is positively correlated to the moisture index in fall and winter prior to the growing season and these correlations are likely related to soil moisture recharge. All sites respond even more strongly to the moisture index in spring and summer (Figures 4.15 and 4.16). Leaf out in spring and the start of cambial growth are water demanding and consequently a strong positive response to spring moisture is seen in this season. Less available water increases the resistance to flow from the soil to the tree, so less photosynthesis can occur (Kozlowski et al. 1991; Larcher 2003). Furthermore, water stress during the summer can cause bud damage and overall heat stress. In oaks, growth of the trunk is a low priority, and during moisture stress the trees divert their carbon resources elsewhere, particularly to roots (Hanson and Weltzin 2000). White oaks in other areas also respond positively to soil moisture in the growing season (LeBlanc and Foster 1992; Kelly et al. 1989; LeBlanc and Terrell 2001), and so this study helps validate the use of a moisture index as one of the best predictors of oak tree growth, although persistence in the Palmer Drought Severity Index should be considered (Heim 2002).

Dendrochronological response to moisture availability was not equally expressed at all 18 stands. Rather, a negative latitudinal gradient is seen in which the importance of spring moisture availability in controlling growth increases in relation to how far south the stand is located (latitude, CF Mix Spr, r = -0.538). Similarly, the importance of ground recharge during fall and winter and the relationship between growth and the moisture index in summer become more pronounced as latitude decreases (Figure 4.16). The growth at five of the stands, three east of the Cascade Mountains (SKC, BRG, and JNC) and the two most southern stands (CCR and TRR), positively respond to soil moisture availability in each month of the climatic growth window.

White oak trees are commonly considered drought tolerators (Abrams 1990, 1996), reflecting their ability to grow where other tree species cannot rather than their immunity to drought. Soil water content is lowest in summer and drought conditions during this time can greatly influence the growth of mature trees (Keen 1937; Heikkinen 1984; Tivy 1993; Ettl and Peterson 1995; Swetnam and Betancourt 1998; Hidalgo et al. 2001; Fritts 2001; Gamache and Payette 2004; Dalen and Hofgaard 2005). Drought effects on oak trees have also been documented in the laboratory (Poulos et al. 2007). Graumlich (1987) and Knapp et al. (2002) used tree-rings to reconstruct summer drought in the region and many of these coincided with years of low growth in Oregon white oak, particularly 1922, 1924, 1931, 1939, 1955, 1970, 1973, and 1992. Xylem deformities and twig dieback are possible reasons that oaks often show multi-year reductions in growth following drought (Jacobi and Tainter 1988; Tyree and Sperry 1988; Foster and LeBlanc 1992; Orwig and Abrams 1997) and drought years were shown to be the dominant climatic factor in the mortality of other North American white oaks (Pedersen 1998). Importantly, long-lived trees exhibit a resource storage effect, mitigate effects of drought, and can display a strong temporal lag when responding to changes in precipitation and available soil moisture. Even so, moisture availability is the best climatic predictor of growth and is likely the dominant climatic influence on the growth of mature Oregon white oak trees.

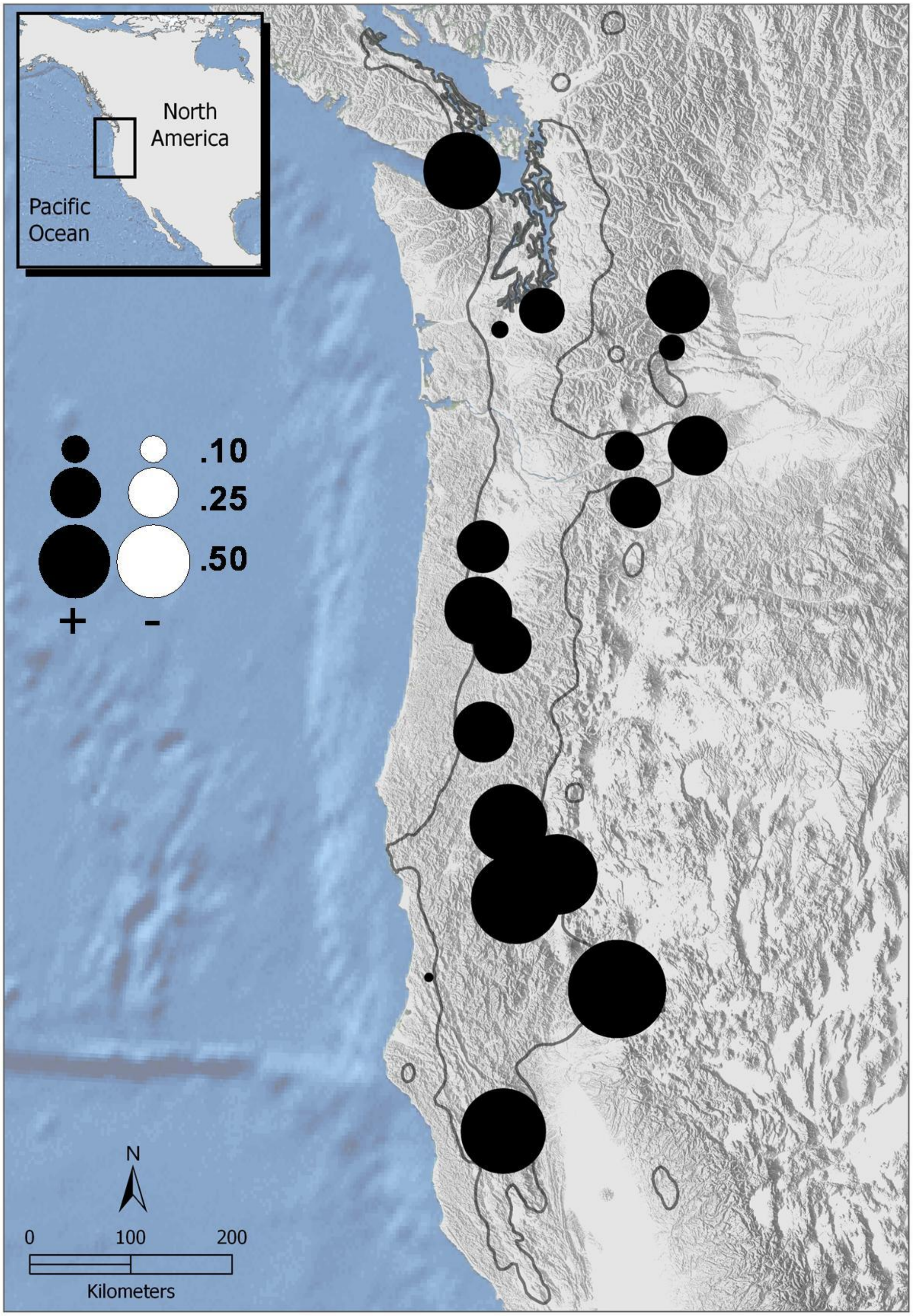

Figure 4.15. Correlation coefficients between the monthly moisture index in spring and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

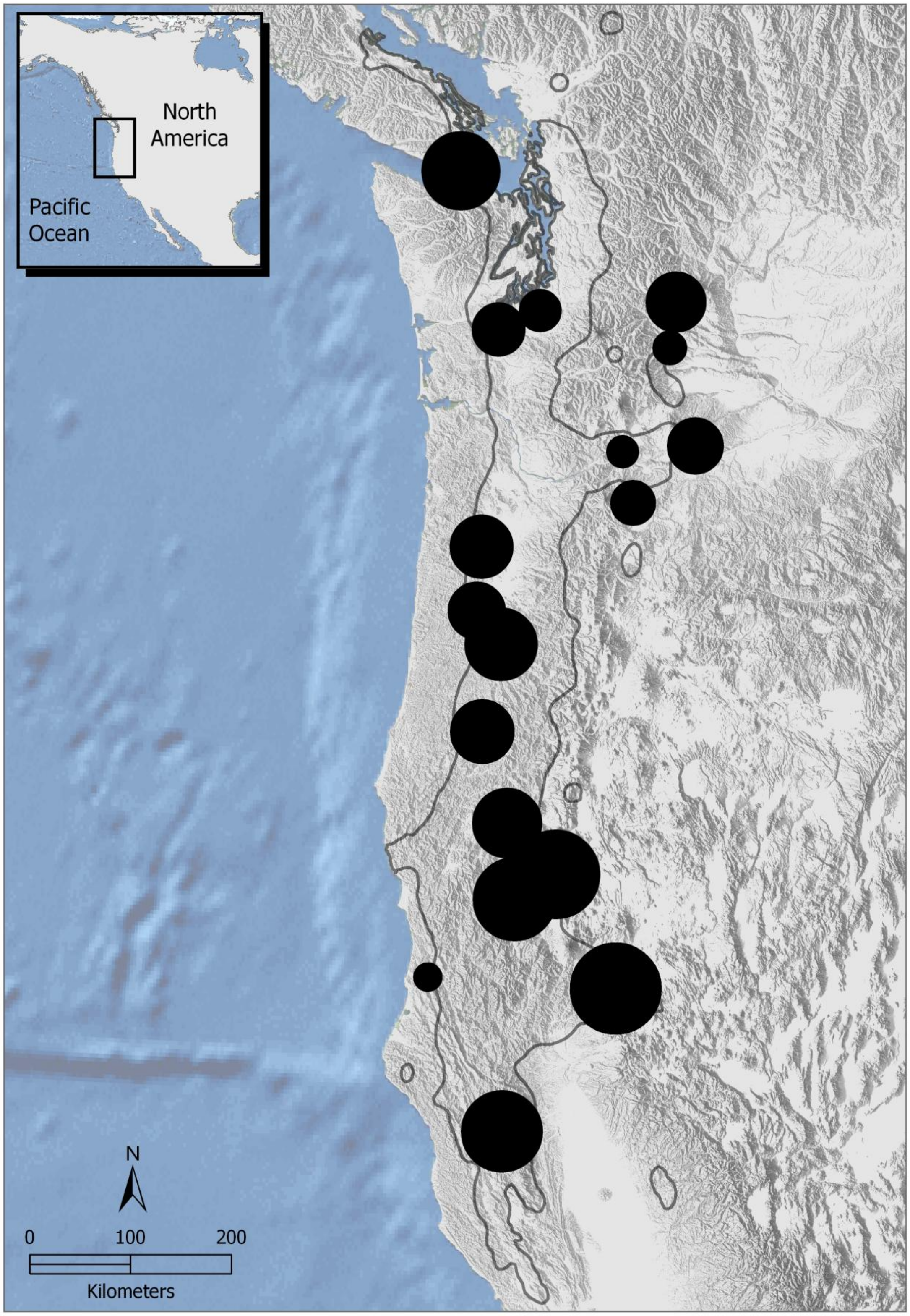

Figure 4.16. Correlation coefficients between the monthly moisture index in summer and the annual radial-growth of Oregon white oak. Symbols as in Figure 4.6.

Quasi-periodic forcings

Quasi-periodic forcings are irregular disruptions of climate that bring characteristic temperatures and amounts of precipitation to a region. El Niño Southern Oscillation, the Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation are associated with changes in sea surface temperatures that precede and influence climate and ecological processes in Pacific North America, especially the growth of trees.

With the aim of quantifying the stands' responses to these three climatic indices, we assessed the growth at each stand in relation to seasonal values of each quasi-periodic forcing index. This analysis shows weak but mostly coherent responses characteristic to each quasi-periodic forcing (Figure 4.17). In addition, we correlated ring-widths to the annual values of the three indices (i.e., hydrologic years, September through August) to understand the climatic forcings' overall influence on the growth of the oak trees. The annual radial-growth of Oregon white oak at most stands in this study is negatively correlated to the Southern Oscillation Index, and positively correlated to indices of the Pacific Decadal Oscillation and the Atlantic Multidecadal Oscillation (Figures 4.18 through 4.20). However, these responses are not equally expressed at all 18 stands.

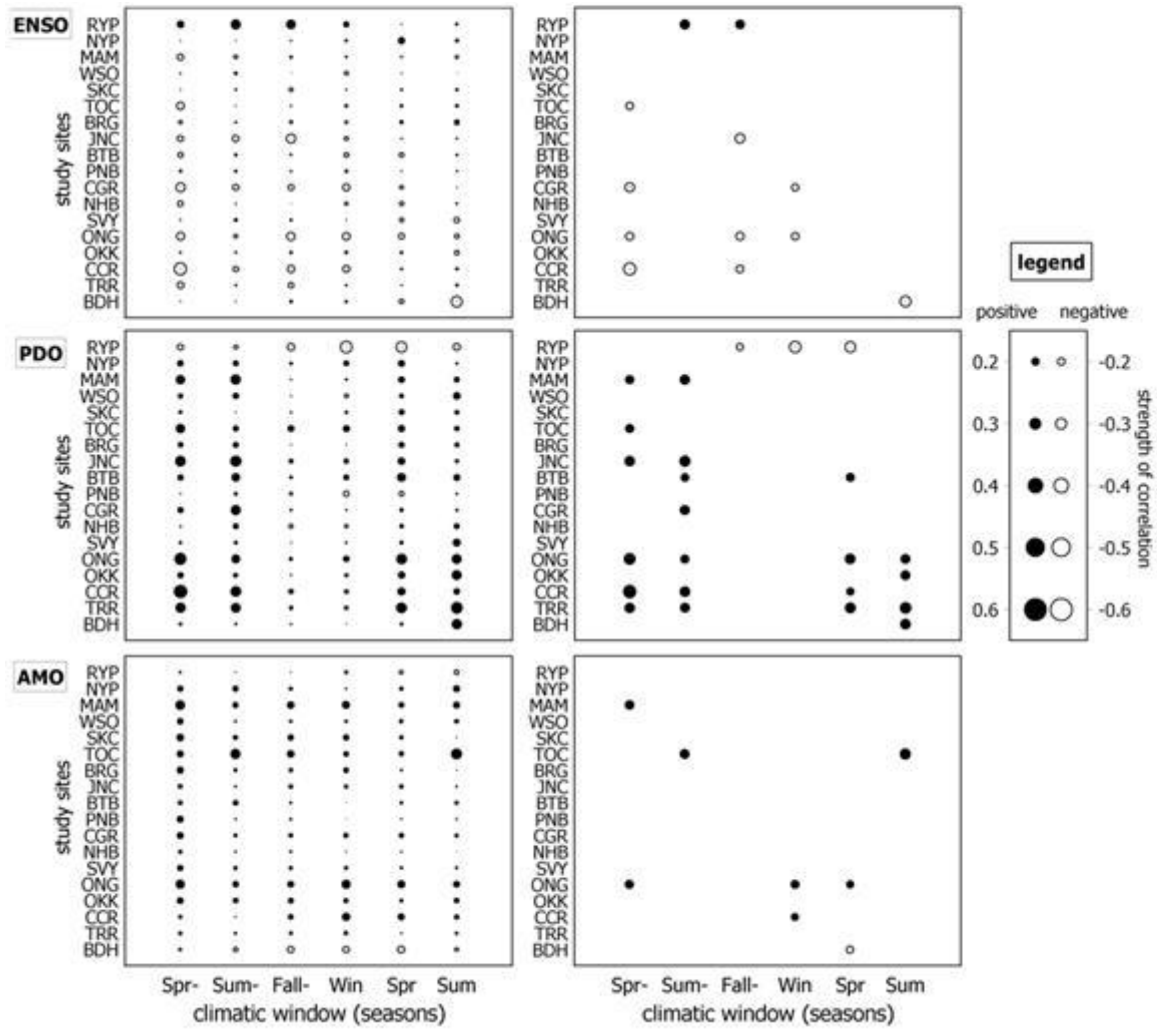

Figure 4.17. Correlation coefficients of seasonal values of quasi-periodic forcings to the annual ring-widths. Only significant correlations are presented in the right panel. Symbols as in Figure 4.3.

With the exception of the two most northern sites and one other, all stands are negatively correlated to the Southern Oscillation Index (SOI), a measurement of El Niño Southern Oscillation (Figure 4.18). Negative values of the SOI, El Niño events, are associated with warmer winters in the northernmost part of Oregon white oak's distribution. In the more southern part of Oregon white oak's distribution, negative values of the SOI are associated with wetter winters, springs, and summers.

In the correlation function analyses just described, we found a positive relationship between increased rainfall and an increase in Oregon white oak's radial-growth, especially in the southern half of Oregon white oak's range. The wetter years associated with El Niños, then, are also associated with increased radial-growth in this species. Some of the strongest correlations between annual growth and the seasonal values of the SOI occur in fall and winter prior to the growing season, again more so in the southern half of the species' range, which supports the interpretation that increased precipitation is the mechanism driving this relationship. Furthermore, the three sites that respond in the opposite direction to this quasi-periodic forcing (i.e., RYP, NYP, PNB) also show uncharacteristic responses to some winter climatic variables: RYP and NYP are not controlled by winter precipitation; RYP and PNB respond negatively to minimum winter temperatures. Some of the strongest El Niño events of the last 50 years are associated with some of Oregon white oak's years of lowest growth, particularly 1977, 1985, and 1992.

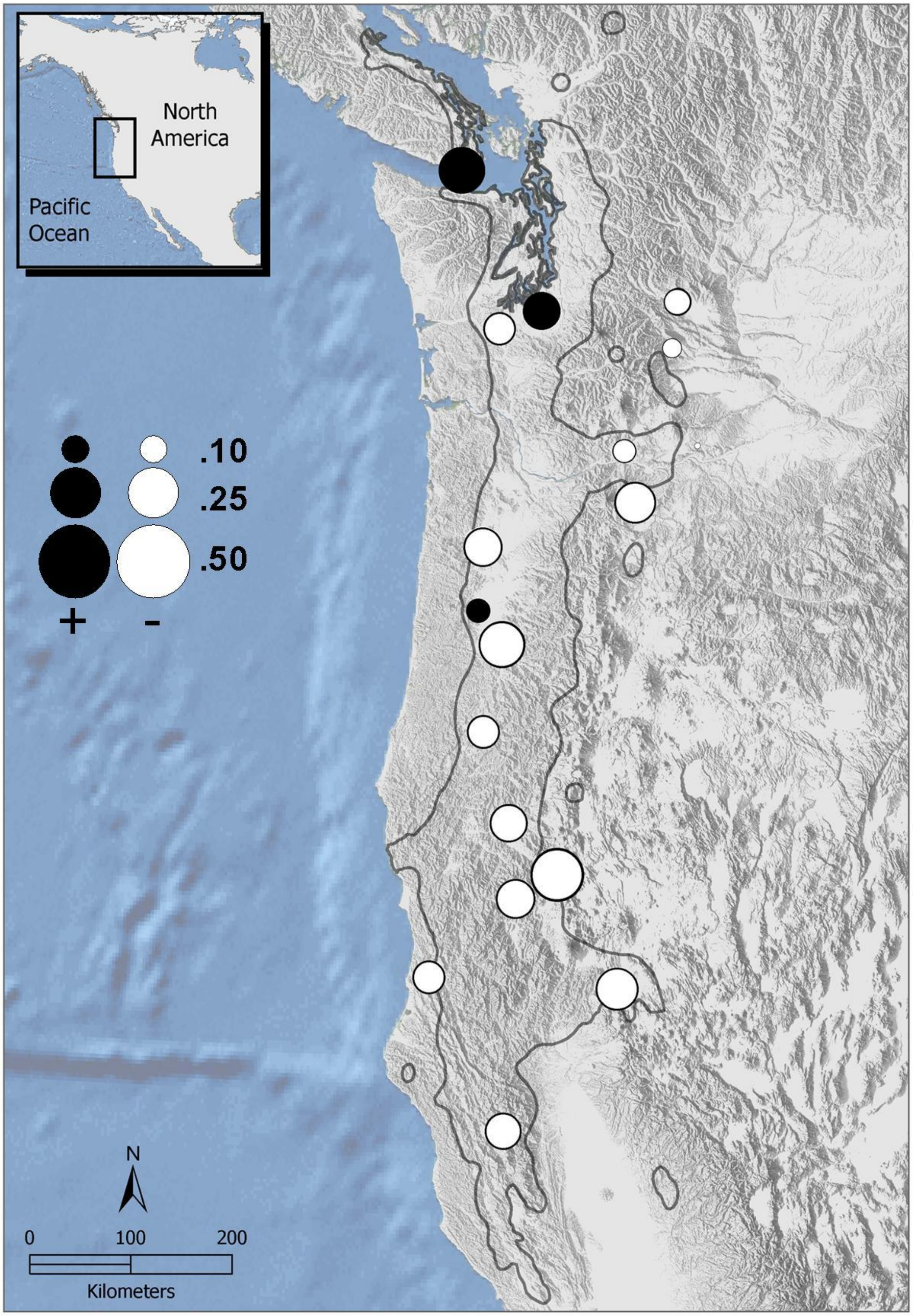

Figure 4.18. Correlation coefficients between annual values of the Southern Oscillation Index (El Niño Southern Oscillation) and annual ring-widths. Symbols as in Figure 4.6.

Positive values of the Pacific Decadal Oscillation (PDO) index are associated with warmer winters and less precipitation in Pacific North America (Minobe 1997). At low elevations, this index has been associated to increased tree growth, seedling establishment, and overall forest productivity at lower elevations (Zhang et al. 1997; Mantua and Hare 2002). The same increase in growth is seen in Oregon white oak: nearly every stand assessed here is positively correlated to the Pacific Decadal Oscillation index (Figure 4.19), again with the exception of Rocky point (RYP) and Pigeon Butte (PNB) which show a decrease in growth in response to warmer winters. The decrease in precipitation associated with this quasi-periodic forcing seems to make little difference to the fully saturated soil common in the region during winter. An increase in minimum temperatures, however, will positively influence growth and it is this response to temperature that likely accounts for the positive correlations between radial-growth and the PDO. The significant correlations between annual growth and seasonal values of the PDO suggest that minimum temperatures in spring and summer are also important in this relationship (Figure 4.17).

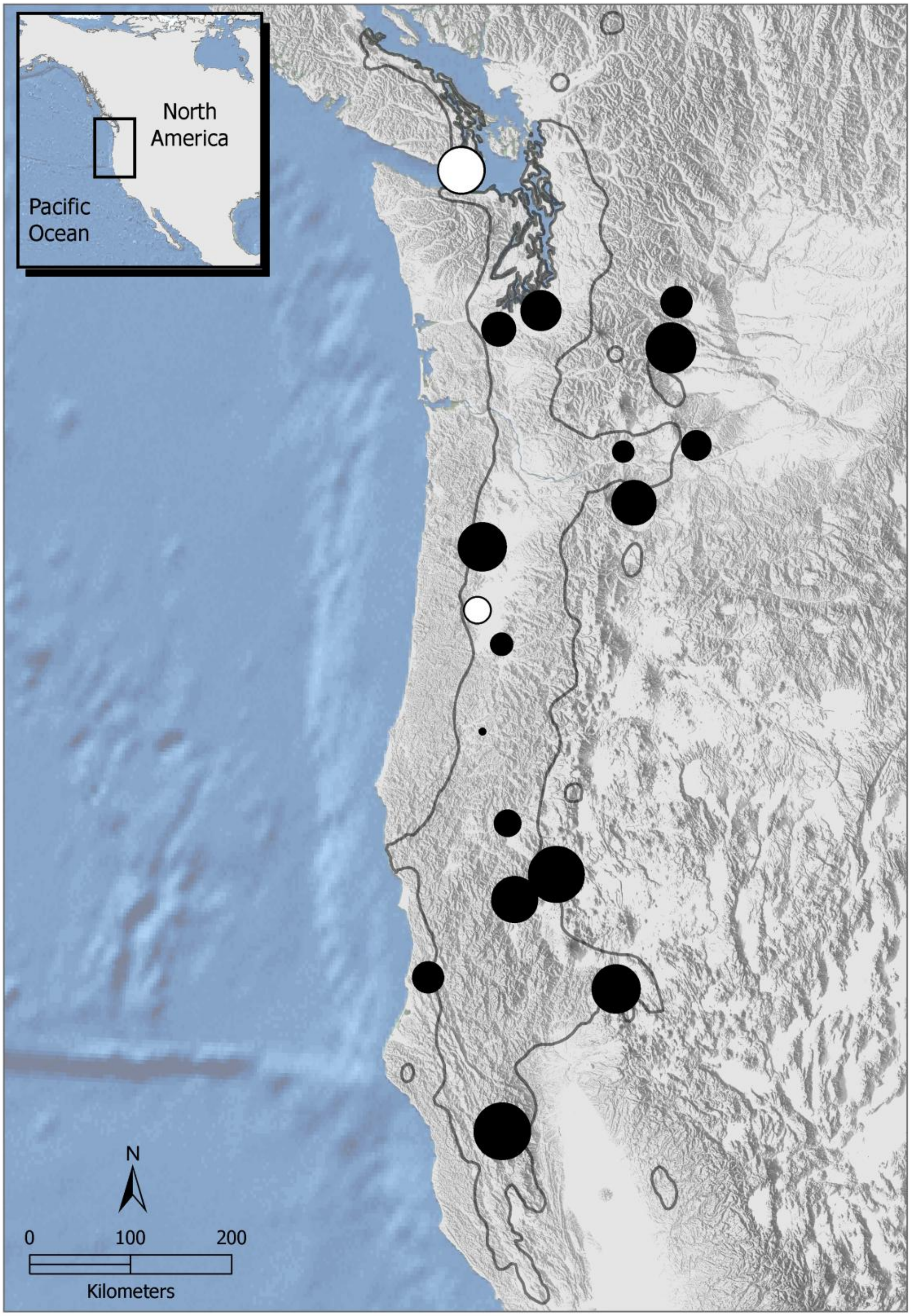

Figure 4.19. Correlation coefficients between annual values of the Pacific Decadal Oscillation index and annual ring-widths. Symbols as in Figure 4.6.

The Atlantic Multidecadal Oscillation (AMO) is associated with climate in Pacific North America: warm temperatures in the Atlantic correspond to low rainfall along the coast in western North America (Enfield et al. 2001; Gray et al. 2004). From the correlation functions just described, a decrease in precipitation is associated with a corresponding decrease in Oregon white oak's radial-growth throughout the species' distribution. Thus, the correlations found between the growth of Oregon white oak and this index are weak. This relationship is mostly coherent: 16 of 18 stands respond positively to the AMO, which is counter-intuitive and highlights the complexity of this forcing (Figure 4.20). The two stands that respond negatively to the Atlantic Multidecadal Oscillation are also those that respond less strongly to precipitation (RYP and BDH).

The similarity of correlations between radial-growth and these three quasi-periodic forcings validate their use in growth projections and dendroclimatic reconstructions. However, these dendrochronological responses are also mixed in that the relative strengths of the climatic controls vary throughout the natural range of the species: a few stands respond to different degrees and occasionally even in opposite directions than the majority of other stands. Therefore, a thorough understanding of a stands' geographic position, the species' unique ecophysiology, and characteristic dendroclimatic response is necessary when employing these indices for biogeographic projections. Significant correlations between growth and these indices suggest that changes in these climatic forcings associated with the current warming may have profound implications for the future growth of Oregon white oak trees.

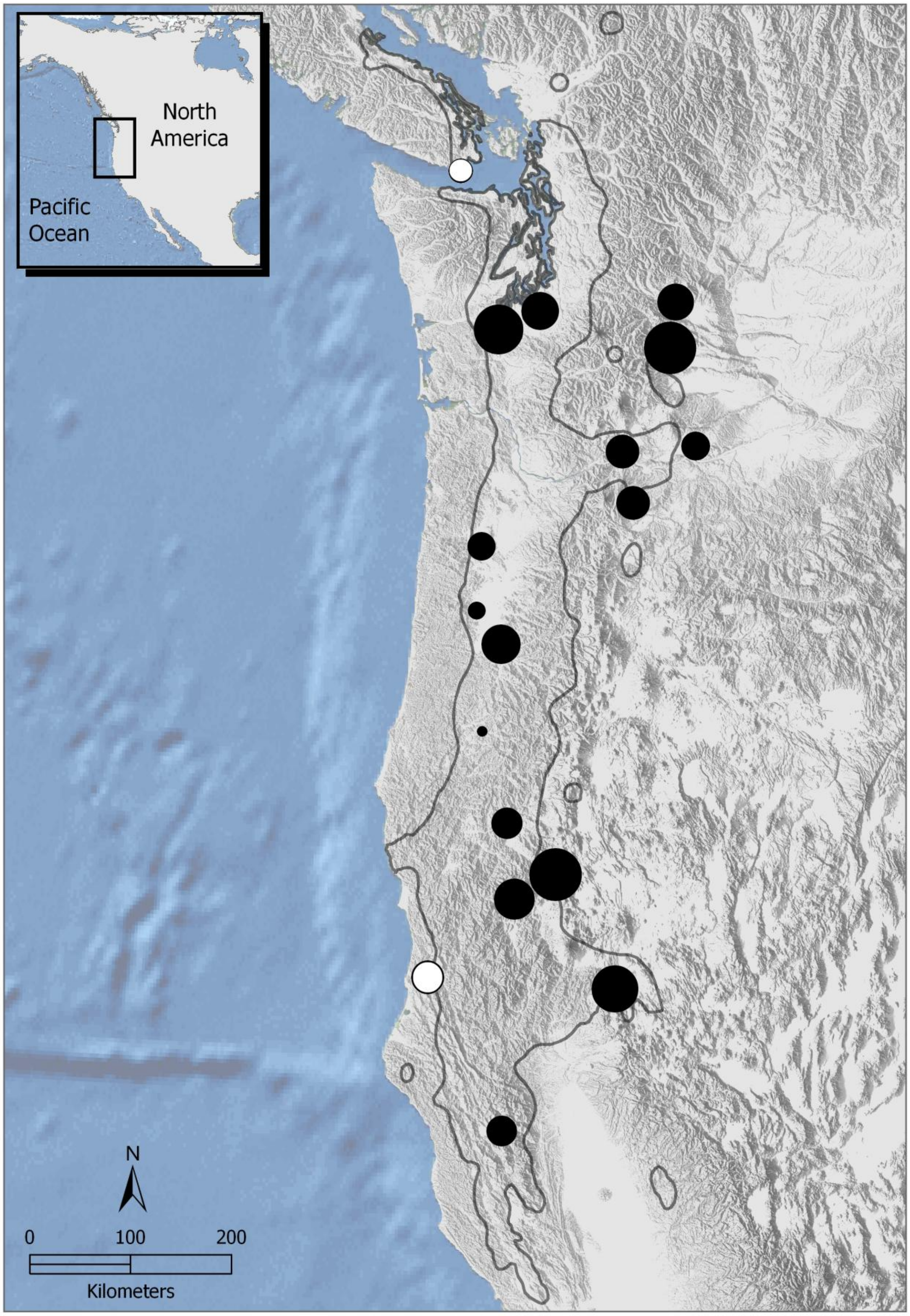

Figure 4.20. Correlation coefficients between annual values of the Atlantic Multidecadal Oscillation index and annual ring-widths. Symbols as in Figure 4.6.

Empirical orthogonal functions

The correlation functions just described identify a characteristic pattern of response indicating the degree to which the radial-growth of Oregon white oak is associated with local climates. Structure detection analyses such as principal components analysis are also widely used in dendrochronology (Briffa 1995). These pattern recognition analyses are especially useful on large highly intercorrelated datasets as they identify orthonogonal modes that account for the most variance. We conducted two principal components analyses here, the first on the matrix of ring-width indices and the second on the matrix of correlation functions between the ring-widths and the climatic variables. These two analyses confirm the strength and synchronicity of the species' dominant response and identify other important growth-climate relationships.

Principal components analysis on the ring-width indices

The principal components analysis performed on the matrix of ring-width indices produces a dendroclimatic pattern similar to the dominant pattern of response evident in the correlation function analyses discussed above and is one of the best indicators of the species' overall growth-response to climate. This analysis reveals only one significant mode of variability. The first eigenvector accounts for 67 percent of all variation in the ring-width indices, while each of the less important eigenvalues represent less than 5 percent of the variation and are not statistically different from zero (Figure 4.21). Each of the other 17 principal components are strongly loaded on by a single chronology, suggesting that site differences rather than regional patterns of climate are also important in determining tree growth.

The leading principal component indicates a coherent regional growth pattern (Figure 4.22). This strength of synchronicity in growth-response is quantified in the empirical orthogonal function loadings, which range from 0.225 to 0.238 (Figure 4.23). The complex but characteristic pattern of growth is expressed very strongly by all stands suggesting the presence of region-wide climatic forcings. Loading values of two stands, NYP and TOC, are slightly different than those of the other stands reflecting disturbance events and the importance of stand dynamics at these sites during these 108 years.

The dominant growth pattern represented by this single eigenvector can be associated with underlying environmental drivers by plotting correlations between the scores of the first principal component and the climatic indices at each site, displaying the strength of climatic influences on the growth of these trees (Figure 4.24). Oregon white oak's characteristic regional pattern of growth is reflected in this first principal component: positive correlations between the first principal component scores to temperatures in April and May prior to the year of growth, negative correlations to maximum temperatures in spring, positive associations to precipitation in spring, and positive correlations between radial-growth and the moisture index in winter, spring, and summer. Furthermore, coherent correlations also occur between these first principal component scores and other climatic variables, especially fall temperatures and winter precipitation. This pattern is the dominant dendroclimatic response of Oregon white oak.

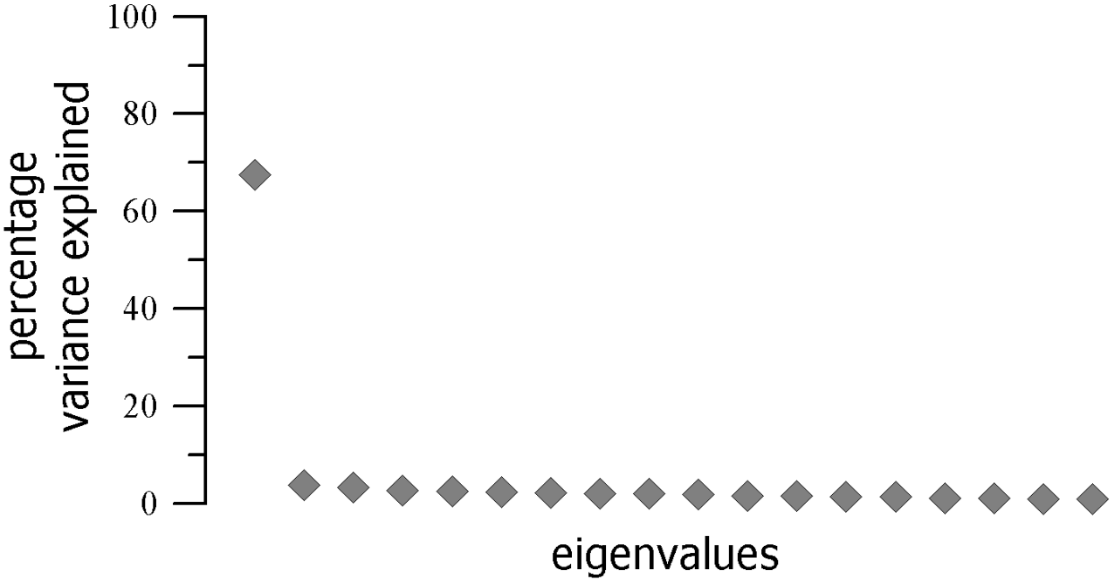

Figure 4.21. Eigenvalues for the principal components analysis performed on the matrix of ring-width indices. Each eigenvalue (diamond) is ordered according to its importance.

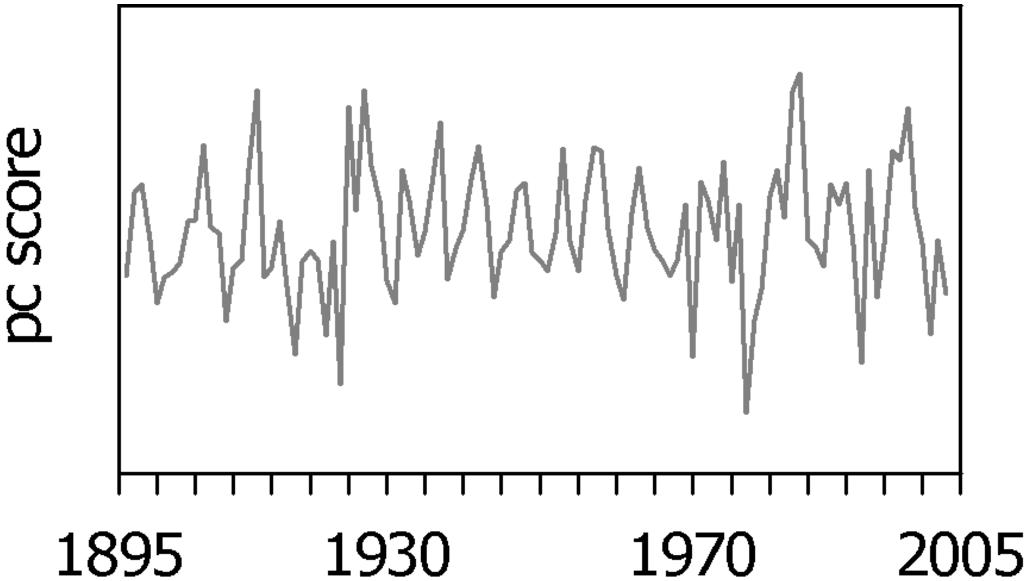

Figure 4.22. The time-series of the first principal component scores from the analysis performed on the matrix of ring-width indices.

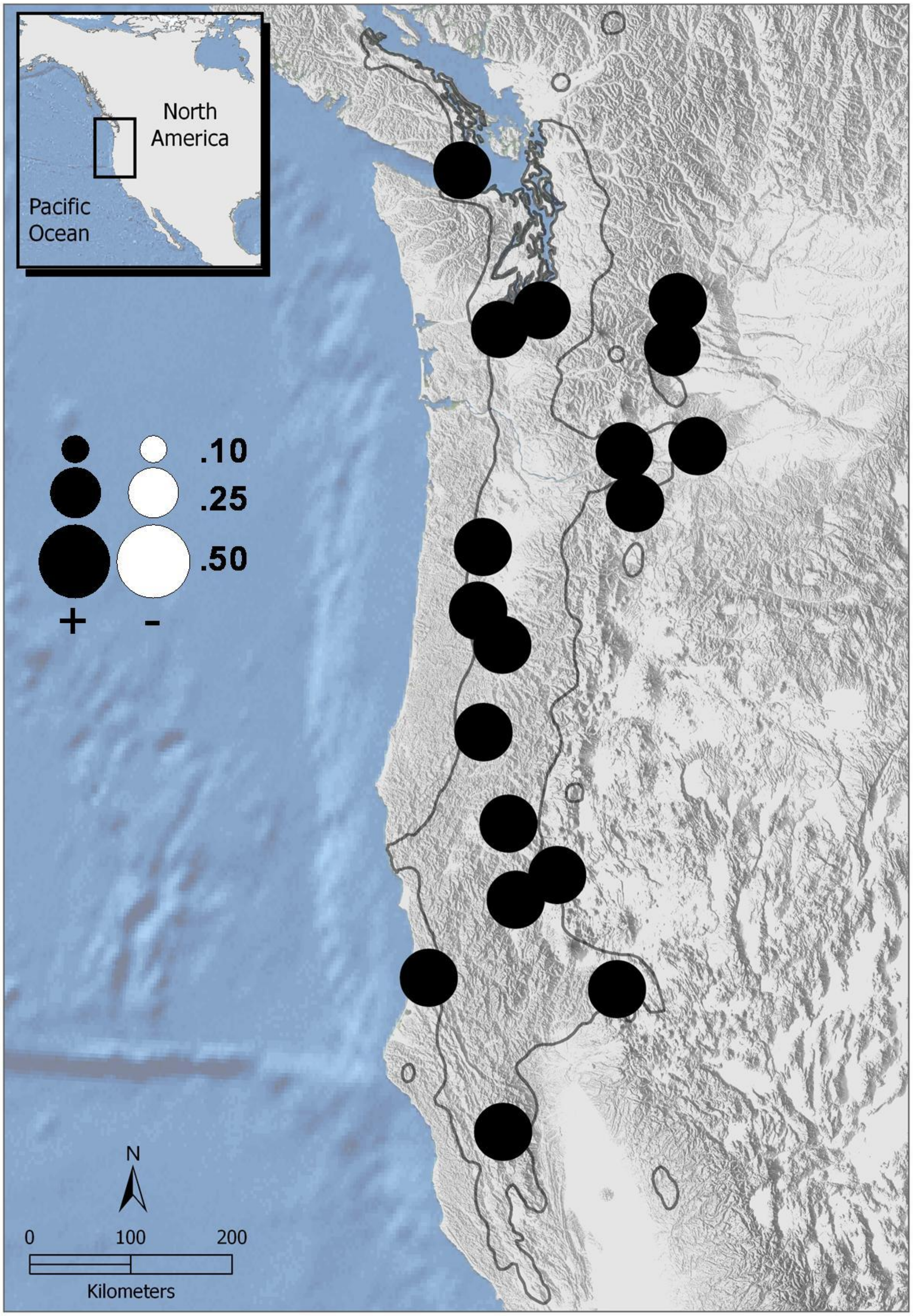

Figure 4.23. Empirical orthogonal loadings associated with the first principal component of the analysis conducted on the matrix of ring-width indices. Symbols as in Figure 4.6.

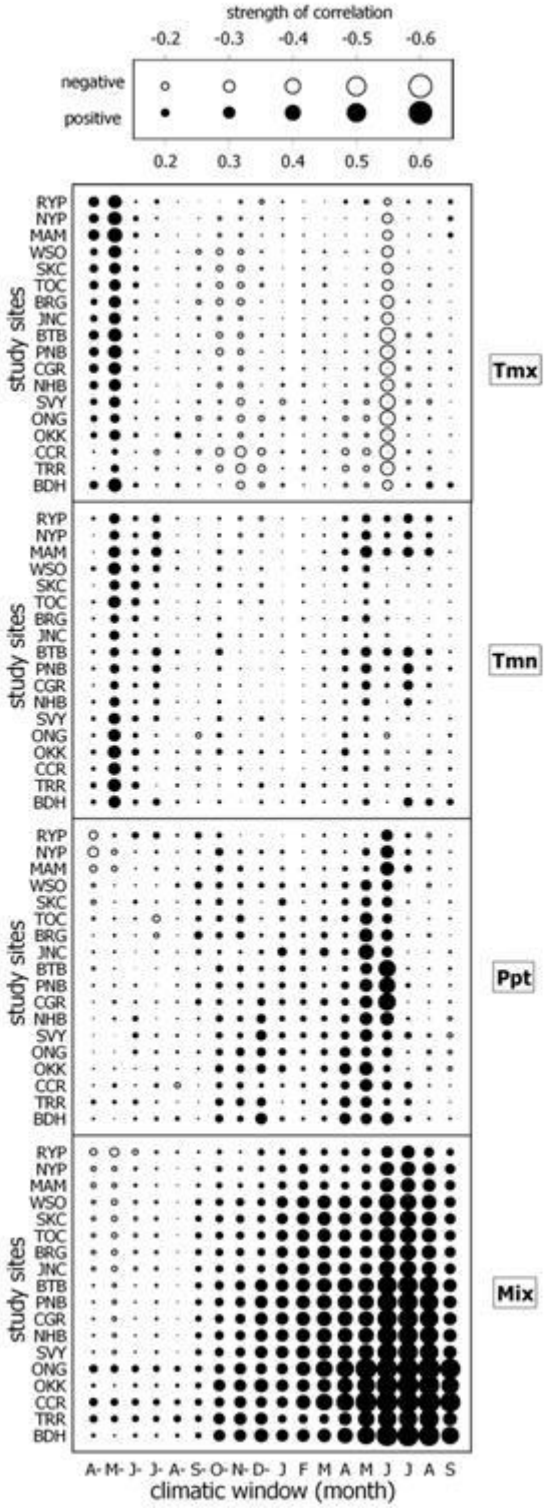

Figure 4.24. Correlations between the first principal component scores performed on the ring width indices and the climatic variables. Black circles represent positive correlation coefficients and white circles represent negative correlations, while the size of the circles represents the strength of the relationship.

Principal components analysis on the correlation functions

The same dominant pattern of climatic response in Oregon white oak identified by the correlation functions analysis and the principal components analysis performed on the matrix of ring-width indices is also found by conducting a second principal components analysis, this on the correlation functions themselves. In addition, the second principal components analysis also uncovered other informative but less obvious patterns. The first three eigenvalues are statistically significant, describing 27, 12, and 10 percent of the variation in the correlation functions, respectively (Figure 4.25).

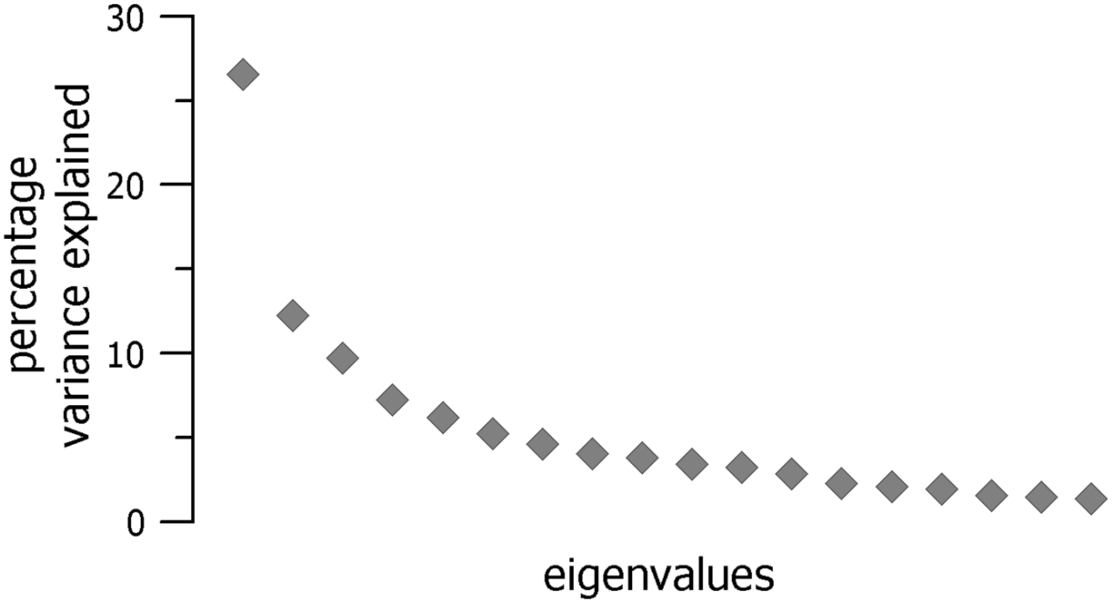

Figure 4.25. Eigenvalues for the principal components analysis performed on the matrix of correlation functions. Each eigenvalue (diamond) is ordered according to its importance.

The degree to which correlation functions are associated with each empirical orthogonal function is seen in diagrams created by plotting the respective principal component scores alongside the correlation variables. The first principal component with its associated empirical orthogonal loadings produces a pattern very similar to Oregon white oak's characteristic dendroclimatic response. The first empirical orthogonal function explains 27 percent of the variation in response. This pattern is nearly identical to the dominant pattern expressed in both of the first two analyses: a strongly negative response to maximum temperatures in June, a positive response to temperatures in May prior to the year of growth, a positive response to the amount of precipitation in spring, and strong positive responses to moisture availability in fall, winter, spring, and summer (Figure 4.26). Sites that load heaviest (e.g., ONG, OKK, CCR, TOC) reflect this pattern to a greater degree (Figure 4.27).The pattern of loading values is very similar to the pattern of response to soil moisture availability in spring (Figure 4.15).

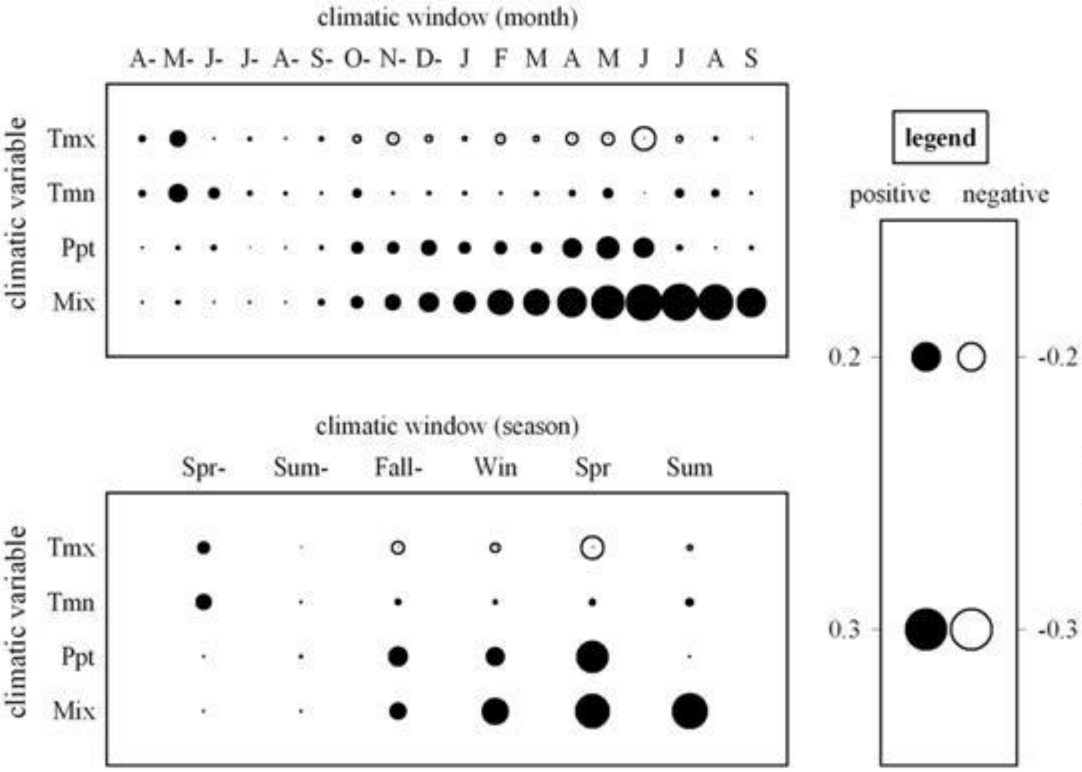

Figure 4.26. The first principal components scores derived from the analysis performed on the correlation functions and the climatic variables. Black circles represent positive scores and white circles represent negative scores.

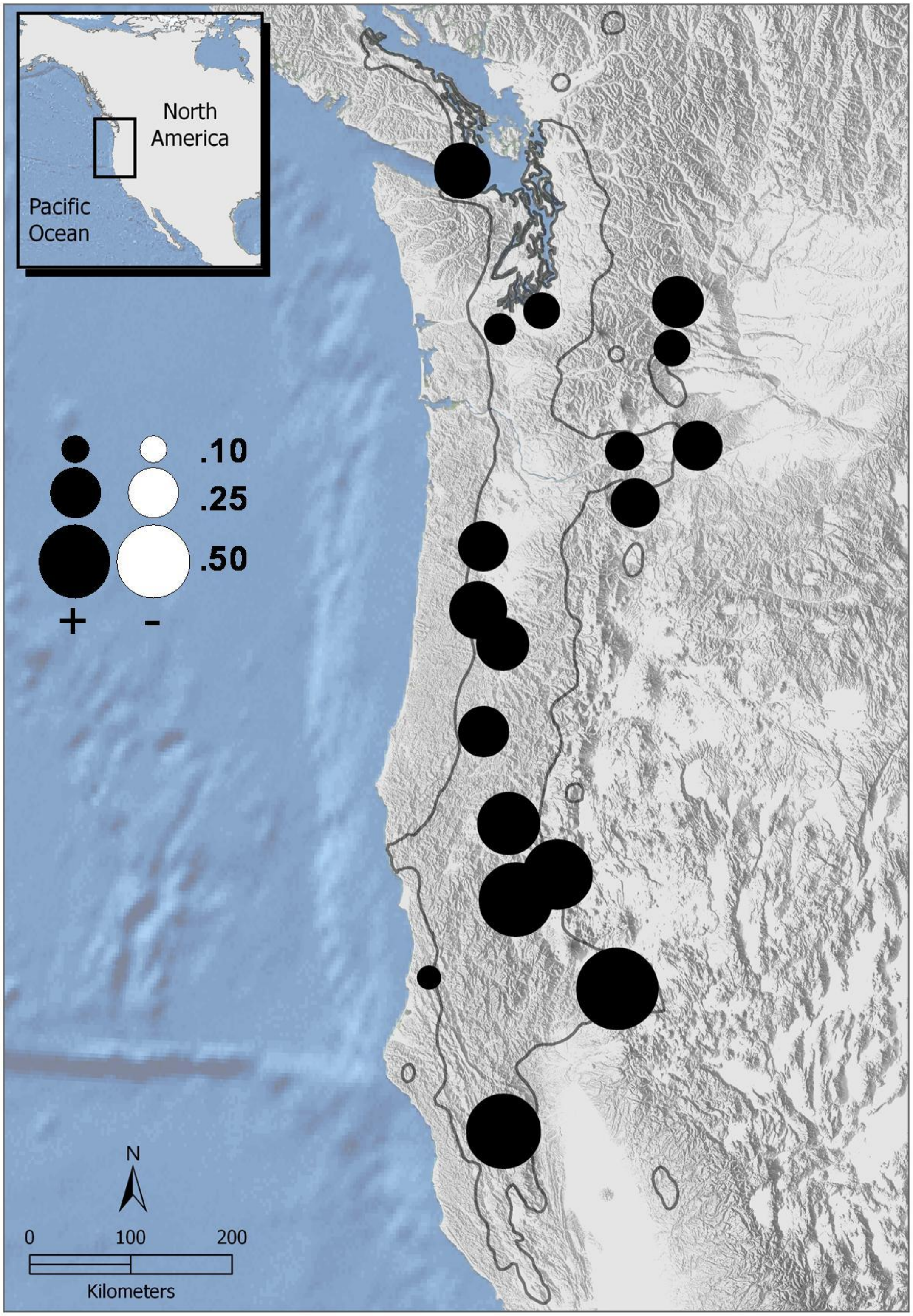

Figure 4.27. Empirical orthogonal loadings associated with the first principal component of the analysis conducted on the matrix of correlation functions. Symbols as in Figure 4.6.

The second eigenvector pattern representing 12 percent of the variation in the species' response shows strong positive correlations to minimum temperatures during spring and summer (Figure 4.28). Notably, a negative response to minimum temperatures in November is also evident, representing the increased negative correlations between temperature and growth in the higher elevation, more southerly stands. Furthermore, this second principal component is related to a negative response to moisture availability during the year prior to growth.

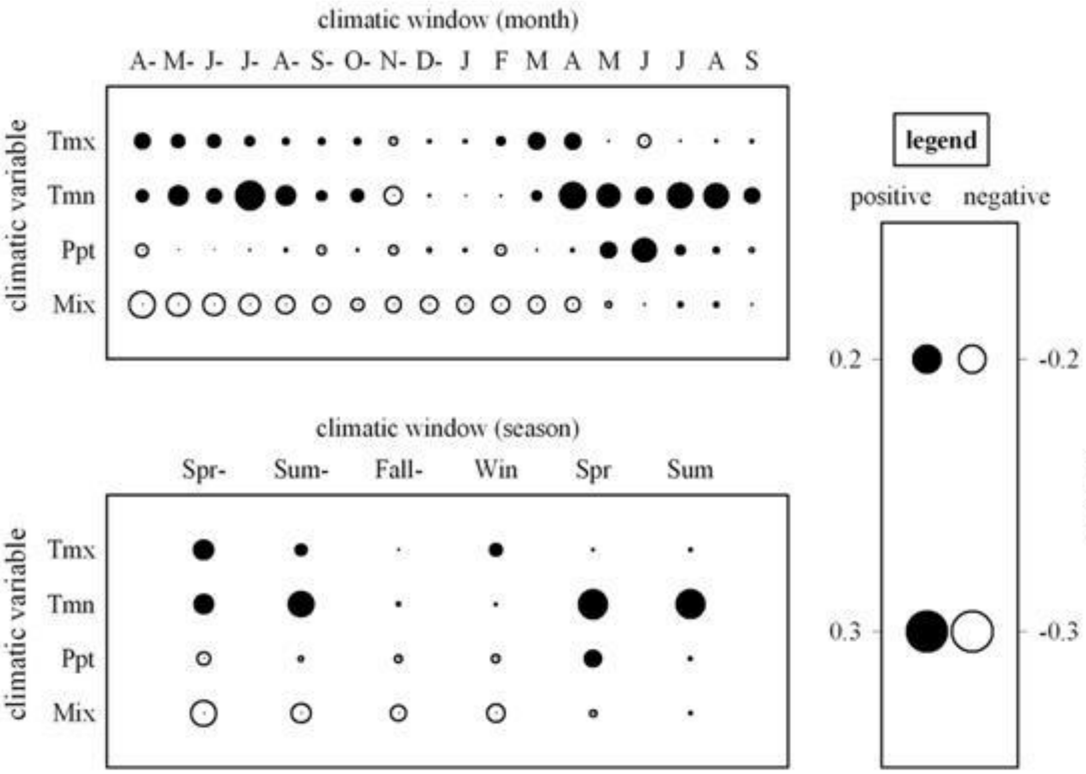

Figure 4.28. The second principal components scores derived from the analysis performed on the correlation functions and the corresponding climatic variables. Symbols as in Figure 4.26.

Stands that load positively on this second principal component are those in which minimum temperatures are positively correlated to growth and moisture availability is less of a control (e.g., NYP, MAM, TOC, and NHB) (Figure 4.29). These stands tend to be at the lowest elevations for their latitude (Figure 3.2, upper panel). Those sites that load positively are those that respond more to minimum temperatures rather than maximum temperatures, and explain why this pattern is more related to correlations to precipitation rather than to correlations to the amount of available soil moisture. This pattern of response is similar to that shown to the correlations between growth and minimum temperatures in spring and fall prior to the growing season (Figures 4.9 and 4.10). Conversely, those sites that load negatively on this principal component are those that are less limited by minimum temperatures (e.g., RYP, BRG, and SVY).

About 10 percent of the variation in the correlation functions is described by the third eigenvector. The strongest associations between the principal component scores and the climatic variables are again found to minimum temperatures, but several other relationships are evident (Figure 4.30). For instance, positive relationships between the principal component scores and maximum temperatures occur in November, December, and January prior to the growing season and in May. This eigenvector also shows the tendency of some stands to respond positively to soil moisture availability even in the year prior to growth.

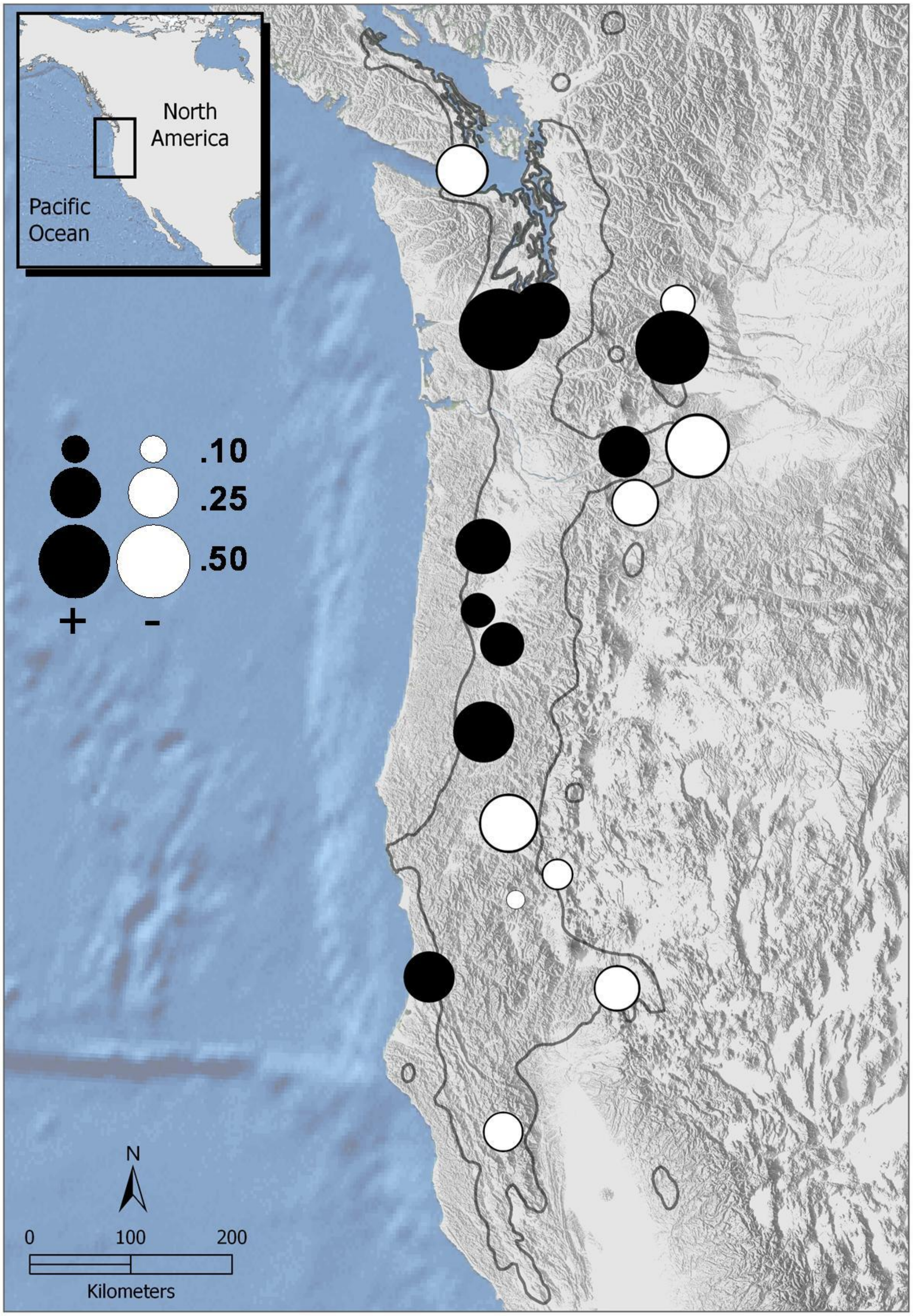

Figure 4.29. Empirical orthogonal loadings associated with the second principal component of the analysis conducted on the matrix of correlation functions. Symbols as in Figure 4.6.

The stands that load positively on this third eigenvector (Figure 4.31), for instance, those east of the Cascades, are those that are at relatively high elevations for their latitude in that they lie furthest above the latitude-elevation trendline in the species' biogeographic profile (Figure 3.2, upper panel). These stands inhabit some of the warmest and driest sites, depending on soil moisture availability even in the year prior to growth and responding positively to temperatures during winter and on the cusps of that season. Conversely, stands that load negatively on this principal component (e.g., RYP and NHB) are those stands that are little affected by minimum temperatures. The spatial patterns of response evident in this third eigenvector are similar to those correlations to average minimum temperatures and amounts of precipitation in the spring and summer prior to growth and to temperatures in the fall prior to the growing season.

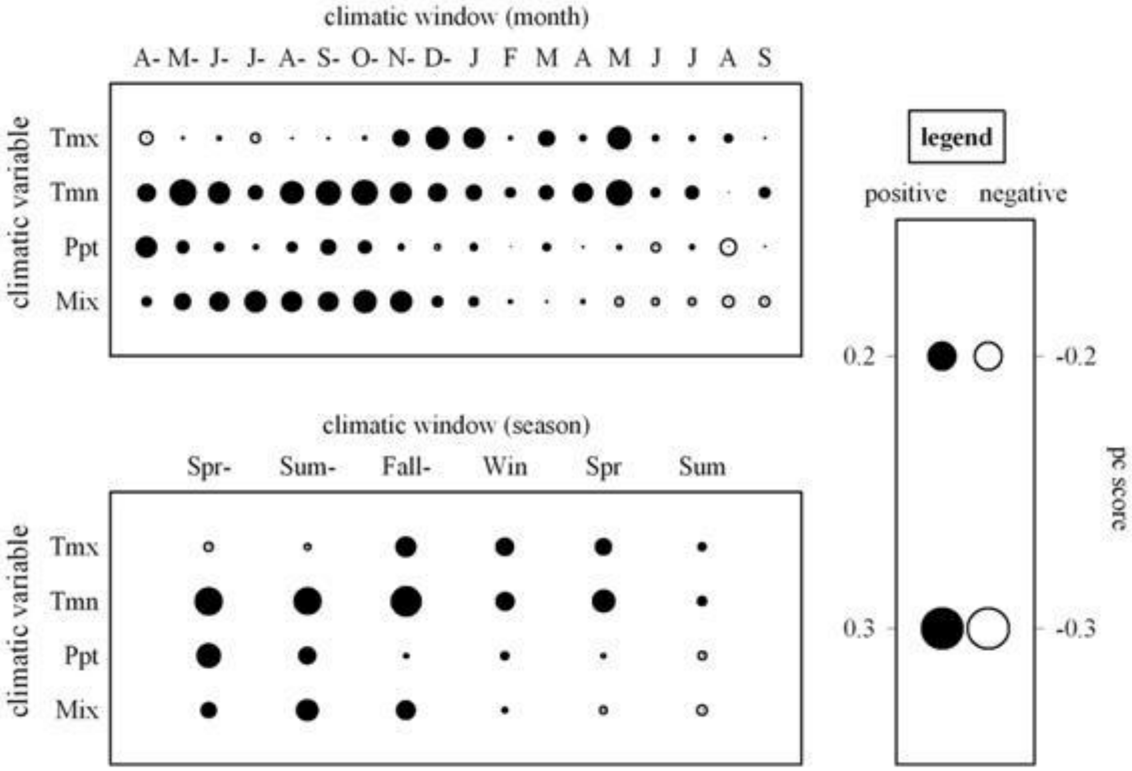

Figure 4.30. The third principal components scores derived from the analysis performed on the correlation functions and the corresponding climatic variables. Symbols as in Figure 4.26.

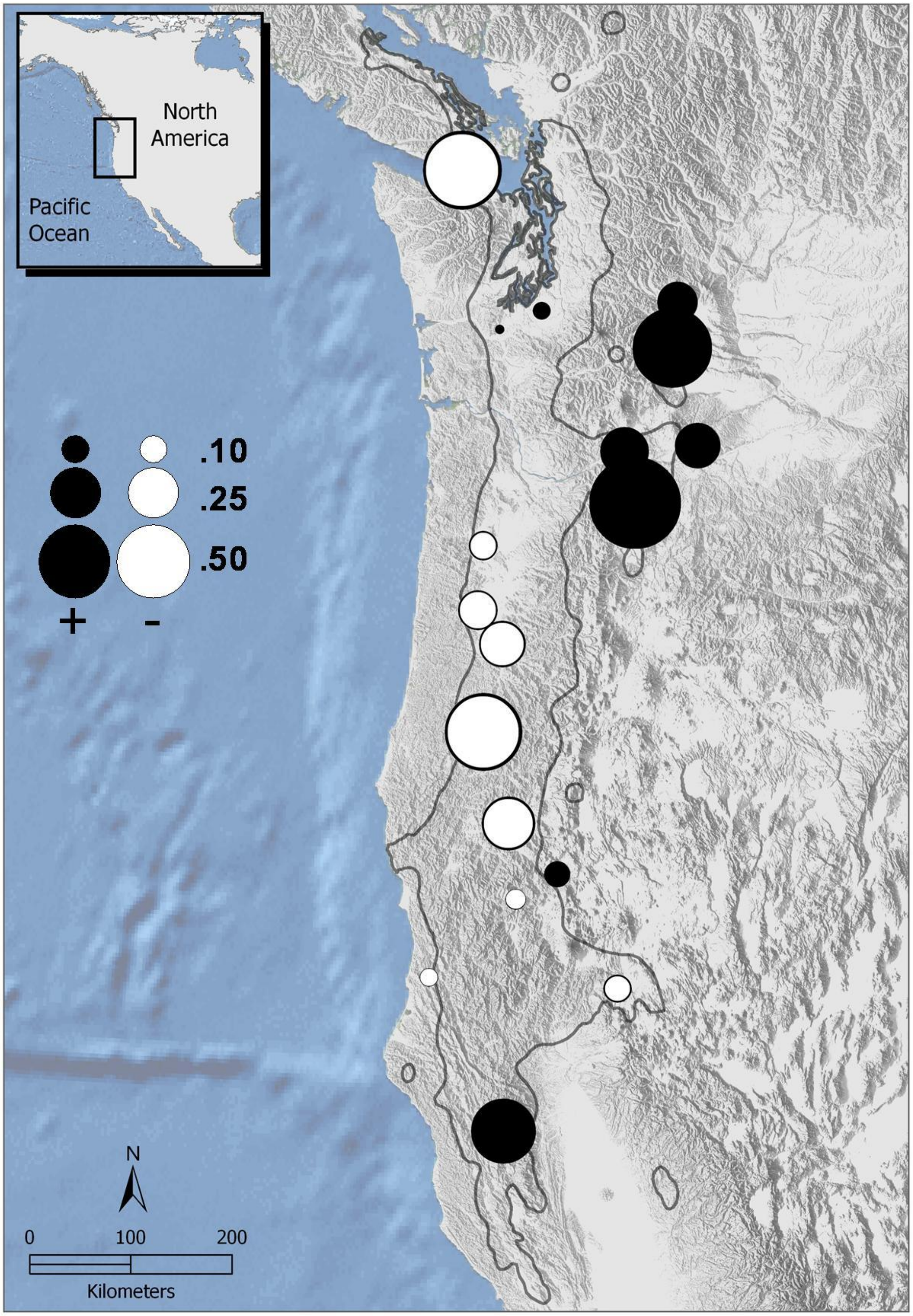

Figure 4.31. Empirical orthogonal loadings associated with the third principal component of the analysis conducted on the matrix of correlation functions. Symbols as in Figure 4.6.

Site influences

To fully understand the spatial patterns in Oregon white oak's dendroclimatic response, one must be aware of the geographic differences between sites. Some stands do not show strong correlations between radial-growth and the climatic variables, those where climatic threshold effects rather than linear relationships are important or where mechanisms other than climate influence growth. The local geographic position and ecological situation all play a role in the average dendroclimatic response of a stand and can obscure the species' overall climatic signal. These confounding variables include topographic factors such as elevation, slope angle, slope position, and exposure; available light due to slope aspect, amount of arboreal canopy coverage, or tree-specific gaps; soil depth, texture, and available nutrients; hydrologic inputs; fire; and biotic influences on growth: competition and facilitation from botanical and fungal associates, herbivory, and anthropogenic disturbances. These are not isolated influences; rather, combinations of these factors, interactions between them, and emergent properties are just as important in determining a stand's growth response to its climate. Specific site descriptions are presented in Appendix A.

Here, it is important to note the numerous partial correlations existing within these datasets. Temperature and precipitation are correlated to each other and to the moisture index. More problematic for interpretation of the climatic signal is that latitude, elevation, the amount of arboreal canopy coverage, and average ring-width are correlated to each other. That is, the northernmost sites are also the lowest in elevation, have the lowest amount of canopy coverage, and include the fastest growing trees. This limits a strict interpretation of a stand's dendroclimatic response. Still, gradients in the stands' responses are seen and should be considered in context of the stand's biogeographical position.

Elevation

Differences in elevation seem to alter the influence of climate on the growth of Oregon white oak, and this has been documented in other tree species (Villalba et al. 1992, 1994; Buckley et al. 1997; Tardif et al. 2003). A positive correlation between elevation and an oak stand's response to minimum temperatures in the winter (elevation, CF Tmn Win-, r = 0.638) may reflect an important influence on Oregon white oak's radial growth (Figure 4.32). That is, higher elevation stands tend to respond more positively to minimum temperatures in winter. The lowest elevation stand shows a significant negative association to winter temperatures and the highest elevation stand responds significantly positively to minimum temperatures in winter suggesting a real difference in dendroclimatic response. However, these associations between radial-growth and winter conditions are generally very low correlations, mostly insignificant. In addition, a strong negative correlation (elevation, Wav, r = -0.610) was found between the elevation of the 18 sites and the average width of the tree-rings. The faster-growing stands tend to be found at lower elevations.

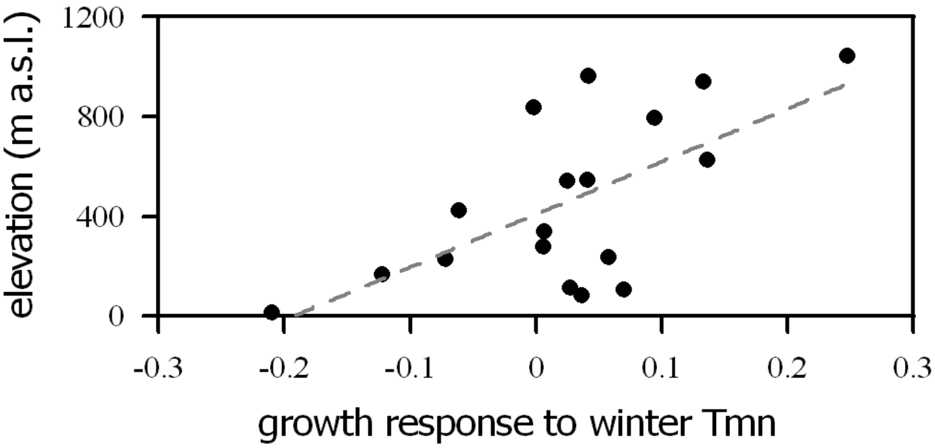

Figure 4.32. The relationship between elevation and minimum temperatures during the winter season prior to growth.

Canopy

The amount of arboreal canopy coverage and Oregon white oak's response to moisture conditions in the spring are related (canopy, CF Mix Spr, r = -0.675). That is, the greater the percentage of light intercepted by leaves, the less positive the response to moisture availability in spring (Figure 4.33). A more open-canopy stand experiences greater diurnal variation in ground-level air and upper-horizon soil temperatures. A closed canopy lessens the influence of available soil moisture (Orwig and Abrams 1997; Villalba et al.1992; Franks 2007).

So, the temporally complex and spatially mixed response of these Oregon white oak stands is likely attributable to specific geographic and ecological influences, especially elevation and the amount of arboreal canopy coverage. Furthermore, site characteristics undoubtedly interact with each other, with local climatic conditions, and with other site-specific characteristics such as soil properties. These interactions confound the interpretation of the species' growth as it directly relates to the regional climate and highlights the complexity of this species' dendroecological response.

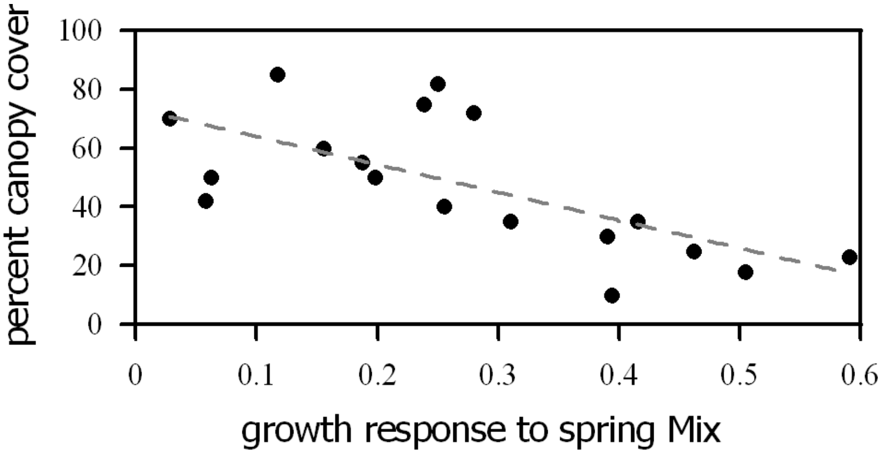

Figure 4.33. The relationship of canopy cover to spring moisture availability. (Note the independent variable on the y-axis.)

A mixed growth response to climate

Documented here is Oregon white oak's strong, mostly synchronous response to its climate. The majority of stands respond similarly to their local climates: the response to certain climatic variables is coherent throughout much of the natural range of the species. The characteristic pattern of Oregon white oak's dendroclimatic response is found in all three statistical analyses: a strongly negative response to maximum temperatures in June, a positive association with both maximum and minimum temperatures in May prior to the year of growth, a positive association to the amount of precipitation in spring, and increasingly strong positive responses to moisture availability in fall, winter, spring, and summer.

However, the 18 stands in this analysis show an asymmetric biogeographic response: not all Oregon white oak trees respond to local climatic forcings to the same degree and sometimes not even in the same direction as those trees in other stands. Rather, the specific climatic limiting factors varied spatially. That is, the pattern of response is mixed in that the relative importance of climatic controls varies according to each stands' particular geographic situation.

In particular, the more northerly stands tend to respond more strongly to temperatures in both the month of July as well as in the winter season. More easterly sites are less strongly correlated to average maximum temperatures in the spring prior to growth but more strongly correlated to minimum temperatures in this season than other stands. These more continental stands, east of the Cascades, also respond more positively to temperatures in the fall prior to growth and to minimum temperatures in spring during the growing season than other Oregon white oaks west of the Cascade Mountains. These stands further east also respond positively to precipitation in spring and summer priior to the growing season, whereas many stands west of the Cascades respond negatively. More southerly stands of Oregon white oak respond negatively to temperatures in the summer, especially in July. Furthermore, the lower the latitude at which a stand is located, the more negatively the trees tend to respond to average maximum temperatures in the fall and winter prior to growth, especially in February, and in spring during the growing season. Sites at lower latitudes tend to respond more positively to precipitation in these same seasons: fall, winter, and spring. Related to these patterns of dendroclimatic response is the increasing importance of moisture availability at lower latitudes, highlighting the mixed response of Oregon white oak. Responses to the quasi-periodic forcings are mostly coherent, but some variation occurs.

The first significant empirical orthogonal function describes a pattern of response very similar to that identified by the correlation function analyses. This characteristic dendroclimatic pattern in Oregon white oak is one which accounts for 67 percent of all the variation in the ring-width indices and on which all sites load heavily. The first significant principal component of the empirical orthogonal functions analysis conducted on the correlation functions captures much of the same pattern, especially the dominance of spring moisture availability in controlling growth. This relationship accounts for 27 percent of the variation in the stands' climatic response, again a principal component on which all sites load strongly. Two other principal components representing Oregon white oak's patterns of dendroclimatic response are also significant, both of which relate most strongly to the response of these trees to minimum temperatures and the soil moisture availability.

This growth-climate model is one part of the realized niche of Oregon white oak. Oregon white oak stands express a characteristic dendroclimatic response throughout the year with correlations during spring being the strongest and associated with the most synchronous responses. While this dendroclimatic pattern is characteristic of most Oregon white oak stands, the relative importance of climatic controls varies according to geographic position. Correlations between ring-width indices and local climatic variables suggest underlying climatic mechanisms. Quantifying these responses in a spatial framework and assessing their coherence contributes to a better understanding of how the specific geographies of the sites alter the influence of climate on the growth of individual trees.

Conclusions Chapter 5

This thesis emphasizes both the coherence and complexity of Oregon white oak's dendroclimatological response and the value of viewing the growth-climate relationship of a tree species in terms of a stand's geographic context. Dendroecological techniques help document the ways in which climate influences the growth of Oregon white oak, identifying a characteristic response of the species to climatic variability. The relative importance of climatic factors in controlling Oregon white oak's radial-growth, however, varies throughout the species' natural range according to a site's ecogeographic situation. Findings resulting from this study contribute to biogeographic scholarship, facilitating the understanding of patterns and processes relating to Oregon white oak's growth and distribution, providing insight into temperate forest-grassland dynamics as they relate to climate, and leading to more accurate species and ecosystem modeling important for both resource and conservation management efforts.

Synthesis of findings

Correlations between the 18 Oregon white oak tree ring chronologies and their local climates are very similar, reflecting the physiological tolerances of the species. Evidence that Oregon white oak responds coherently as a species comes from the correlation function and principal components analyses. The correlation function analyses uncovered a complex spring growth response to temperature, precipitation, and moisture availability. The principal components analysis performed on the matrix of ring-width indices showed that much of the variation in annual radial-growth is controlled by climate, 67%, and that all stands respond similarly in a characteristic white oak pattern.

The second principal components analysis, that performed on the correlation functions, showed that this pattern of growth is strongly associated with soil moisture availability in the spring during ring formation, but that climatic influences in other seasons are also important in controlling growth, especially minimum temperatures.

The growth-response of Oregon white oak trees is one dominantly controlled by spring conditions. A temporally complex growth-response to spring temperatures occurs, with trees at most sites responding positively to temperatures in April and May of the year prior to growth but negatively to maximum temperatures during June in the year that the ring is formed. A positive response to spring rainfall is consistent in stands throughout the range of the species. The strongest correlations found in this study are the positive growth associations with soil moisture availability in winter, spring, and summer.

However, a higher degree of variability in growth-response to some climatic variables shows that some Oregon white oak stands do not respond in the same way to all climatic forcings: differences in the timing, direction, and magnitude of growth-responses between stands to the same climatic factors indicate a mixed response (Brubaker 1980; Pilcher and Gray 1982; Gedalof and Smith 2001a; Lloyd and Fastie 2002; Carrer et al. 2007). Spatial patterns include latitudinal gradients: stands at lower latitudes tend to respond more negatively to maximum temperatures and more positively to precipitation and soil moisture availability in fall, winter, and spring. Northern sites respond more positively to temperatures in winter. Longitudinal gradients in response reflect the influence of drier continental climates and extreme diurnal and seasonal variability: more easterly sites respond more positively to minimum temperatures in the spring and in the fall than other Oregon white oaks west of the Cascade Mountains. The radial-growth response reflects the interaction of local climate with the ecogeographic position of the stand, and so suspected mechanisms vary by site (Brubaker 1980; Villalba 1992).

Biogeographic scholarship

An identification of the extent to which climate controls the growth of Oregon white oak provides insight into long-term biogeographical and ecological processes relevant to this species and its ecosystem as well as the underlying environmental determinants of Oregon white oak distribution. Some patterns become evident by examining processes at larger and longer scales such as those assessed here.

Information about this species’ growth-climate relationship provides insight into the vegetation dynamics of Pacific North America and is crucial for understanding local and regional controls on the species’ growth and distribution. While the study is specific to the growth-climate relationship of Oregon white oak, knowledge of the underlying environmental determinants of Oregon white oak's growth and extending this to trees in other regions, especially deciduous oak species, may add to the understanding of other forests’ distribution patterns, the processes that control them, the spatial and temporal nature of ecotones, and the semi-successional development of woodland from savanna. Furthermore, by exploring growth responses to commonly available ecophysiologically-relevant climate proxies, this research also assesses the importance of temperature, precipitation, and moisture availability in phytogeography. These findings exemplify the complex manner in which climate can affect a species’ growth and distribution.

The direct ecophysiological effects of climatic change on these ecosystems are complex in part because the growth of oak trees is influenced by temperature, shifting precipitation patterns, and corresponding changes in the region’s water balance. Seasonal variability is important, as wetter winters and drier summers combined with year-round warming will likely decrease the water available to plants even with increased rainfall (Mote 2003; Mote et al 2005; Barnett et al 2005), especially in moisture-limited systems. The longevity of this tree species plus facilitation and inhibition by associated organisms result in ecological inertia: an ecosystem's persistence beyond its bioclimatic envelope. Thus, changes due to the environment may not be readily apparent. However, climatic change does not occur in isolation (Hannah et al. 2002), so the spatially-fragmented habitats, limited dispersal abilities of Oregon white oak, and the projected rapid changes in climate may exacerbate this species' decline on the landscape. As an indicator of future climatic response at decadal scales, the response of Oregon white oak to the Pacific Decadal Oscillation may loosely mimic the species' response to future warming projected for 2040 (IPCC 2007). As most stands show increased growth during warm phases of the PDO, we speculate that many of these Oregon white oak stands will show increased growth under short-term future climate change scenarios due to rising minimum and winter temperatures (IPCC 2007). However, increased evapotranspiration in spring and summer will strongly limit growth, especially in populations at lower latitudes, lower elevations, and on xeric sites. Threshold responses not identified in this thesis may cause mortality.

The analyses presented here assume linear relationships between growth and climatic variables, threshold values are not considered. Still, these findings illuminate aspects of temperate forest-grassland dynamics and support the use of physiologically based models to inform projections of future growth response, stand structure, and distribution. The coherent response to some climatic variables helps validate methods employed in pattern-based bioclimatic envelope models and those used in reconstructing climate based on a tree's growth-climate relationship (e.g., Iverson and Prasad 1998; Shafer et al. 2001). Identifying Oregon white oak's characteristic response to climatic variability facilitates reconstructions of climate, but the mixed-response evident here leads to questions about the use of inferring a species' growth-climate relationship from any chronology derived from a single site without regard to its biogeographic position. Furthermore, synergistic effects between climate and a stand's ecology will play a role in its dendroclimatic response (e.g., mycorrhizal associates, invasive plants in the understory, changes in fire regime). These influences may facilitate or inhibit the growth of Oregon white oak in complex and interacting ways. Oregon white oak as a species may have broader climatic tolerances than it currently experiences, and so for this reason pattern-based and process-based models may underestimate the ability of the species to respond to impending changes in climate. It is important to note that although climate may not be limiting to the radial-growth of a mature Oregon white oak tree, conditions may still be beyond the ecophysiological tolerances of the plant at other life-history stages (e.g. seedling) and may limit reproduction or establishment.

Ecosystem management

The future of this ecosystem is uncertain in part because its dynamics have not been well understood, and this limits the effectiveness of management models. Organizations in both the United States and Canada aim to preserve remaining Oregon white oak stands by conducting research, establishing reserves, and mitigating factors contributing to the deterioration of the stands (GOERT 2002). An understanding of Oregon white oak at the level required for management should consider the unique geography of the species at multiple scales in space and time, so important for both resource management and the conservation of these unique ecosystem types is the identification of species-specific climatic controls on growth at the stand-scale.

Dendrochronological methods shed light on the complex ecological and environmental tolerances of the species and establish a baseline of variability in Oregon white oak’s radial growth, quantifying the sensitivity of the tree to its recent climate. This is some of the regional, site, and species-specific information needed to help mitigate the effects of a changing climate on the species and its associated ecosystems. Study sites likely to be suitable for long-term growth and conservation can now be more accurately identified, as can those sites where non-climatic factors play large roles. Oregon white oak's climatic response may be indicative of associated species’ response to ecological and climatic variability, although this transferability should be applied with caution since species tend to respond individualistically to shifts in climate.

Ecosystems with foundation species are often managed too late and at inappropriate scales (Ellison et al. 2005), especially when the habitat losses occur in a mosaic like these oak ecosystems rather than in a continuous wave-like manner, and this can exacerbate an ecosystem's threshold responses (Gosz 1993; Thysell and Carey 2001). The pattern of decline in space will influence ecosystem function (Ellison et al. 2005). Populations of Oregon white oak are especially vulnerable to the synergy between climate change and fragmentation, due in part to their large seeds and consequent dependence on animal dispersal, so this analysis plays an essential part in the understanding, predicting, and managing of these ecosystems.

Findings from this research allow a more accurate assessment of the integrity of particular oak ecosystems at longer time scales: setting restoration goals and facilitating the discrimination of sites suitable for conservation efforts. Sampling a number stands in different ecoregions can improve estimates of other stands' likely responses within the same ecoregion. Successful management of sustainable Oregon white oak populations will certainly benefit from knowledge of the growth-climate relationship of the species as well as the role that site geography plays in mediating climatic influences.

Works Cited

Abrams, M.D. (1990). Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology 7:227-238.

Abrams, M.D. (1996). Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Ann. Sci. For. 53(:2–3): 487–512.

Abrams, M.D. (2003). Where Has All the White Oak Gone? BioScience: Vol. 53(10): 927–939.

Abrams, M. D., M. E. Kubiske, and S. A. Mostoller (1994). Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology 75:123-133.

Adams, H. D. and T. E. Kolb (2004). Drought responses of conifers in ecotone forests of northern Arizona: tree ring growth and leaf C^{13}. Oecologia 140:217-225.

Adler, P. B. and J.M. Levine (2007). Contrasting relationships between precipitation and species richness in space and time. Oikos 116:221-232.

Agee, J. K. (1993). *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, D.C.

Agee, J. K. (1996). Achieving conservation biology objectives with fire in the Pacific Northwest. Weed Technology 10:417-421.

Akkemik U., R. D'Arrigo, P. Cherubini, N. Kose, and G.C. Jacoby (2007). Tree-rings reconstructions of precipitation and streamflow for northwestern Turkey. Int J Climatol., in press.

Akkemik, U., H. Cinar Yilmaz, and O. Sevgi (2006). Cambial Activity of the Sessile Oak (*Quercus petraea*) in Belgade Forest, Istanbul. Turk J Agric For 30:429-438.

Allen, C. D. and D. D. Breshears (1998). Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climatic variation. Proc Natl Acad Sci USA 95:14839-14842.

Allen, G.B., K.J. Brown, and R.J. Hebda (1999). Surface pollen spectra from southern Vancouver Island, British Columbia, Canada. Canadian Journal of Botany. 77(6):786–799.

Anderson, Stanley H. (1972) Seasonal variations in forest birds of western Oregon. Northwest Science 46 (3):194-206.

Anderson, R.C., J.S. Fralish, and J.M. Baskin, eds. (1999). *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge University Press, Cambridge, United Kingdom.

Aranda I., L. Castro, M. Pardos, L. Gil, J.A. Pardos (2005). Effects on the interaction between drought and shade on water relations, gas exchange and morphological traits in cork oak (*Quercus suber* L.) seedlings. Forest Ecology and Management 210: 117-129.

Araújo M.B. and R.G. Pearson (2005). Equilibrium of species' distributions with climate. Ecography 28: 693–695.

Archibold, O.W. (1995). *Ecology of World Vegetation*, Chapman & Hall, London.

Arora, D. (1986). *Mushrooms Demystified*. Ten Speed Press, Berkley, California.

Avise, J.C. (2001). Comparative phylogeography as an integrative approach to historical biogeography. Journal of Biogeography 28: 819-825.

Bachelet, D., R.P. Neilson, J.M. Lenihan, and R.J. Drapek (2001). Climate change effects on vegetation distribution and carbon budget in the U.S. Ecosystems 4:164–185.

Baldocchi, D. and R. Valentini (2004). Geographic and Temporal Variation of the Mechanisms Controlling Carbon Exchange by Ecosystems and their Sensitivity to Environmental Perturbations. In: Towards CO2 stabilization: Issues, Strategies and Consequences, A SCOPE/GCP Rapid Assessment Project. Chris Field and Michael Raupach, eds. pp 295-316.

Barlow, M., S. Nigam and E.H. Berbery (2001). ENSO, Pacific Decadal Variability, and U.S. Summertime Precipitation, Drought, and Stream Flow. Journal of Climate 14(9):2105-2128.

Barnett, T. P., J.C. Adams, and D.P. Lettenmaier (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303-309.

Barnhart, S. J., J.R. McBride, C. Cicero, P. da Silva, and P. Warner (1987). Vegetation dynamics of the northern oak woodland. pp. 53-58 in T. R. Plumb and N. H. Pillsbury (eds.) Proceedings of the symposium on multiple-use management of California's hardwood resources. USDA Forest Service General Technical Report PSW GTR-100. Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Barnhart, S.J., J.R. McBride, and P. Warner (1996). Invasion of northern oak woodlands by Pseudotsuga menziesii Mirb. Franco in the Sonoma mountains of California. Madroño 43:28-45.

Barry, R.G. and A.M. Carleton. (2001). Synoptic and dynamic climatology. Routledge, London and New York. 2001. 620 pp.

Bartolome, J.W., J.S. Fehmi, R.D. Jackson and B. Allen-Diaz (2004). Response of a native perennial grass stand to disturbance in California's Coast Range grassland. Restoration Ecology, 12, 279–289.

Biondi, F. and T.W. Swetnam (1987). Box-Jenkins models of forest interior tree-ring chronologies. Tree-Ring Bulletin 47: 71-96

Biondi, F., A. Gershunov, and D. Cayan (2001). North Pacific decadal climate variability since AD 1661. J. Clim. 14, pp. 5–10.

Biondi F., J. Kozubowski, A.K. Panorska, K.T. Redmond, and S. Strachan (2004). Drought Risk Estimation from Tree Rings. Abstracts of the Mountain Climate Sciences Symposium, South Lake Tahoe, California.

Blasing, T.J., D.N. Duvick, and D.C. West (1984). Dendroclimatic calibration and verification using regionally averaged and single station precipitation data. Tree-Ring Bulletin 41: 37-43.

Bond, N.A. and D.E. Harrison (2000). The Pacific Decadal Oscillation, air-sea interaction and central north Pacific winter atmospheric regimes. Geophys. Res. Lett. 275: 731-734.

Briffa, K.R. (1995). Statistical aspects of the interpretation of high-resolution proxy climate data: the example of dendroclimatology. In: *Analysis of Climate Variability: Applications of Statistical Techniques*. H. von Storch and A. Navarra, eds., pp.77-94. Springer, Berlin.

Briffa, K.R. and Wigley, T.M.L. (1985). Soil moisture reconstruction using tree-rings. Climate Monitor 14, 106-113 Climatic Research Unit, University of East Anglia, Norwich, UK.

Brown, J.H. (1999) Macroecology: progress and prospect. Oikos 87: 3–14.

Brown, JR, and S. Archer (1990). Water relations of a perennial grass and seedling versus adult woody plants in a subtropical savanna, Texas. Oikos 57:366-374.

Brown, K.J. and R.J. Hebda. (2002a). Ancient fires on southern Vancouver Island, British Columbia, Canada: A change in causal mechanisms at about 2,000 ybp. Environmental Archaeology 7:1-12.

Brown, K.J., and R.J. Hebda. (2002b). Origin, development, and dynamics of coastal temperate conifer rainforests of southern Vancouver Island, Canada. Canadian Journal of Forest Research 32:353–372.

Brudvig, L.A., and I. Asbjornsen (2005). Oak regeneration before and after initial restoration efforts in a tall grass oak savanna. American Midland Naturalist 153:180-186.

Brubaker L.B. (1980). Spatial patterns of tree growth anomalies in the Pacific Northwest. Ecology 61: 798–807.

Brubaker, L.B., (1986). Responses of tree populations to climatic change. Vegetation 68:119-130.

Buckley, B.M., E.R. Cook, M.J. Peterson, M. Barbetti, (1997). A changing temperature response with elevation for *Lagarostrobos Jrankhnii* in Tasmania, Australia. Climatic Change 5:477-498.

Buckley, B.M., R.J.S. Wilson, P.E. Kelly, D.W. Larson, and E.R. Cook (2004). Inferred summer precipitation for southern Ontario to AD 610, reconstructed from ring widths of Thuja occidentalis. Canadian Journal of Forest Research 34: 2541-53.

Cane M. (2004). The evolution of El Nino, past and future. Earth and Planetary Science Letters 164: 1–14.

Castello A, Shelton M (2004) Winter precipitation on the US Pacific coast and El Niño-Southern Oscillation events. International Journal of Climatology, 24, 481–497.

Carrer, M. and C. Urbinati (2003). Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. Ecology, 85(3): 730-740.

Carrer M., P. Nola, J.L. Eduard, R. Motta, and C. Urbinati (2007). Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. Journal of Ecology 95: 1072-1083.

Cayan, D.R., M.D. Dettinger, H.F. Diaz, and N.E. Graham, (1998): Decadal climate variability of precipitation over western North America. *J. of Clim*., 11(12): 3148-3166.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio, and D.H. Peterson (2000). Changes in the Onset of Spring in the Western United States. Bulletin of the American Meteorological Society, Vol. 82(3), 399-415.

Cedro, A. (2007). Tree-Ring Chronologies of Downy Oak, Pedunculate Oak, and Sessile Oak in the Bielinek Nature Reserve: Comparison of the Climatic Determinants of Tree-Ring Width. Geochronometria 26:1733-8387.

Chapin, S.F., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman. (1997). "Biotic control over the functioning of ecosystems". in: Science 277:500-504.

Chapin, S., F. Osvaldo, E. Sala, I. C. Burke, J. P. Grime, D. U. Hooper, W. K. Lauenroth, A. Lombard, H. A. Mooney, A. R. Mosier, S. Naeem, S. W. Pacala, J. Roy, W. L. Steffen, D. Tilman. (1998). Ecosystem Consequences of Changing Biodiversity. BioScience 48(1): 45-52.

Chesson, P.L. and Robert R. Warner (1981). Environmental Variability Promotes Coexistence in Lottery Competitive Systems. *The American Naturalist* 117(6): 923-943.

Chhin, S., G. G. Wang, and J. Tardif. (2004). Dendroclimatic analysis of White Spruce at its Southern Limit of Distribution in the Spruce Woods Provincial Park, Manitoba, Canada. Tree-Ring Research 601: 31-43.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr and P. Whetton (2007) In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, Eds., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Christopherson, R.W. (2005). *Geosystems: An Introduction to Physical Geography*. Prentice-Hall Canada, Inc., Toronto, Canada.

Churkina, G. and Y. Suirezhev (1995). Dynamics and forms of ecotone under the impact of climatic change: mathematical approach. Journal of Biogeography 22(2/3): 565-569.

Cochard and M. T. Tyree. (1990). Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. Tree Physiology 6: 393–407.

Cole, D. (1977). Ecosystem dynamics in the coniferous forest of the Willamette Valley, Oregon, U.S.A. Journal of Biogeography 4: 181-192.

Cole, M. M. (1986). *The Savannas: Biogeography and Geobotany*. Academic Press Inc., London, UK.

Cole, K.L., J. Fisher, S.T. Arundel, J. Cannella, and S. Swift (2008). Geographical and climatic limits of needle types of one- and two-needled pinyon pines. Journal of Biogeography 35: 257-269.

Connell, J.H. (1978). Diversity in tropical rain forest and coral reefs. Science 199:1302-1310.

Cook, E.R. and Briffa, K.R. (1990) in *Methods of Dendrochronology* eds. Cook, E. R. & Kairiukstis, L. A. 153−162.

Cook E.R., and R.L. Holmes (1986). Users manual for Program ARSTAN. In: Holmes RL, Adams RK, Fritts HC, editors. Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Chronology Series VI, Laboratory of Tree-Ring Research, University of Arizona. p. 50–60.

Cook, E. R., and R. L. Holmes (1996). ARSTAN: Chronology development.75–87. in H. D. Grissino-Mayer, R. L. Holmes, and H. C. Fritts, editors. The international tree-ring data bank program library version 2.0 user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.

Cook, E.R. and Kairiukstis, L.A., (1990). In: *Methods of Dendrochronology*, Kluwer Academic Publishing, Boston 394 pp .

Cook, E.R. and P.J. Krusic (2005). Program Arstan, a tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. Tree-ring Laboratory Lamont Doherty Earth Observatory of Columbia University, Palisades, NY.

Cook, E.R. & Peters, K. (1981) The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree Ring Bulletin 41: 45–53.

Cook, E. R., and K. Peters. (1997). Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7: 361–370.

COSEWIC (2003). COSEWIC Assessment Results, November 2003. Committee on the Status of Endangered Wildlife in Canada. 44 pp.

Cox, C.B. and P.D. Moore (2005). *Biogeography: An Ecological and Evolutionary Approach*. Seventh ed. Blackwell Publishing, Malden, Massachusetts, USA.

Cropper, J.P. 1982. Climate Reconstructions (1801 to 1938) inferred from Tree-Ring Width Chronologies of the North American Arctic. Arctic and Alpine Rsearch 14(3): 223-241.

Cullen L.E., J.G. Palmer, R.P. Duncan, and G.H. Stewart (2001). Climate change and tree-ring relationships of Nothofagus menziesii tree-line forests. Can J For Res 31: 1981–1991.

Curtis, J. T. (1959). *Vegetation of Wisconsin*. University of Wisconsin Press, Madison.

Dai A, Trenberth KE, Qian T (2004). A global data set of Palmer drought severity index for 1870–2002: relationships with soil moisture and effects of surface warming. Journal of Hydrometeorology 5: 1117-1130.

Dalen, L., and A. Hofgaard (2005). Differential regional treeline dynamics in the Scandes Mountains. Arctic, Antarctic, and Alpine Research, 37(3): 284-296.

Daly, C., R.P. Neilson, and D.L. Phillips (1994): A Statistical-Topographic Model for Mapping Climatological Precipitation over Mountanious Terrain. J. Appl. Meteor. 33: 140-158.

Daly, C., G. Taylor, and W. Gibson (1997). The PRISM Approach to Mapping Precipitation and Temperature, 10th Conf. on Applied Climatology, Reno, NV. Amer. Meteor. Soc. 10-12.

D’Arrigo, R., G. Jacoby, et al. (1999). Northern hemisphere temperature variability for the past three centuries: tree-ring and model estimates. Climatic Change 42: 663 - 675.

D ’Arrigo R, Villalba R, Wiles G (2001). Tree-ring estimates of Pacific decadal climate variability. Climate Dynamics 18:219–224

D ’Arrigo R, Yamaguchi D, Wiles G, Jacoby G, Osawa A, Lawrence D (1997). A Kashiwa oak (*Quercus dentata*) tree-ring width chronology from northern coastal Hokkaido, Japan. Can J For Res 27:613–617

Daubenmire, R. (1968). *Plant Communities: A Textbook of Synecology*. Harper and Row, New York. 300 pp.

Davy, L.E. (2008). *TheInfluence of Competitive Interactions on Soil Moisture Dynamics in an Invaded Garry Oak Savanna.* MSc Thesis, University of Guelph, Guelph, Ontario.

Delcourt, P. A., and H. R. Delcourt (1992). Ecotone dynamics in space and time. BioScience 45(5): 19-54.

Dettinger, M.D., D.R. Cayan, H.F. Diaz, and D.M. Meko, (1998): North-south precipitation patterns in western North America on interannual-to-decadal time scales. J. Clim., 11(12), 3095-3111.

Devine, W. D. and C. A. Harrington (2005). Root System Morphology of Oregon White Oak on a Glacial Outwash Soil. Northwest Science 79(2 and 3): 179-189.

Devine, W. and C. Harrington (2006). Changes in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) following release from overtopping conifers. Trees 20:747-756.

Dewitt, E. and Ames, M. (1978). Tree-ring chronologies of Eastern North America. Chronology Series IV, vol. 1. Laboratory of Tree-ring Research. University of Arizona, Tucson, AZ.

di Castri, F., A. J. Hansen, and M. M. Holland (1988). *A new look at ecotones*. Biology International Special Issue 17.

Douglass, A.E. (1920). Evidence of climatic effects in the annual rings of trees, Ecology 1, pp. 24–32.

Du, S., N. Yamanaka, Fukuju Yamamoto, Kyoichi Otsuki, Shengqi Wang and Qingchun Hou. The effect of climate on radial growth of *Quercus liaotungensis* forest trees in Loess Plateau, China 2007. Dendrochronologia 25:(1) 29-36.

Dunwiddie, P. (2002). Management and restoration of grasslands on Yellow Island, San Juan Islands. Pages 78–87 In: Garry oak ecosystem restoration: progress and prognosis. British Columbia Chapter of the Society for Ecological Restoration, P. Burton, ed., Victoria, Canada.

Easterling D.R., G.A. Meehl, C. Parmesan, S.A. Changnon, T.R. Karl, and L.O. Mearns. Climate extremes: Observations, modeling, and impacts. Science. 289:2068–2074.

Ebenman, B. and T. Jonsson (2005). Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20: 568– 57.

Eckstein, D. and E. Frisse (1982). The influence of temperature and precipitation on vessel area and ring width of oak and beech. In Hughes, M. K., Kelly, P. M., Pilcher, J. R., LaMarche Jr, V. C. (eds.), Climate from Tree Rings. Cambridge: Cambridge University Press, p. 12.

Eldridge, N. 1998. *Life in the balance: humanity and the biodiversity crisis*. Princeton, NJ: Princeton University Press.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. V. Holle, J. R. Webster (2005). Loss of foundation species: consequences for structure and dynamics of forested ecosystems. Front Ecol Environ 3(9):479-486.

Enfield, D.B., A.M. Mestas-Nunez, and P.J. Trimble (2001). The Atlantic Multidecadal Oscillation and its relationship to rainfall and river flows in the continental U.S. Geophys. Res. Lett., 28: 2077-2080.

Erickson, W. (2000). Garry oak communities in Canada: classification, characterization and conservation. International Oaks 10:40-54.

Erickson, W. R. (2002). Environmental Relationships of Native Garry oak (*Quercus Garryana*) Communities at Their Northern Margin. Pages 179-190 in U.S.D.A., ed. Forest Service Gen. Tech. Rep. PSW-GTR-184.

Ettl, G. J. and D. L. Peterson (1995). Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). Global Change Biology 1: 231 - 241.

Farrar, J.L. 2006. *Trees in Canada.* Fitzhenry and Whiteside Ltd., Markham, Ontario, Canada.

Field, C.B., L.D. Mortsch,, M. Brklacich, D.L. Forbes, P. Kovacs, J.A. Patz, S.W. Running and M.J. Scott, (2007). North America. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of theIntergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, UK, 617-652.

Foley J.A., R. Defries, G.P. Asner, C. Barford, G. Bonan, S.R. Carpenter, F.S. Chapin, M.T. Coe, G.C. Daily, H.G. Gibbs. (2005). Global Consequences of Land Use. Science 309:570–574.

Foster, J.R. and D.C. LeBlanc, (1993). A physiological approach to dendroclimatic modelling of oak radial growth in the Midwestern United States. Canadian Journal of Forest Research, 23, 783–798.

Foster, B. L., and D. Tilman (2003). Seed limitation and the regulation of community structure in oak savanna grassland. Journal of Ecology 91:999-1007.

Fralish, J.S. (2004). The Keystone Role of Oak and Hickory in the Central Hardwood Forest. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. pp. 78-87.

Franklin, J.F. and C.T. Dyrness (1988). Natural vegetation of Oregon and Washington. USDA Forest Service, General Technical Report PNW-8. Portland, OR.

Franklin, J.F., F.J. Swanson, M.E. Harmon, D.A. Perry, T.A. Spies, V.H. Dale, A. McKee, W.K. Ferrell, J.E. Means, S.V. Gregory, J.D. Lattin, T.D. Schowalter, and D. Larsen (1991). Effects of global climatic change on forests in northwestern North America. Northwest Environmental Journal 7:233-254.

Franks, J. (2007). *Competition Effects on Drought Sensitivity of Oregon White Oak (Quercus garryana) and Douglas-fir (Pseudotsuga menziesii).* MSc Thesis, University of Guelph, Guelph, Ontario.

Fritts, H. C. (1962). The relation of growth ring widths in American beech and white oak to variations in climate. Tree-Ring Bull. 25: 2-10.

Fritts, H. C. (2001). *Tree Rings and Climate*. Blackburn Press, Caldwell, New Jersey, USA.

Fritts, H. C., and T. W. Swetnam (1989). Dendroecology: a tool for evaluating variations in past and present forest environments. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA.

Fuchs, M.A., P.G. Krannitz, and A.S. Harestad (2000). Factors affecting emergence and first-year survival of seedlings of Garry oaks Quercus garryana in British Columbia, Canada. Forest Ecology and Management 137:209-219.

Fuchs, M.A. (2001). Towards a Recovery Strategy for Garry Oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review. Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region.

Gamache I. & Payette S. (2004) Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. Journal of Ecology 92: 835–845.

Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press, New York.

Gaston, K.J., S.L. Chown, and K.L. Evans (2007). Ecogeographical rules: elements of a synthesis. Journal of Biogeography 35(3): 483-500.

Gavin D.G., D. Hallett, F.S.Hu, K. Lertzman, S.J. Prichard, K.J. Brown, J.A. Lynch, P. Bartlein, and D.L. Peterson (2007). Forest fire and climate change: Insights from sediment charcoal records. Frontiers in Ecology and the Environment 5: 499-506.

Gedalof, Z. and A..A. Berg *in review*. Evidence for limited CO2 fertilization of forests over the 20th century.

Gedalof, Z. and D. J. Smith (2001a). Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America. Canadian Journal of Forest Research 31: 322-332.

Gedalof, Z. and D. J. Smith (2001b). Interdecadal climate variability and regime-scale shifts in Pacific North America. Geophysical Research Letters 288: 1515 - 1518.

Gedalof, Z., N.J. Mantua and D.L. Peterson (2002). A multi-century perspective of variability in the Pacific Decadal Oscillation: new insights from tree rings and coral. Geophysical Research Letters, Vol. 29, No. 4, p. 2204.

Gedalof, Z., M.G. Pellatt, D.H. Lewis and D.J. Smith (2004). Paleoenvironmental Analysis of Garry Oak Ecosystems on Southern Vancouver Island. Paleoecology Laboratory, University of Guelph. Report #0402.

Gedalof, Z., D.L. Peterson, and N.J. Mantua (2005). Atmospheric, climatic and ecological controls on extreme wildfire years in the northwestern United States. Ecological Applications. 15: 154 - 174.

Gedalof, Z., D.L. Peterson and D.J. Smith (2006). From prairie to forest: three centuries of environmental change at Rocky Point, Vancouver Island, B.C. Northwest Science, Vol. 80, No. 1, pp. 34-46.

Gershunov, A. and T. Barnett (1998). Interdecadal modulation of ENSO teleconnections. Bulletin of the American Meteorological Society Vol. 79: pp 2715-2726.

Gilkey, H.M. and L.R.J. Dennis (2001). *Handbook of Northwestern plants*. Rev. Corvallis, OR: Oregon State University. 494 p.

Glantz, M.H. (1998). A La Niña Summit: A Review of the Causes and Consequences of Cold Events. Executive Summary of the workshop held 15-17 July 1998 in Boulder, Colorado. Environmental and Societal Impacts Group, NCAR: Boulder, Colorado.

GOERT (2002). Recovery Strategy for Garry Oak and Associated Ecosystems and their Associated Species at Risk in Canada, 2001 - 2006. Garry Oak Ecosystem Recovery Team.

GOERT (2008). Website: http://www.goert.ca/, Accessed: August 1, 2008.

Goldblum, D. and L. S. Rigg (2005). Tree growth response to climate change at the deciduous-boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research 35: 2709-2718.

Garcia-Gonzalez, I.G. and D. Eckstein (2003). Climatic signal of earlywood vessels of oak on a maritime site, *Tree Physiology* 23: 497–504.

Gosz, J.R. (1993). Ecotone Hierarchies. Ecological Application 3(3): 369-376.

Graumlich, L.J. and L.B. Brubaker (1986). Reconstruction of annual temperature 1590 - 1979 for Longmire, Washington, derived from tree rings. Quaternary Research 25: 223 - 234.

Graumlich, L.J. (1987). Precipitation variation in the Pacific Northwest (1675-1975) as reconstructed from tree rings. Annals of the Association of American Geographers. 77: 19-29.

Graumlich, L.J. (1991). Subalpine tree growth, climate, and increasing CO_2: an assessment of recent growth trends. Ecology 72: 1–11.

Graumlich, L.J. (1993). A 1000-year record of temperature and precipitation in the Sierra Nevada. Quaternary Research 39: 249 - 255.

Gray, S.T., J.L. Graumlich, J.L. Betancourt, and G.T. Pederson (2004): A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. Geophysical Research Letters.

Gray, S.T., J.L. Betancourt, C.L. Fastie and S.T. Jackson (2003). Patterns and sources of multi-decadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. Geophysical Research Letters 30:491-494.

Grime, J.P.(1973). Competitive exclusion in herbaceous vegetation, Nature 242, pp. 344–347.

Grime J.P. (1979). *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.

Grissino-Mayer, H.D. and H.C. Fritts (1997). The international tree-ring data bank: an enhanced global database serving the global scientific community, The Holocene 7: 235–238.

Grissino-Mayer, H.D. (2001). Evaluating cross-dating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57: 205–221.

Grivet, D., M.F. Deguilloux, R.J. Petit, and V.L. Sork (2006). Contrasting patterns of historical colonization in white oaks (*Quercus* spp.) in California and Europe. Molecular Ecology 15: 4085-4093.

Guiot, J. (1986). ARMA techniques for modelling tree ring response to climate and for reconstructing variations in paleoclimates. Ecological Modelling 33: 149-171.

Guyette, R.P., R.M. Muzika, J. Kabrick, M.C. Stambaugh (2004). A Perspective on *Quercus* Life History Characteristics and Forest Disturbance. In: Spetlich, M. A., ed. Upland oak ecology symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station. 311 p.

Hacke, U. and J.J. Sauter (1996). Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* and *Alnus glutinosa*. Plant Physiology 111: 413-417.

Hagar, J.C. and M.A. Stern (2001). Avifauna in Oak Woodlands of the Willamette Valley, Oregon. Northwestern Naturalist, Vol. 82, No. 1, pp. 12-25.

Halpern, C.B., D. McKenzie, S.A. Evans (2005). Initial responses for forest understories to varying levels of green tree retention. Ecological Application 15: 175-195.

Hamburg S.P. and C.V. Cogbill (1988). Historical decline of red spruce populations and climatic warming. Nature 331: 428-431.

Hamann, A., and T. Wang (2006). Potential Effects of Climate Change on Ecosystem and Tree Species Distribution in British Columbia. Ecology 87:2773-2786.

Hannah, L., T. Lovejoy, G. Midgley, W. Bond, M. Bush, J. Lovett, D. Scott, I. Woodward (2002). Conservation of Biodiversity in a Changing Climate. Conservation Biology 16:11-17.

Hansen A.J. and F. di Castri (1992). *Landscape Boundaries, Ecological Studies*, Springer-Verlag, New York.

Hansen, A.J., R.P. Neilson, V.H. Dale, C.H. Flather, L.R. Iverson, D.J. Currie, S. Shafer, R. Cook, and P.J. Bartlein (2001). Global Change in Forests: Responses of Species, Communities, and Biomes. BioScience 51(9): 765-779.

Hanson P.J, and J.F. Weltzin (2000). Drought disturbance from climate change response of United States forests. Science of the Total Environment. 262:205–220.

Harrington, C.A. (2002). Oak forest ecosystems: ecology and management for wildlife. Forest Science. 484: 792-793.

Hebda, R. and G. Allen (1993). Origin and history of the Garry oak-meadow system. In: R.J. Hebda and F. Aitkens, eds. Garry Oak-Meadow Colloquium Proceedings.

Hebda, R.J., K. Gustavson, A. Golinski and M. Calder (2000). Burns Bog Ecosystem Review Synthesis Report for Burns Bog, Fraser River Delta, South-western British Columbia, Canada. Environmental Assessment.

Heikkinen, O. (1984). Dendrochronological evidence of variations of Coleman Glacier, Mount Baker, Washington, USA. *Arctic Alpine Res.* 16: 53–64.

Heim, R.R. (2002). A Review of Twentieth Century Drought Indices Used in the United States, Bull. Amer. Meteorol. Soc. 83, 1149–1165.

Hessl, A.E., D. McKenzie and R. Schellhaas (2004). Fire and climatic variability in the inland Pacific Northwest. Ecological Applications 14(2): 425-442.

Heyerdahl, E.K., Brubaker, L.B. and Agee, J.K. (2002). Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. The Holocene: 12(5): 597-604.

Hibbs, D.E., and B.J. Yoder (1993). Development of Oregon White Oak Seedlings. Northwest Science 67:30-36.

Hidalgo, H.G., T.C. Piechota, and J.A. Dracup (2001). Alternative Principal Components Regression Procedures for Dendrohydrologic Reconstructions. Water Resources Research 36:3241-3249.

Hitchcock, C.L., and A. Cronquist (1973). *Flora of the Pacific Northwest: an illustrated manual*. University of Washington Press, Seattle.

Holland, M.M., P.G. Risser, and R.J. Naiman, eds. (1991). *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments.* Chapman & Hall, New York.

Holman, M.L. and D.L. Peterson (2006). Spatial and temporal variability in forest growth in the Olympic Mountains, Washington: sensitivity to climatic variability. Can. J. For. Res. 36(1): 92–104.

Holmes, R., (1983). Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 44, pp. 69–74.

Howard, J.L. (2002). *Quercus garryana*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Fire Effects Information System.

Hughes M.K., B. Gray, J. Pilcher, M. Baillie, and P. Leggett (1978). Climatic signals in British Isles tree-ring chronologies. Nature, 272: 605-606.

Huntley, B.P., M. Berry, W. Cramer, and A.P. McDonald (1995). Special Paper: Modelling Present and Potential Future Ranges of Some European Higher Plants Using Climatic Response Surfaces Journal of Biogeography 22(6): 967-1001.

IPCC. (2007). Intergovernmental Panel on Climate Change. Climate Change 2007: The IPCC Fourth Assessment Report. Cambridge, United Kingdon: Cambridge University Press.

Iverson, L.R. and A.M. Prasad (1998). Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68(4): 465-485.

Jackson, R.D. , K.O. Fulgham, and B. Allen-Diaz (1998). *Quercus garryana* Hook. (Fagaceae) stand structure in areas with different grazing histories. Madrono 45: 275-282.

Jackson, R.D., and J.W. Bartolome (2002). A state-transition approach to understanding nonequilibrium plant community dynamics in California grasslands. Plant Ecology 162:49-65.

Jacobi, J.C. and F.H. Tainter (1988). Dendroclimatic examination of white oak along an environmental gradient in the Piedmont of South Carolina. Castanea 53: 252-262.

Jacoby, G.C. and R. D'Arrigo (1995). Tree ring width and density evidence of climatic and potential forest change in Alaska. Global Biogeochemical Cycles 9: 227-234.

Janzen, D.H. (1988). Management of Habitat Fragments in a Tropical Dry Forest. Annals of the Missouri Botanical Garden 75(1): 105-116.

Johnson, E.A. (1992). *Fire and vegetation dynamics: studies from the North American boreal forest.* Cambridge University Press; Cambridge, UK.

Johnson, E.A. and K. Miyanishi (2008). Testing the assumptions of chronosequences in succession. Ecology Letters, 11(5): 419-431.

Kaplan, A., M. Cane, Y. Kushnir, A. Clement, B. Blumenthal, and B. Rajagopalan (1998). Analysis of global sea surface temperature 1856–1991. *J. Geophys. Res.* 103: 18567–18589.

Keen, F.P. (1937). Climatic cycles in eastern Oregon indicated by tree rings. Monthly Weather Review 65:183–88.

Kelly P.M., M.A.R. Munro, M.K. Hughes, C.M. Goodess (1989). Climate and signature years in west European oaks, Nature 340: 57-59.

Kienast F, F.H. Schweingruber, O.U. Bräker, E. Schär (1987). Tree-ring studies on conifers along gradients and the potential of single-year analyses. Can J Forest Res 17:687–696.

Kikuzawa, K. (1983). Leaf survival of woody plants in deciduous broad-leaved forests. Tall trees. Canadian Journal of Botany 61: 2133–2139.

Kimmins, J.P. (2004). *Forest Ecology*. Macmillan, New York.

Knapp A.K., P.A. Fay, J.M. Blair, S.L. Collins, M.D. Smith, J.D. Carlisle, C.W. Harper, B.T. Danner, M.S. Lett, and J.K. McCarron (2002). Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. Science. 298:2202–2205.

Koike, T. (1988). Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Pl. Species Biol. 3: 77-87.

Koenig, W.D. and J.M.H. Knops (2000). Patterns of annual seed production by northern hemisphere trees: a global perspective. Am. Nat. 155: 59–69.

Köppen, W. (1923). *Die Klimate der Erde – Grundriss der Klimakunde*. Walter de Gruyter & Co., Berlin, Leipzig, 369 pp.

Koole, R., D. Jordan, and G. Jordan (2004). Mapping Garry oak meadows: a case study of ecological transition zones. Environmental Science and Geography Programs, Trinity Western University, Langley, BC.

Kolasa, J. and M. Zalewski (1995). Notes on ecotone attributes and functions. Hydrobiologia 303: 1-7.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy (1991). The physiological ecology of woody plants. Academic Press, San Diego, California, USA.

Kronberg, B. I., M. J. Watt, and S. C. Polischuk (1996). Forest-Climate Interactions in the Quetico-Superior Ecotone Northwest Ontario and Northern Minnesota. Environmental Monitoring and Assessment 50: 173-187.

Kullman, L. (1993). Tree-limit dynamics of *Betula pubescens ssp. tortuosa* in relation to climate variability: evidence from central Sweden. Journal of Vegetation Science 4, 765–772.

Kurz W.A, G. Stinson, G. Rampley (2008). Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? Phil. Trans. R. Soc. B. 363:2261–2269.

Lamb, E.G. and A.U. Mallik (2003). Plant species traits across a riparian zone/forest ecotone. Journal of Vegetation Science 14: 853-858.

Larcher W. (2003). *Physiological Plant Ecology. Ecophysiology and Stress Physiology of Functional Groups.* Springer-Verlag, Berlin.

Laroque, C.P. and D.J. Smith (1999). Tree-ring analysis of yellow cedar (*Chamaecyparis nootkatensis*) on Vancouver Island, British Columbia. Canadian Journal of Forest Research 21: 115-123.

Laroque, C.P. and D.J. Smith (2003). Radial-growth forecasts for five high-elevation conifer species on Vancouver Island, British Columbia. Forest Ecology and Management 1831-3:313-325.

Laroque, C.P. and D.J. Smith (2005). Predicted short-term radial-growth changes of trees based on past climate on Vancouver Island, British Columbia. Dendrochronologia 223:163-168.

Larsen, E.M. and J.T. Morgan (1998). Management recommendations for Washington's priority habitats: Oregon white oak woodlands. Olympia, WA: Washington Department of Fish and Wildlife. 37 p.

Larson, D.W., U. Matthes, and P.E. Kelly (2000). *Cliff ecology. Pattern and process in cliff ecosystems*. Cambridge University Press, Cambridge, UK.

Latif, M. and T. P. Barnett (1996): Decadal climate variability over the North Pacific and North America: dynamics and predictability. J. Climate 9: 2407–2423.

Lea, T. (2002). Historical Garry oak ecosystems of Greater Victoria and the Saanich Peninsula: a 1:50,000 map. Terrestrial Information Branch, British Columbia Ministry of Sustainable Resource Management, Victoria, BC, Canada.

Leblanc, D.C. and J.R. Foster (1992). Predicting effects of global warming on growth and mortality of upland oak species in the midwestern United States: a physiologically based dendroecological approach. Can. J. For. Res. 22: 1739-1752.

LeBlanc, D. and M. Terrell (2001) Dendroclimatic analyses using the Thornthwaite–Mather-type evapotranspiration models: a bridge between dendroecology and forest simulation models. Tree-Ring Research, 57: 55–66.

LeBourgeois, F., G. Cousseau, and Y. Ducos (2004). Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Berce ("Futtaie de Clos", Sarthe, France). Annals of Forest Science 61:361-372.

Lewis, I.M. (1911). The seedling of *Quercus virginiiana*. Plant World 14:119-123.

Leibold M.A., M. Holyoak, N. Mouquet, P. Amarasekare, J.M. Chase, M.F. Hoopes, R.D. Holt, J.B. Shurin, R. Law, D. Tilman, M. Loreau, A. Gonzalez (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Little, E.L. (1971). Atlas of United States trees, volume 1, conifers and important hardwoods. U.S. Department of Agriculture Miscellaneous Publication 1146. 9 p., 200 maps.

Lloyd A, Fastie C (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Clim Change 52:481–509.

Loehle, C. (2000). Forest ecotone response to climate change: sensitivity to temperature response functional forms. Canadian Journal of Forest Research 30: 1632-45.

Loehle, C. and D.C. LeBlanc (1996). Model-based assessments of climate change effects on forests: A critical review. Ecological Modelling 90: 1-31.

Lomolino, M.V., B.R. Riddle, and J.H. Brown (2006a) *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.

Lomolino, M.V., D.F. Sax, B.R. Riddle, and J.H. Brown (2006b) The island rule and a research agenda for studying ecogeographical patterns. Journal of Biogeography 33: 1503–1510.

Lorimer, C.G. (2003). The decline of oak forests. Bioscience 53:915.

Lortie, C.J., R.W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F.I. Pugnaire, and R.M. Callaway (2004). Rethinking plant community theory. Oikos 107:2.

Luckman, B.H. and T.A. Kavanagh (1998). Documenting the effects of recent climate change at treeline in the Canadian Rockies. In: The Impacts of Climate Variability on Forests, Berlin, Springer-Verlag: 121-144.

MacArthur, R.H., E.O. Wilson (1967). *The theory of island biogeography*. Princeton University Press, Princeton , New Jersey .

MacArthur, R.M. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Harper and Row, New York. 269 pp.

MacDougall, A.S. (2004). Responses Of Diversity And Invasibility To Burning In A Northern Oak Savanna. Ecology 86(12): 3354–3363.

MacDougall, A.S., B.R. Beckwith, and C.Y. Maslovat (2004). Defining conservation strategies with historical perspectives:a case study from a degraded oak grassland ecosystem. Conservation Biology 18:455–465.

MacDougall, A.S., and R. Turkington (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42-55.

Mann, M.E. (2002). The value of multiple proxies. Science 297: 1481-82.

Manos, P.S., J.J. Doyle, and K.C. Nixon (1999). Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (*Fagaceae*). Molecular Phylogenetic Evolution 12 (3):333-49.

Mantua, N. and S. Hare (2002). The Pacific decadal oscillation. Journal of Oceanography 58: 35-44.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, R.C. Francis (1997). A Pacific climate interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78: 1069-1079.

McCann, K.S. (2000). The diversity-stability debate. Nature 405: 228-233.

McCarty, J.P. (2001). Ecological Consequences of Recent Climate Change. Conservation Biology, Vol. 15(2): 320-331.

McCulloch, W.F. (1940). Oregon oak: tree of conflict. American Forest: 264–266, 286–288.

McGarigal, K, S. Cushman, and S. Stafford (2000). *Multivariate Statistics for Wildlife and Ecology Research*. Springer: New York, 277 pp.

McKenzie, D., Z. Gedalof, D.L. Peterson, and P. Mote (2004). Climatic change, wildfire, and conservation. Conservation Biology 18(4): 890-902.

McMenamin, M.A.S. (1992). The Cambrian transition as a time-transgressive ecotone. Geological Society of America Abstracts with Program 24:62.

McPherson, G.R. (1997). *Ecology and Management of North American Savannas*. The University of Arizona Press, Tucson.

McPherson, B.A., D.L. Wood, A.J. Storer, P. Svihra, D.M. Rizzo, N.M. Kelly and R.B. Standiford (2000). Oak Mortality Syndrome: Sudden Death of Oaks and Tanoaks. Tree Notes 26: 1-6.

McShea, W.J., and W.M. Healy, eds. (2002). *Oak Forest Ecosystems: Ecology and Management for Wildlife*. The John Hopkins University Press, Baltimore, Maryland.

Millspaugh, S.H., C. Whitlock, P.J. Bartlein (2000). Variations in fire frequency and climate over the past 17,000 yr in central Yellowstone National Park. Geology 28(3): 211-214.

Minobe, S. (1997). A 50-70 year climatic oscillation over the North Pacific and North America. Geophysical Research Letters 24: 683-686.

Mitchell, J. M. (1976). An Overview of Climatic Variability and Its Causal Mechanisms. Quaternary Research 6, pp. 481-493.

Morgan P., C.C. Hardy, T.W. Swetnam, M.G. Rollins and D.G. Long (2001). Mapping fire regimes across time and space: understanding coarse and fine-scale fire patterns. International Journal of Wildland Fire 10: 329-342.

Mosteller, F. and J.W. Tukey (1977). *Data Analysis and Regression: A Second Course in Statistics.* Reading MA: Addison-Wesley.

Mote, P.W. (2003). Trends in temperature and precipitation in the Pacific Northwest. Northwest Science 77: 271–282.

Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier (2005). Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86: 39-49.

Muzika, R. and R.P. Guyette (2004). A dendrochronological analysis of red oak borer abundance. Pages 102-105 in Proceedings of the Upland Oak Ecology Symposium, (M. Spetich, ed.) Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Dept. of Agriculture, Forest Service, Southern Research Station. 311 p.

Myers, A.A. and P.S. Giller (1988). Process, pattern and scale in biogeography. pp. 3-14 in *Analytical Biogeography* (ed.) Myers, A. A. and P. S. Giller. Chapman and Hall, London, England.

Nakawatase, J.M., and Peterson, D.L. (2006). Spatial variability in forest growth–climate relationships in the Olympic Mountains, Washington. Can. J. For. Res. 36: 77–91.

Neilson, R.P. (1993). Transient ecotone response to climatic change: some conceptual and modeling approaches. Ecological Applications 3(3): 385-395.

Neilson, R.P., L.F. Pitelka, A.M. Solomon, R. Nathan, G.F. Midgley, J.M.V. Fragoso, H. Lischke, and K. Thompson (2005). Forecasting regional to global plant migration in response to climate change. BioScience 55:749–759.

Niemiec, S.S., G.R.Ahrens, S. Willits, D.E. Hibbs (1995). *Hardwoods of the Pacific Northwest*. Research Contributions 8. Corvallis, OR: Oregon State University. 115 p.

Nigam, S., M. Barlow, and E.H. Berbery (1999). Analysis Links Pacific Decadal Variability to Drought and Streamflow in United States. EOS 80(61).

Nixon, K.C. (2002). The Oak (*Quercus*) Biodiversity of California and Adjacent Regions. USDA Forest Service Gen. Tech. Rep. PSW-GTR-184.

Nixon, K. C. (1997). Quercus: In: Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 445-447.

Noss, R.F., E.T. LaRoe, and J.M. Scott (1995). Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological report 28. U.S. National Biological Service, Washington, D.C.

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

Nowacki G.J. and Abrams M.D. (2008) The Demise of Fire and “Mesophication” of Forests in the Eastern United States. BioScience 58(2): 123–138

Nuzzo, V.A. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. Natural Areas Journal 6:6-36.

Oberhuber W. (2004). Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. Tree Physiol 24: 291–301.

ODFW (2005). Oregon's comprehensive wildlife conservation strategy. Oregon Department of Fish and Wildlife, Salem, Oregon.

Orwig, D.A. and M.D. Abrams (1997). Variation of radial growth responses to drought among species, site, and canopy strata. Trees 11: 474-84.

Pacific Northwest Ecosystem Research Consortium (1998.) Willamette River Basin: A planning atlas. Institute for a Sustainable Environment, Eugene, Oregon.

Palmer, W.C.(1965). Meteorological drought. Research Paper No. 45. United States Department of Commerce Weather Bureau. Washington, D.C. 58 p.

Pan, C., S. J. Tajchman And J. N. Kochenderfer (1997). Dendroclimatological analysis of major forest species of the central Appalachians. For. Ecol. Manag. 98: 77-87.

Parmesan, C. and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature. 421:37-42.

Parmesan, C. (2005). Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. 2006.37:637-669.

Pederson, B.S. (1998). The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. Ecology 79: 79-93.

Pederson, N, E.R. Cook, G.C. Jacoby, D.M. Peteet and K.L. Griffin (2004). The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia, 22: 7-29.

Pellatt, M.G., R.J. Hebda, and R.W. Mathewes (2001). High resolution Holocene vegetation history and climate from core 1034B ODP leg 169S, Saanich Inlet, Canada. Marine Geology 174:211-226.

Pellatt, M.G., Z. Gedolof, M. McCoy, K. Bodtker, A. Canon, S. Smith, B. Beckwith, R.W. Mathewes, and D. Smith (2007). Fire History and Ecology of Garry Oak and Associated Ecosystems in British Columbia. Final Report for the Interdepartmental Recovery Fund Project 733. WNSC Publication.

Peter, D. and C.A. Harrington (2002). Site and tree factors in Oregon white oak production in western Washington and Oregon. Northwest Science. 76(3): 189-201.

Peterson, D.L. (1998). Climate, limiting factors and environmental change in high-altitude forests of Western North America. In: Beniston M. and Innes J.L., eds. The impacts of climate variability on forests. Lecture Notes in Earth Science, vol 74. Springer-Verlag, Berlin, pp 191-208

Peterson, D.W., and P.B. Reich (2001). Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics Ecological Applications 11:914-927.

Peterson, D.W. and D.L. Peterson (1994). Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. Canadian Journal of Forest Research 24: 1921-1932.

Peterson, D.W. and D.L. Peterson (2001). Mountain hemlock growth responds to climatic variability at annual and decadal time scales. Ecology 8212: 3330-3345.

Peterson, D.W., D.L. Peterson and G.J. Ettl (2002). Growth responses of subalpine fir to climatic variability in the Pacific Northwest. Canadian Journal of Forest Research 32: 1503–1517.

Peterson, D.L., M.C. Johnson, J.K. Agee, T.B. Jain, D.M. McKenzie, and E.R. Reinhardt (2005). Forest structure and fire hazard in dry forests of the Western United States. Gen. Tech. Rep. PNW-GTR-628. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 30 p.

Petit, J.R, J. Jouzel, D. Raynaud, N.I. Barkov, J.M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V.M. Kotlyakov, M. Legrand, V.Y. Lipenkov, C. Lorius, L.P. Épin, C. Ritz, E. Saltzman and M. Stievenard (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399: 429–436.

Phipps, L.R. (1982). Comments on interpretation of climatic information from tree rings, eastern North America. Tree-Ring Bulletin 42: 11–22.

Pielou, E.C. (1991). *After the ice age: the return of life to glaciated North America*. University of Chicago Press, Chicago and London, 366 pp.

Pilcher J.R., and B. Gray (1982). The relationships between oak tree growth and climate in Britain. J. Ecol. 70: 297-304.

Pitelka, L.F.and the Plant Migration Workshop Group (1997). Plant migration and climate change. *Am. Sci.* 85, 464–473.

Poulos, H.M., U.M. Goodale and G.P. Berlyn (2007). Drought response of two Mexican oak species, *Quercus laceyi* and *Q. sideroxyla* (Fagaceae), in relation to elevational position. Am. J. Bot. 94: 809-818.

PRISM (2007). PRISM Group, Oregon State University. Website: http://www.prismclimate.org Accessed January 20, 2007.

Raper, S.B.and F. Giorgi (2005). Climate change projections in T.E. Lovejoy and L. Hannah eds: *Biodiversity and Climate Change*, Yale.

Rasmussen, E.M. and J.M. Wallace (1983). Meteorological aspects of the El Niño/Southern Oscillation. Science, 222: 1195–1202.

Regan, A.C., and J.K. Agee (2004). Oak Community and Seedling Response to Fire at Fort Lewis, Washington. Northwest Science 78:1-11.

Reid, W.V., H.A. Mooney, A. Cropper (2005). Millennium ecosystem assessment synthesis report. Washington D. C.: Millennium Assessment and World Resources Institute.

Reigel, G.M., Franklin, J.F., and Smith, B.G. (1992). Foothill oak woodlands of the interior valleys of southwestern Oregon. Northwest Science 66: 66-76.

Ricklefs, R.E. (1997). *The Economy of Nature* (fourth edition). W. H. Freeman, New York.

Riitters, K.H., J.W. Coulston and J.D. Wickham (2003). Localizing national fragmentation statistics with forest type maps. Journal of Forestry 101(4).

Risser, P.G. (1993). Ecotones at local to regional scales from around the world. Ecological Applications 3(3): 367-368.

Risser, P.G. (1995). The status of the science examining ecotones. Bioscience 45:318–325.

Ritland K., L.D. Meagher, D.G.W. Edwards, and Y.A. El-Kassaby (2005). Isozyme variation and the conservation genetics of Garry oak. Canadian Journal of Botany 83(11): 1478-1487.

Rizzo, B. and E. Wiken (1992). Assessing the sensitivity to Canada’s ecosystems to climatic change. Climatic Change 21: 37-55.

Roemer, H.L. (1972). Forest vegetation and environments of the Saanich Peninsula, Vancouver Island. Ph.D. Thesis. University of Victoria, Victoria, BC. pp. 405.

Roemer, H. (1993). Vegetation and ecology of Garry oak woodlands. In: Garry Oak-Meadow Colloquium Proceedings: Victoria, BC. edited by R.J. Hebda and F. Aitkens. Garry Oak Meadow Preservation Society, Victoria, BC:19-24.

Roemer, H. (unpublished). An ecosystem creating its own space?

Ropelewski, C.F. and M.S. Halpert (1986). North American Precipitation and Temperature Patterns Associated with the El Nino Southern Oscillation (ENSO). Monthly Weather Review 114 (12).

Roxburgh, S.H., K. Shea, and J.B. Wilson (2004). The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. Ecology 85(2):359-371.

Rozas V. (2001). Detecting the impact of climate and disturbances on tree-rings *of Fagus sylvatica* L. and *Quercus robur* L. in a lowland forest in Cantabria, Northern Spain, Ann. For. Sci. 58:237-251.

Rozas, V. (2005). Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: establishment patterns and the management history. Ann. For. Sci. 62:13–22.

Rubino, D.L. and B.C. McCarthy (2000). Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-growth forest of southeastern Ohio, USA. Journal of the Torrey Botanical Society 127(3): 240-250.

Ryan, L.A. and Carey, A.B. (1995). Biology and management of the western gray squirrel and white oak woodlands: with emphasis on the Puget Trough. USDA Forest Service Gen. Tech. Rep. PNW-GTR-348. Pacific Northwest Forest Research Station, Portland, Oregon.

Schoennagel,, T., T.T. Veblen, W.H. Romme, J.S. Sibold, E.R. Cook (2005). ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. *Ecol. Appl.* 15.

Scholes, R.J., and S.R. Archer (1997). Tree-Grass Interactions in Savannas. Annual Reviews of Ecology and Systematics 28:517-544.

Schweingruber, F.H. (1996). *Tree Rings and Environment Dendroecology*. Paul Haupt Publishers, Berne, 609 p.

Scott, J.M., F.W. Davis, R.G. McGhie, R.G. Wright, C.G. and J. Estes (2001). Nature reserves: do they capture the full-range of biological diversity? Ecological Applications 11(4): 999-1007.

Shafer, S.L., P.J. Bartlein and R.S. Thompson (2001). Potential changes in the distributions of western North American tree and shrub taxa under future climate scenarios. Ecosystems, 4: 200-215.

Sheppard, P.R. and Graumlich, L.J. (1996). A reflected-light video imaging system for tree-ring analysis of conifers, p. 879-889. In: J.S. Dean, D.M. Meko and T.W. Swetnam, eds., Tree-rings, Environment and Humanity: Proceedings of the International Conference, Tucson, Arizona, 17-21, May 1994. Radiocarbon, University of Arizona, Tucson.

Siau, J.F. (1971). *Flow in Wood*. Syracuse University Press. Syracuse, New York. 131 p.

Smith, S.J. (2007). *Garry oak savannah stand history and change in coastal southern British Columbia*. MSc Thesis, University of Guelph, Guelph, Ontario.

Smith, D.J. and C.P. Laroque (1998). Mountain Hemlock Growth Dynamics on Vancouver Island. in J.A. Trofymow and A. MacKinnon, editors. Proceedings of a workshop on Structure, Process, and Diversity in Successional Forests of Coastal British Columbia, February 17-19, 1998, Victoria, British Columbia. Northwest Science 72(2): 67-70.

Sork, V.L., J. Bramble, and O. Sexton (1993). Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology. 74(2): 528–541.

Speer, J. (2001).*Oak mast history from dendrochronology: A new technique demonstrated in the southern Appalachian region.* Ph.D. Dissertation, Department of Geography, University of Tennessee.

Stearns, S.C. and R.E. Crandall (1981). Bet hedging and persistance as adaptations of colonizers. - In: Scudder, G. G. E. and Reveal, J. L. (eds), Evolution today. - Proc. Second Int. Congr. Syst. Evol. Biol., pp. 371-383.

Stein, W.I. (1990). (*Quercus garryana* Dougl. ex Hook.) Oregon White Oak. in Silvics of North America. R. M. Burns and B. H. Honkala. Washington, U.S. Dept. of Agriculture, Forest Service.

Stinson, D.W. (2005). Washington State Status Report for the Mazama Pocket Gopher, Streaked Horned Lark, and Taylor’s Checkerspot. Washington Department of Fish and Wildlife, Olympia. 138 pp.

Stokes, M.A. and T.L. Smiley (1996). *An Introduction to Tree-Ring Dating*. University of Arizona Press, Tucson, Arizona, USA.

Sugihara, N.G.; Reed, L.J. (1987). Vegetation ecology of the Bald Hills oak woodlands of Redwood National Park. Tech. Rep. 21. Orick, CA: Redwood National Park, South Operations Center. 78 p.

Swetnam, T.W. and J.L. Betancourt (1990). Fire-Southern Oscillation Relations in the southwestern United States. Science 249: 1017-1020.

Tardif, J. (1996). Earlywood, latewood and total ring-width of a ring-porous species (*Fraxinus nigra* Marsh.) and their relationship to climatic and hydrologic factors, In Dean, J.S., Meko, D.M. and Swetnam, T.W., editors, *Tree-ring, environment and Humanity*, Radiocarbon, Arizona, pp. 315-324.

Tardif, J. and Y. Bergeron (1997). Comparative dendroclimatic analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet, NW Quebec. Canadian Journal of Forest Research 27: 108-116.

Tardif, J. and Stevenson, D. (2002). Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. Dendrochronologia 19: 1-9.

Tardif, J., J.J. Camarero, M. Ribas, and E. Gutiérrez (2003). Spatiotemporal variability in radial growth of trees in the Central Pyrenees: climatic and site influences. Ecological Monographs 73: 241–257.

Tardif, J., F. Conciatori, P. Nantel, and D. Gagnon (2006). Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Quebec, Canada. Journal of Biogeography 33(9): 1657-1669.

Thilenius, J.F. (1968). The *Quercus Garryana* Forests of the Willamette Valley, Oregon. Ecology 49: 1124-1133.

Thysell, D.R., and A.B. Carey (2000). Effects of forest management on understory and overstory vegetation: a retrospective study. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-488.

Thysell, D.R. and A.B. Carey (2001). *Quercus garryana* communities in the Puget Trough, Washington. Northwest Science 753: 219-235.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Sieman (1997). The influences of functional diversity and composition ecosystem processes. Science 277: 1300-1302.

Tivy, J. (1993). *Biogeography: A Study of Plants in the Ecosphere*. Addison Wesley Longman Limited, Essex, England.

Trenberth, K.E. and J.W. Hurrell (1994): Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9: 303-319.

Turner, N.J. (1999). Time to burn: Traditional use of fire to enhance resource production by aboriginal peoples in British Columbia. in Indians, fire and the land in the Pacific Northwest. R. Boyd. Corvallis, OR, Oregon State University Press: 185-218.

Tveten, R.K., and R.W. Fonda (1999). Fire Effects on Prairies and Oak Woodlands on Fort Lewis, Washington. Northwest Science 73:145-158.

Tyree, M.T. and H. Cochard. (1996). Summer and winter embolism in oak: Impact on water relations. Ann. Sci. For. 53:173–180.

Tyree, M.T. and J. S. Sperry (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* 88: 574–580.

USDA (2007). *The Encyclopedia of Wood*. Skyhorse Publishing, Inc. New York, NY.

Valentine, L.L., T.L. Fieldler, A.A. Hart, C.A. Petersen, H.K. Berninghausen, and D. Southworth (2004). Diversity of ectomycorrhizas associated with *Quercus garryana* in southern Oregon. Canadian Journal of Botany, 82, 123–135.

Vallardes and Pearcy (2002). Interactions between water stress, sun-shade, acclimation, heat tolerance, and photoinhibition in the sclerophyll *Hetromeles arbutifolia*. Plant, Cell, and Environment 20: 25-36.

van Breemen, N., A.F. Finzi, and C.D. Canham (1997). Canopy tree-soil interactions within temperate forests: Effects of fine-scale variation in soil texture and elemental composition on species distributions. Canadian Journal of Forest Research 27:1110-1116.

Villalba, R., R.L. Holmes and J.A. Boninsegna (1992). Spatial patterns of climate and tree growth variations in subtropical northwestern Argentina. Journal of Biogeography 196:631-649.

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

Walther, G.R. (2002). Ecological responses to recent climate change. Nature 416, 389-395.

Weltzin, J.F. & McPherson, G.R. (1997). Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia 112: 156–164.

Weltzin, J.F. and McPherson, G.R. (1999). Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. Ecological Monographs 69: 513-534.

Weltzin, J.F. and McPherson, G.R. (2000). Implications of precipitation redistribution for shifts in temperate savanna ecotones. Ecology 81(7): 1902-1913.

White, K. L. (1999). Revisiting native *Pinus radiata* forests after twenty-five years. Madrono. 46:80–87.

Whitlock, C. (1992). Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. Northwest Environmental Journal. 8: 5–28.

Whitlock, C. and T. Knox In: J. N. Mastr (2003a). Fire, Native Peoples, and the Natural Landscape. Annals of the Association of American Geographers 93(2): 498-500.

Whitlock, C., S. L. Shafer, and J. Marlon (2003b). The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. Forest Ecology and Management 178, 5–21.

Wimberly M.C. and Spies T.A. (2001). Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. Ecology 82: 1443–1459.

Wolff, J.O. (1996). Population fluctuations of mast-eating rodents are correlated with the production of acorns. Journal of Mammology 77: 850–856.

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

Yarnall, B. and H. F. Diaz (1986). Relationships between extremes of the Southern Oscillation and the winter climate of the Anglo-American Pacific coast. Journal of Climatology 6: 197-219.

Zhang, Y., J.M. Wallace and D.S. Battisti (1997). ENSO-like interdecadal variability: 1900-93. Journal of Climate 10: 1004-1020.

Zhang, X., L.A. Vincent, W.D. Hogg, and A. Niitsoo (2000). Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38:395-429.

Rocky Point

Oregon white oak and Douglas-fir are scattered throughout savannas and woodlands on Rocky Point on southern Vancouver Island (Figure A.1). This site on the San Juan de Fuca strait has some of wettest and coolest summers and some of the fastest-growing trees among those in this analysis.

Oak trees inhabiting woodlands, those experiencing greater interspecific competition, and those growing in more mesic sites tend to be more sensitive to temperatures than other stands (Franks 2007). Consequently, the trees at Rocky Point respond negatively to monthly average maximum temperatures in the fall, winter, and spring, and this stand is one of the few in this study that responds negatively to minimum temperatures. The most dominant aspect of Rocky Point's oak tree's growth-climate relationship is a positive response to soil moisture availability in winter, spring, and summer (Figure A.2).

Any study using RYP as an indicator of Oregon white oak’s growth response to climate must consider the fact that the population there displays somewhat different patterns of growth response to both temperature and precipitation than other more southerly populations, although these are more in degree of response rather than in direction. Differences in soil and hydrology of Rocky Point compared to other stands of Oregon white oak, the stand's proximity to the strait of Juan de Fuca, North-South movement of the jet stream over the area, and the high latitude of the stand likely account for its unique response to minimum temperature and the lack of the stand's response to precipitation.

Figure A.1. Photograph of the sampled Oregon white oak stand at Rocky Point, British Columbia.

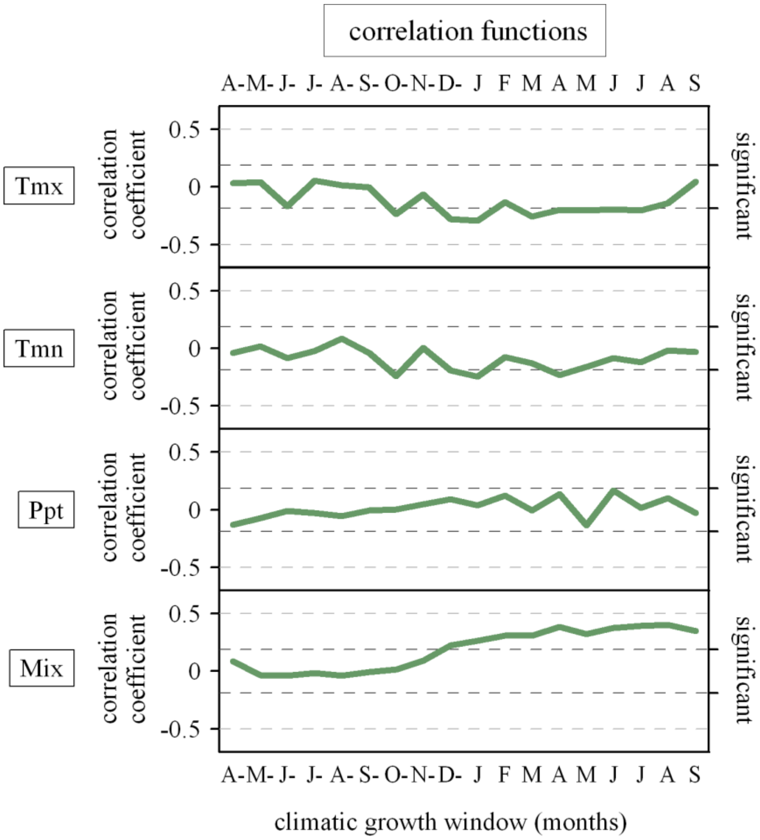

Figure A.2. Graph of correlation functions for the Oregon white oak stand at Rocky Point.

Nisqually Plain

The Oregon white oak stand assessed at Fort Lewis in Washington consists of moderate-sized oak trees on the edge of a conifer-dominated woodland (Figure A.3). A few Douglas-fir and ponderosa pine (*Pinus ponderosa*) occur within this stand. The oak trees display growth forms characteristic of woodland trees. This oak stand experiences the wettest summers assessed here which likely accounts for its rapid growth in recent years and certainly influences the stand's overall response to climatic forcings. Stand dynamics due to fire and restoration efforts also influence the clarity of the climate signal, so this stand has the highest interseries correlation but its growth-climate relationship may be of questionable utility in the identification of the species' characteristic dendroclimatic response.

This stand's response to temperature and precipitation are characteristic of the species as a whole: a positive response to minimum temperatures in the spring prior to growth and a negative response to maximum temperatures in June during the growing season. The stand responds positively to rainfall in spring. Uncharacteristically, the growth of the trees at Nisqually Plain shows little correlation to the moisture index (Figure A.4.).

Figure A.3. Photograph of an Oregon white oak stand on Nisqually Plain, Washington.

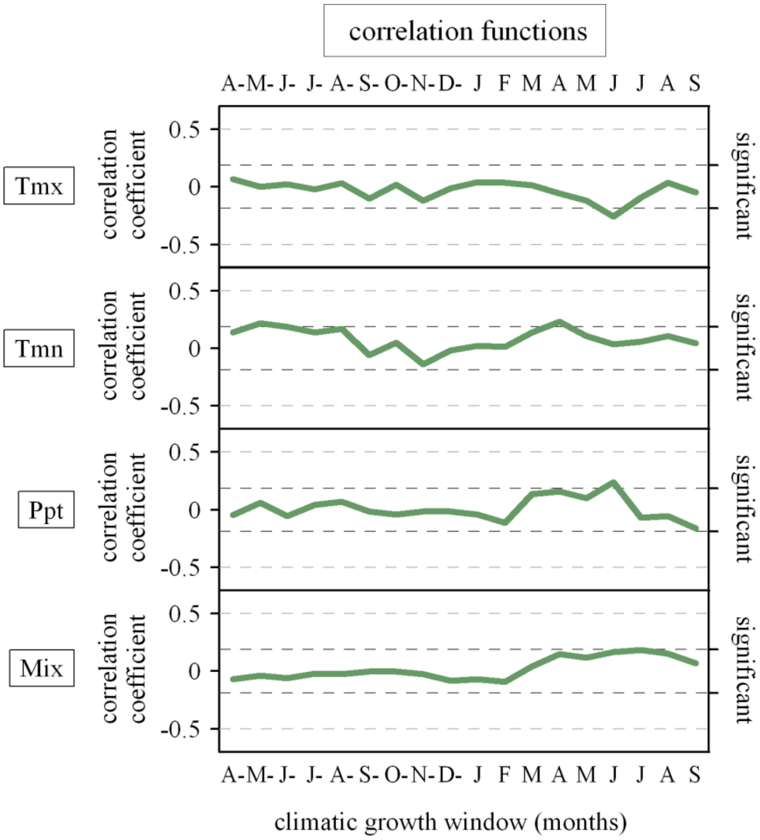

Figure A.4. Graph of correlation functions for an oak stand on Nisqually Plain.

Mima Mounds

The seasonally inundated site at Mima Mounds consists of medium sized oak trees scattered under a closed canopy among many other tree species, including Douglas-fir, red alder (*Alnus rubra*), willow (*Salix* spp.) and numerous shrubs (Figure A.5). Similar to the nearby stand on Nisqually Plain, this site has wet summers, moderate temperatures, and fast-growing trees when compared to other sites in this study.

The Oregon white oaks near Mima Mounds respond to temperatures much as do most other trees in this study: negatively to maximum temperatures in June, July, and in the previous November. However, the stand responds more strongly to minimum temperatures in spring and summer than most of the other stands surveyed, a trait of these oak trees when growing in mixed-species woodlands or on mesic sites (Franks 2007). Like all Oregon white oak, this stand responds positively to precipitation in June, but these trees show a negative growth-response to soil moisture availability in the months prior to ring formation, probably reflecting decreased soil gas concentrations resulting from flooded conditions peculiar to this site (Figure A.6).

more to sum mix than spr mix

Figure A.5. Photograph of the Oregon white oak stand at Mima Mounds.

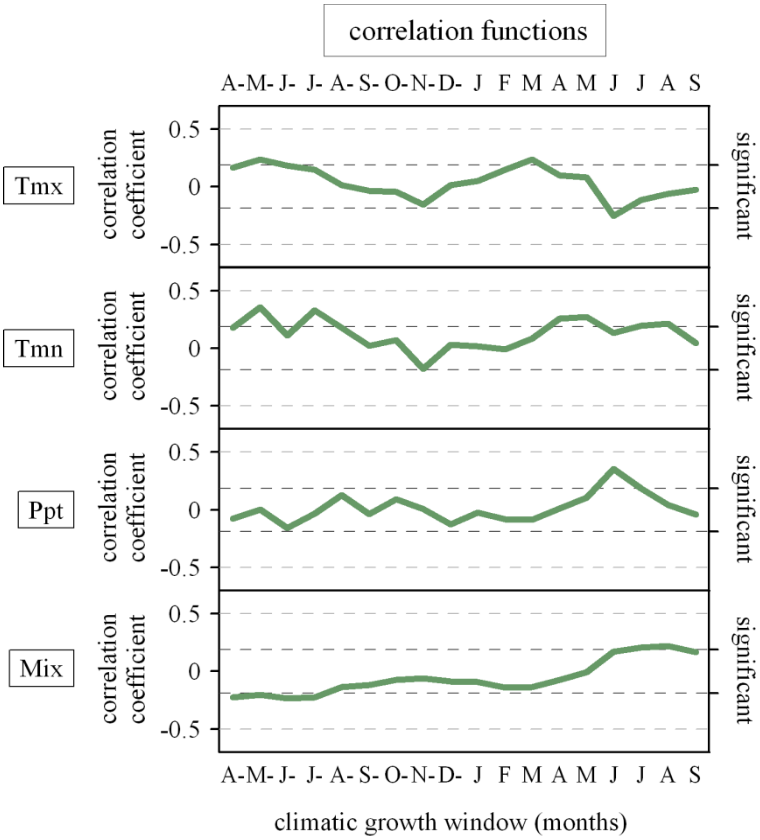

Figure A.6. Graph of correlation functions for the oak stand at Mima Mounds.

White Salmon Oaks

White Salmon Oaks is a Natural Resource Conservation Area and habitat important for local wildlife. This shaded woodland stand near the Columbia Gorge in Washington is on a gentle slope where Oregon white oak is codominant with Douglas-fir, bigleaf maple (*Acer macrophyllum*), and ponderosa pine (Figure A.7). Poison-oak (*Toxicodendron diversiloba*) and snowberry are common associates. This site experiences relatively low maximum winter temperatures and high minimum summer temperatures, and these trees are some of the slowest growing among those assessed in this study (Table 4.1).

Although this stand responds in the same direction to climatic variables as the majority of other Oregon white oak stands, these trees are somewhat dendroclimatically complacent and significant correlations are few (Figure A.8). These oak trees are more responsive to temperature than to moisture availability, which supports other studies' findings of characteristic oak responses in mixed-species woodlands (Franks 2007) and results from the increased ability of these shaded stands to moderate humidity levels. Like most stands in the northern half of Oregon white oak's distribution, a positive response to minimum temperatures occurs throughout the year.

Figure A.7. Photograph of an Oregon white oak stand at White Salmon Oaks.

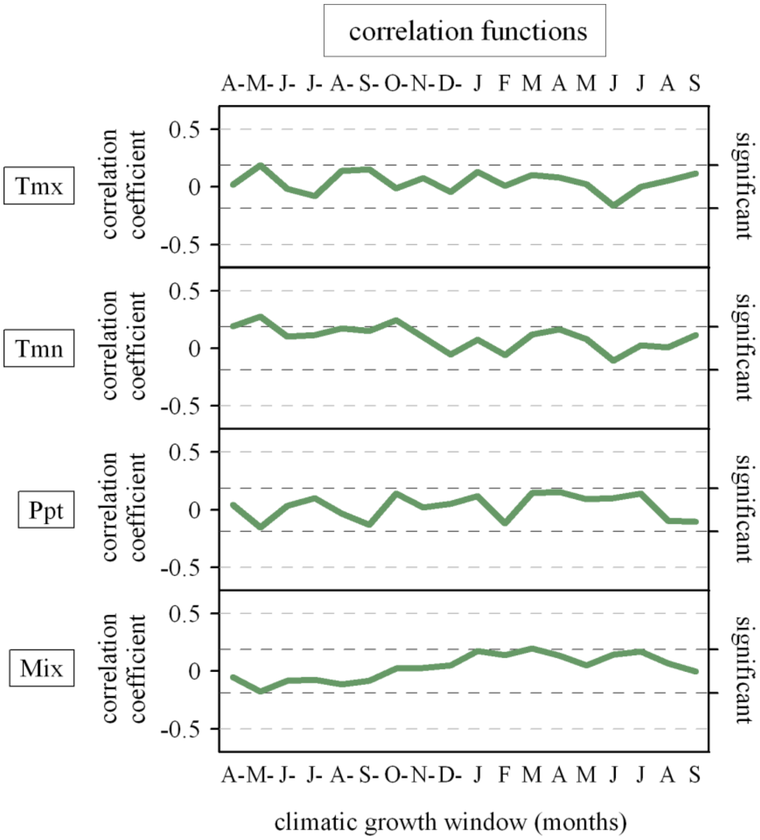

Figure A.8. Graph of correlation functions for the oak stand at White Salmon Oaks.

Swauk Creek

This shady stand of oak, black cottonwood (*Populus trichocarpa*), red alder, and ponderosa pine lies on a rocky floodplain very close to a creek (Figure A.9). The tree's gnarly branches are strongly directed toward gaps in the canopy. Shrubs include snowberry and Oregon grape. This stand in Washington represents the species northern limit east of the Cascade Mountains, experiencing the coldest and driest winters in this study.

These Oregon white oak trees respond positively to minimum temperatures throughout much of the year, as nighttime temperatures can be extremely low in this high desert ecosystem. This stand responds negatively to maximum temperatures in fall, indicating that warmer or longer fall seasons result in decreased growth. Even though, or possibly because this stand is in close proximity to a creek, significant positive responses to soil moisture availability are evident not only in the growing season, but also in the fall and winter prior (Figure A.10).

Figure A.9. Photograph of an Oregon white oak stand at Swauk Creek.

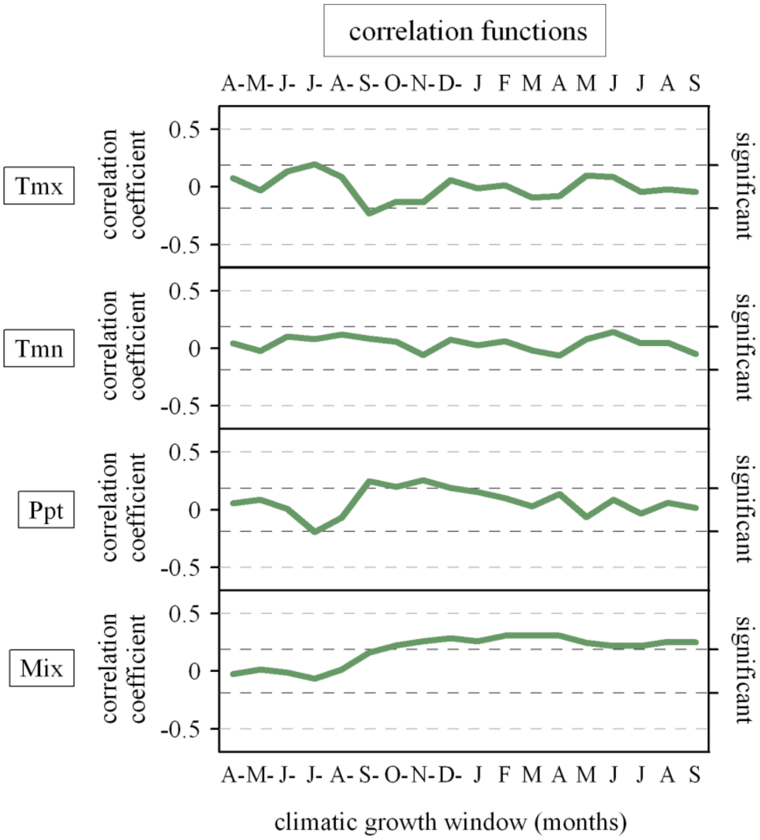

Figure A.10. Graph of correlation functions for the oak stand at Swauk Creek.

Tieton Oaks Creek

Large Oregon white oak trees mixed with a few Douglas-fir and ponderosa pine occur at the toe of a steep slope in Oak Creek Wildlife Area on the eastern side of the Cascade Mountains (Figure A.11). Snowberry is the dominant shrub. The area here at Tieton Bench burned in 2003 (Reese Lolley, personal communication) and seemingly several other times within the last 100 years as two distinct release events are evident (Figure 3.4). This site, like nearby Swauk Creek, experiences some of the driest and coldest winters of any site in this study.

These trees respond strongly to minimum temperatures in spring and summer, a response that uncharacteristically dominates this stand's growth-climate relationship. The strength and coherence of the response to minimum temperatures suggests that this particular stand is at the edge of its bioclimatic envelope (Figure A.12). This stand, like other white oaks east of the Cascade Mountains, responds positively to rainfall in every season.

Figure A.11. Photograph of the Oregon white oak stand at Tieton Oaks Creek.

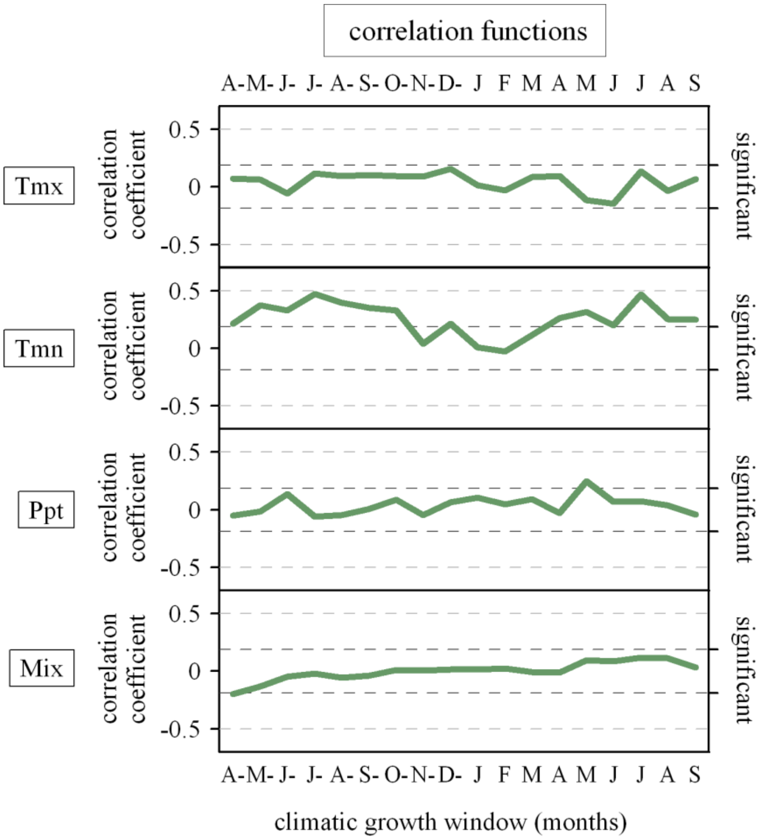

Figure A.12. Graph of correlation functions for the oak stand at Tieton Oaks Creek.

Badger Gulch

In Washington, we sampled Oregon white oak trees adjacent to Badger Gulch Natural Area Preserve that were growing among bigleaf maple in a shaded riparian corridor at the eastern edge of Oregon white oak's natural distribution (Figure A.13). Open-grown Oregon white oak trees, not sampled, were scattered on the dry, rocky slopes and in nearby savannas. This stand experiences cold, dry winters relative to most others in this study.

This stand responds positively to precipitation and even more strongly to soil moisture availability throughout the year. Oak trees at Badger Gulch respond positively to increased fall temperatures, so higher temperatures tends to increase growth. The stand responds negatively to spring temperatures during the growing season, a characteristic response of Oregon white oak trees, especially on more mesic sites (Figure A.14). This stand is likely at the edge of the species' bioclimatic envelope and tends to respond favorably to increased temperatures in fall, lower temperatures in spring and summer, and increased rainfall.

Figure A.13. Photograph of the Oregon white oak stand at Badger Gulch.

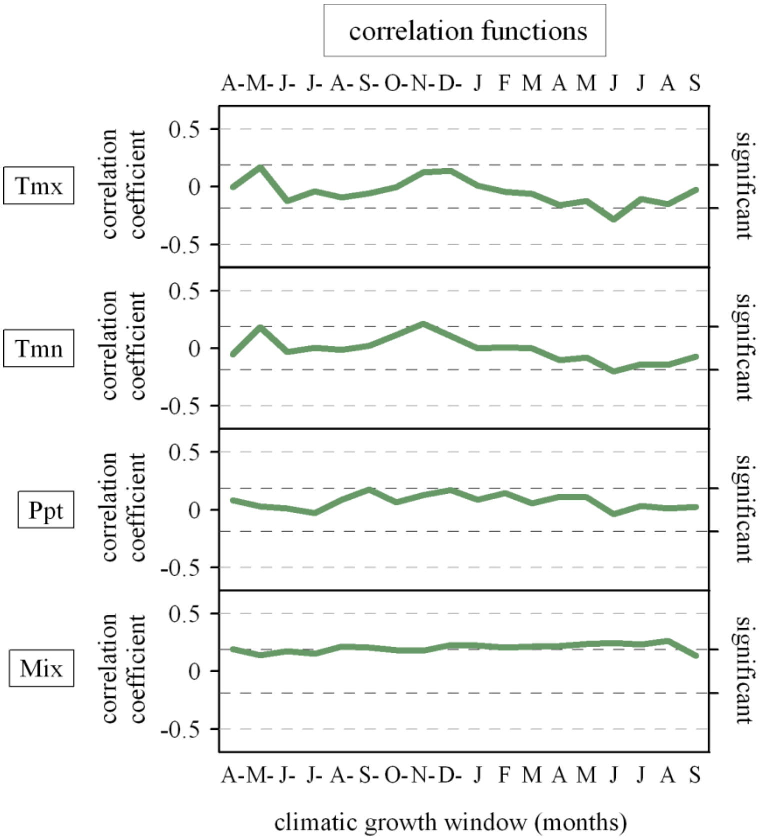

Figure A.14. Graph of correlation functions for the oak stand at Badger Gulch.

Jordan Creek

The Oregon white oak stand on the foothills above Jordan Creek is characterized by herbs, exposed rocks, and bare ground (Figure A.15). Clumps of even-aged oaks, often with rotten centers, grow among ponderosa pine. Like others east of the Cascade Mountains, this site is among the coldest and driest in this study. This site is situated at the southern end of the species' distribution in eastern Oregon, at a high elevation relative to its latitude. The Oregon white oak trees in this stand, along with those at nearby White Salmon Oaks, are the slowest growing in this study.

Also, characteristic of the species as a whole, the Oregon white oaks above Jordan Creek respond negatively to maximum temperatures in most seasons, but these trees respond positively to the longer growing season represented by increased minimum temperatures in May prior to the year of ring formation. The trees here are limited by rainfall: similarly to other sites east of the Cascades, this stand responds to positively to soil moisture availability consistently throughout the year (Figure A.16). Although radial-growth may directly benefit from increases in precipitation, conifers in the area already threaten to encroach on habitat currently occupied by Oregon white oak and will alter the ecosystem if allowed to establish.

Figure A.15. Photograph of the Oregon white oak stand at Jordan Creek in eastern Oregon.

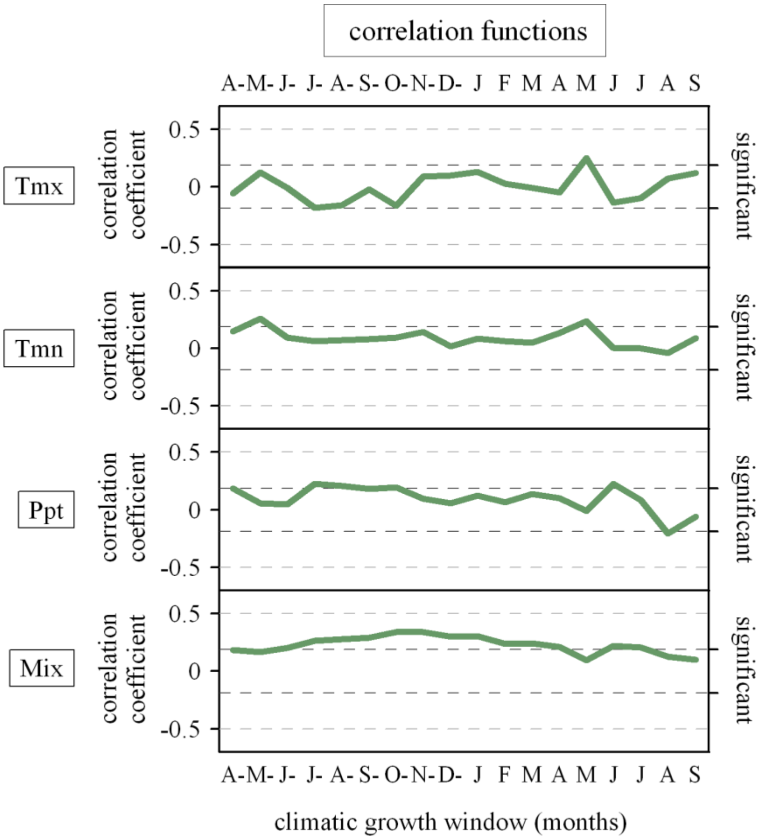

Figure A.16. Graph of correlation functions for the oak stand at Jordan Creek.

Baskett Butte

Baskett Slough National Wildlife Refuge in Oregon is surrounded by agricultural fields and wetlands. Within this Refuge, on the edge of Baskett Butte, is a landscape of mixed prairies and woodlands, these consisting predominantly of Douglas-fir, bigleaf maple, and Oregon white oak. We surveyed a stand of mossy oaks; scattered shrubs include poison-oak, snowberry, and saskatoon (Figure A.17). This site is slightly warmer and wetter than the average site assessed here.

This interior stand responds in the same direction and to the same degree to most climatic forcings as the species as a whole. At Baskett Butte and characteristic of many Oregon white oak stands is the negative response to average monthly maximum temperatures in May, June, and July during the growing season. The trees here respond positively to minimum temperatures throughout the year: the strong positive growth-response to minimum temperatures in June may reflect the site's hilltop exposure. These trees respond favorably to increased temperatures in spring prior to the year of growth. Excessive cloud cover may be the mechanism behind the negative response to April rainfall in the year prior to growth. This stand of Oregon white oak is strongly limited by precipitation and soil moisture availability in spring (Figure A.18). This relationship to soil moisture suggests that actual evapotranspiration rates in spring are greater than Oregon white oak prefers.

Figure A.17. Photograph of the Oregon white oak stand on Baskett Butte.

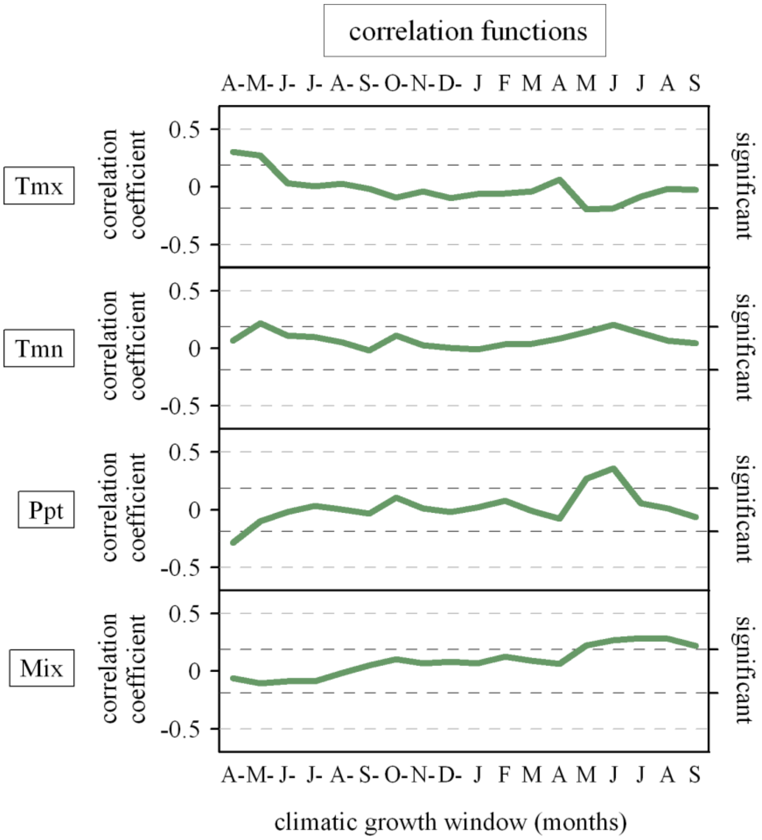

Figure A.18. Graph of correlation functions for the oak stand at Baskett Butte.

Pigeon Butte

In the William L. Finley National Wildlife Refuge in the Willamette Valley, a stand of large oak trees on Pigeon Butte are associated with a few bigleaf maple and a dense shrub layer, blackberry (*Rubus armeniacus*), snowberry, and poison-oak (Figure A.19). This site's climate is only slightly warmer and wetter than the average climatic conditions in this study.

This stand on Pigeon Butte responds positively to temperatures in April and May in the spring prior to the year of growth, but negatively to maximum temperatures in several other months, especially October. This stand does however respond positively to temperatures in November prior to growth. Other research found that higher density woodland stands and those with more intraspecific competition, like this site at Pigeon Butte, the greater the sensitivity to winter precipitation (Franks 2007). We see a relationship between growth and winter rainfall at Pigeon Butte and further associations with moisture availability in winter, spring, and summer (Figure A.20). This strong positive response to winter precipitation may explain the uncharacteristic responses to El Niño Southern Oscillation and the Pacific Decadal Oscillation. Increased temperatures projected for this century will not benefit this stand.

Figure A.19. Photograph of the Oregon white oak stand on Pigeon Butte.

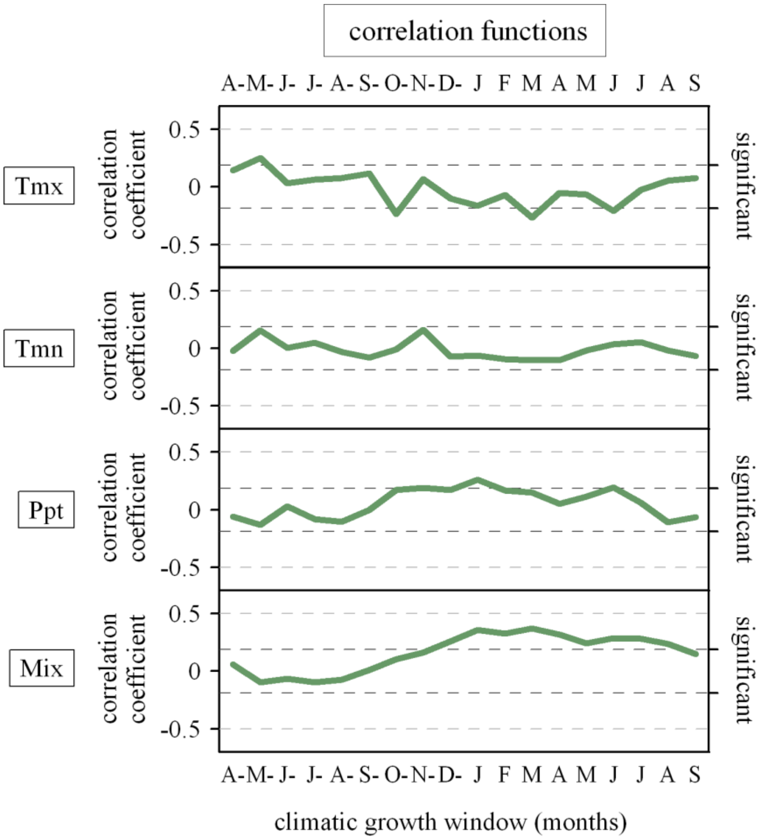

Figure A.20. Graph of correlation functions for the oak stand at Pigeon Butte.

Coburg Ridge

The pure stand of Oregon white oak on Coburg Ridge above Eugene, Oregon includes many small woodland-grown trees and several large open-grown ones. Shrubs include Nootka rose (*Rosa nutkana*) and poison-oak. The stand assessed here is on a convex slope above a small meadow (Figure A.21). This site has higher average monthly minimum temperatures and some of the slowest-growing oak trees when compared to other sites in this study.

This stand of Oregon white oak responds very much like other stands in the Willamette Valley and much like that of the species as a whole. The trees show a complex response to temperature, responding positively to spring temperatures in the year before ring formation and negatively in spring during the growth year. The trees' radial-growth here is strongly associated to precipitation and moisture availability in spring and in this regard responds similarly to stands further south (Figure A.22). Radial-growth, then, is strongly dependant on rainfall in spring and summer and will benefit by lower fall temperatures, neither of which are projected for this coming century.

Figure A.21. Photograph of the Oregon white oak stand on Coburg Ridge.

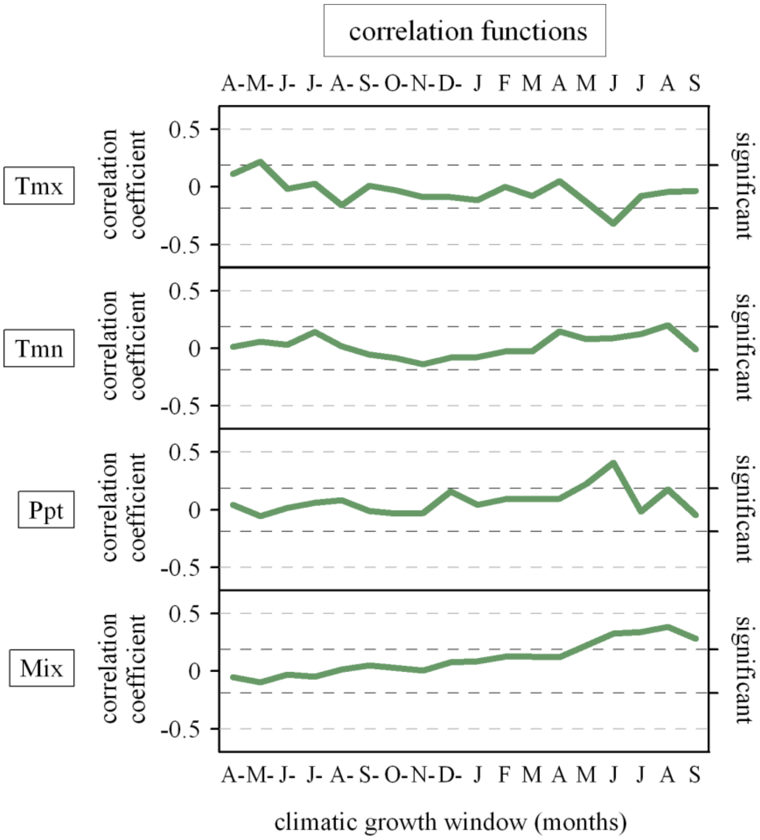

Figure A.22. Graph of correlation functions for the oak stand at Coburg Ridge.

North Bank

The sampled oak stand lies on a saddle high above the Umpqua River in Oregon. This woodland on the edge of a meadow consists of Oregon white oak trees as well as California black oaks (*Quercus kelloggii*) in all size classes (Figure A.23).

Trees in this stand respond similarly to those stands further south, especially in its response to temperatures: an inverse relationship to November in the fall before growth and May and June during ring formation and a positive response to temperatures in the spring prior. This site chronology is strongly correlated to precipitation in December before ring formation and to precipitation in May and June. North Bank, like all Oregon white oak stands analyzed here, is positively associated with moisture availability in spring and summer during the growing season (Figure A.24).

Figure A.23. Photograph of the sampled Oregon white oak stand at North Bank, above the Umpqua River.

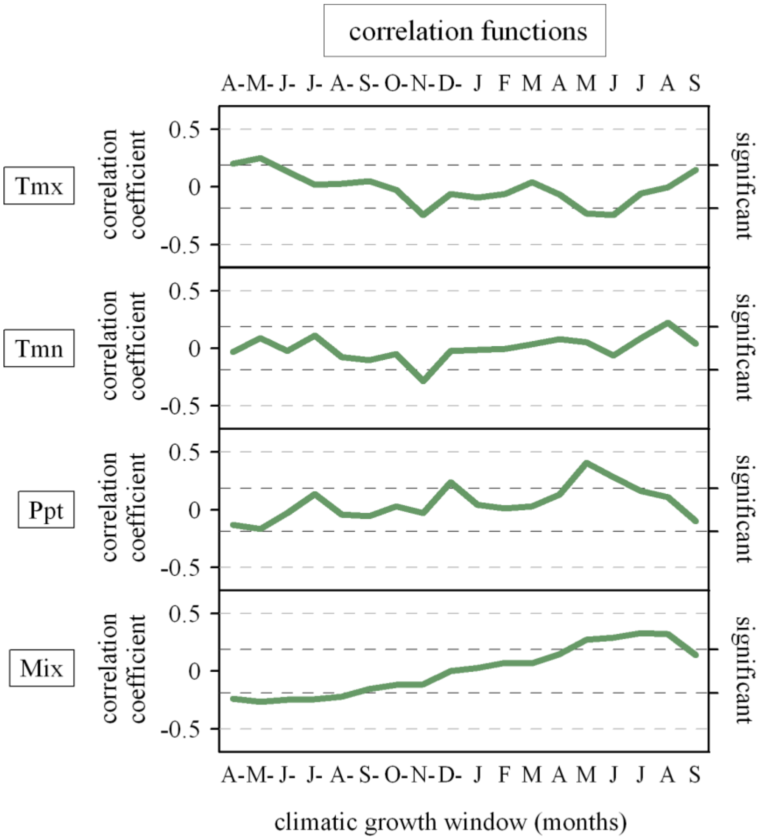

Figure A.24. Graph of correlation functions for the oak stand at North Bank.

Sam's Valley

The open oak savanna in Sam's Valley in southern Oregon consists almost entirely of even-aged Oregon white oak trees. Scattered buckbrush (*Ceanothus cuneatus*) and ponderosa pine also occur on the thin soil (Figure A.25). This stand experiences some of the warmest and driest summers when compared to other sites included in this analysis.

White oak trees in Sam's Valley respond positively to precipitation in the spring and negatively to maximum temperatures. The strongest correlations between radial-growth and the climatic variables are those to soil moisture availability in spring (Figure A.26). Increases in average monthly maximum temperatures projected for this century are likely to result in decreased growth, as will any decrease in winter or spring precipitation.

Figure A.25. Photograph of the Oregon white oak stand in Sam's Valley.

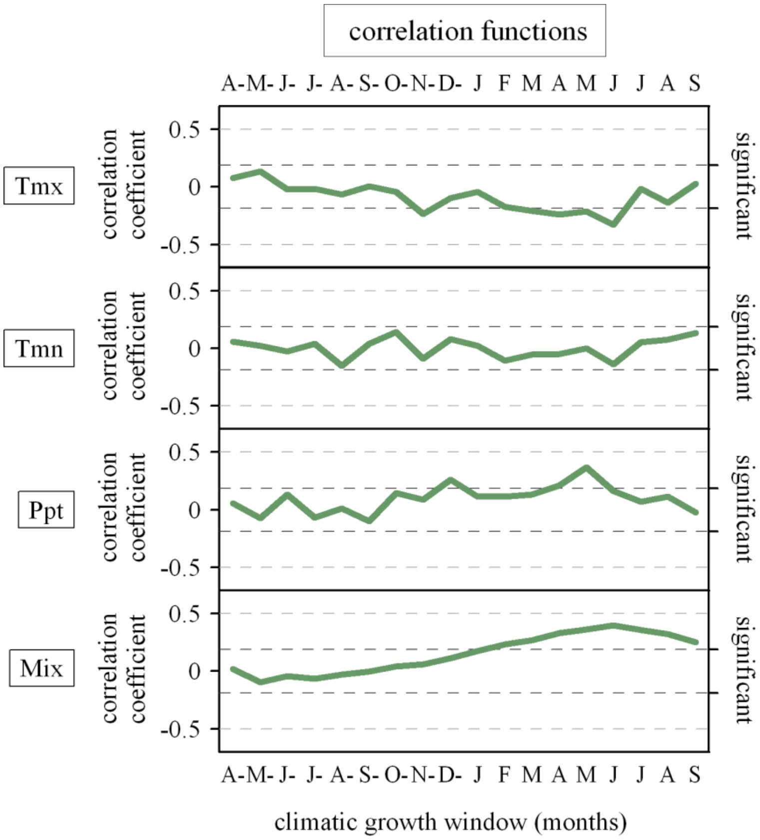

Figure A.26. Graph of correlation functions for the oak stand at Sam's Valley.

Oregon Gulch

Oregon Gulch is a Research Natural Area in southern Oregon, part of the Cascade-Siskiyou National Monument. Here, moderate-sized Oregon white oak trees on the margins of the foothills grow alongside smaller ponderosa pine, juniper (*Juniperus communis*), and buckbrush (Figure A.27). This stand experiences relatively cold, dry winters, and Oregon white oak trees here are some of the slowest-growing among those assessed in this study.

A positive response to precipitation and the index of available soil moisture occurs throughout the year, but these trees are most strongly limited by conditions in the spring. This stand responds negatively to maximum temperatures throughout most of its year, but especially in spring, and especially in June during the growing season. Positive responses to minimum temperatures also characterize the radial-growth of trees at this sit. (Figure A.28).

Figure A.27. Photograph of the Oregon white oak stand near Oregon Gulch.

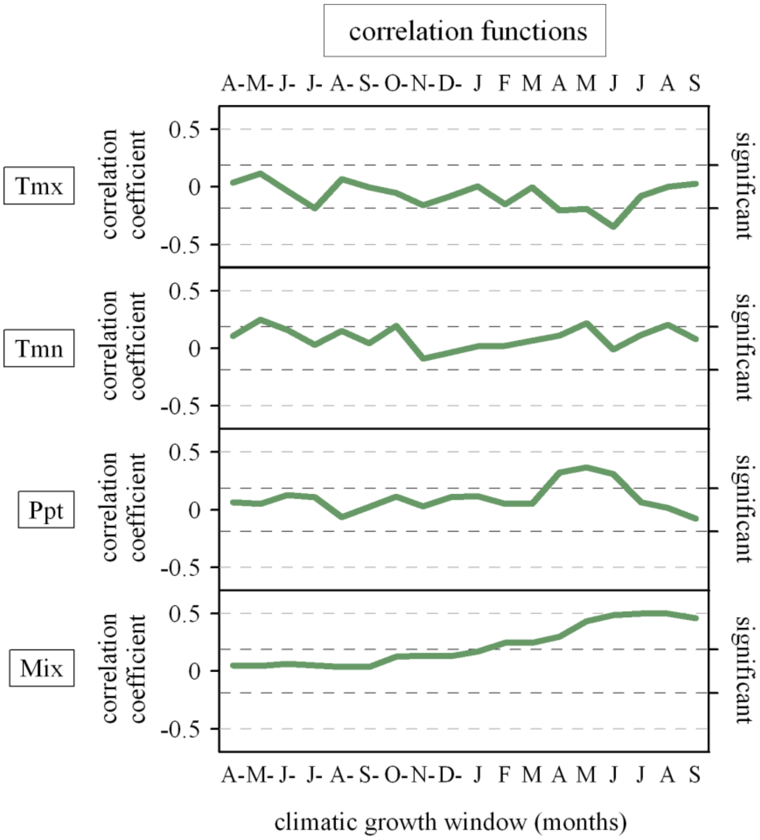

Figure A.28. Graph of correlation functions for the oak stand at Oregon Gulch.

Oak Knoll

Open-grown Oregon white oak trees, mostly with damaged crowns, were scattered in a mixed-stand within the Klamath National Forest in northern California (Figure A.29). A few California black oak, Douglas-fir, and ponderosa pine also inhabit this site, which experiences warm, dry summers relative to other sites in this study,. These trees are relatively slow-growing.

This stand's relationship to temperature is complex, with negative growth-responses to maximum temperatures from February through June and into August but a positive response to temperatures in the spring prior. Any increase in temperature is likely to be detrimental to these trees. Oak trees at this site respond increasingly positively to precipitation and availability of soil moisture in fall, winter, and spring, and rainfall in these seasons can be strongly limiting (Figure A.30).

Figure A.29. Photograph of the Oregon white oak stand at Oak Knoll.

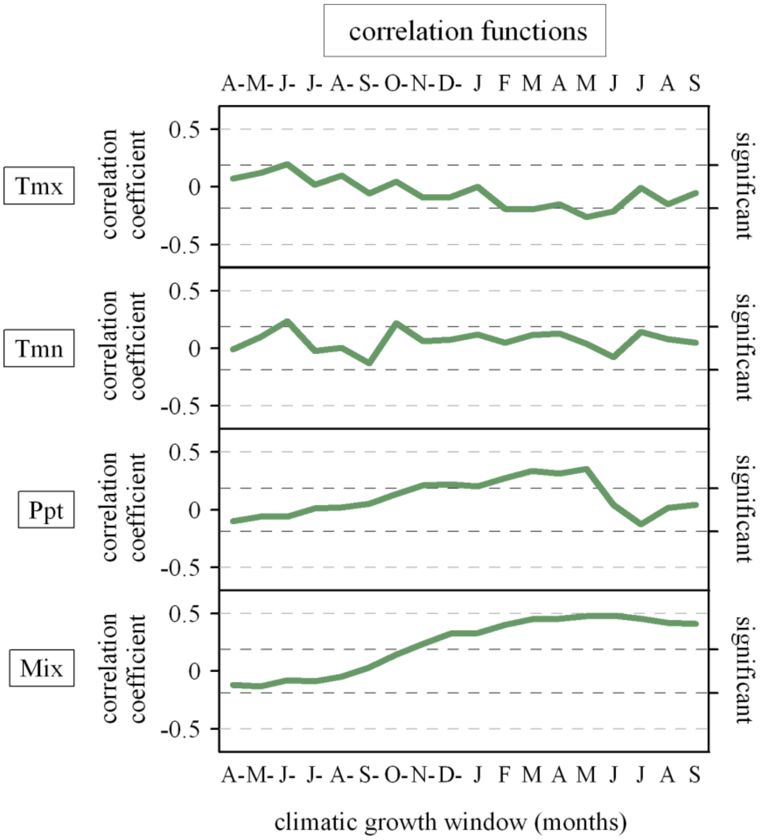

Figure A.30. Graph of correlation functions for the oak stand at Oak Knoll.

Clark Creek

The Oregon white oak trees we sampled near Clark Creek in Lassen National Forest in California are growing in open areas in thin soil along with a few California black oaks, Douglas-fir, and ponderosa pine (Figure A.31). Heartrot in the oak trees is common here. Buckbrush is scattered within these stands, an indicator of the dry summers common at this site. Relative to other sites in this study, Clark Creek is at higher elevation and experiences warmer summers and colder winters.

These Oregon white oak trees above Clark Creek have a negative or inverse growth-response to maximum temperatures in fall prior to growth and in spring, especially June. Radial-growth in this stand is most strongly correlated to precipitation in spring and the moisture index in winter, spring, and summer and this positive relationship holds throughout much of the year (Figure A.32). Any increase in temperature resulting in greater evapotranspiration rates are likely to be result in decreased radial-growth.

Figure A.31. Photograph of the Oregon white oak stand near Clark Creek in California.

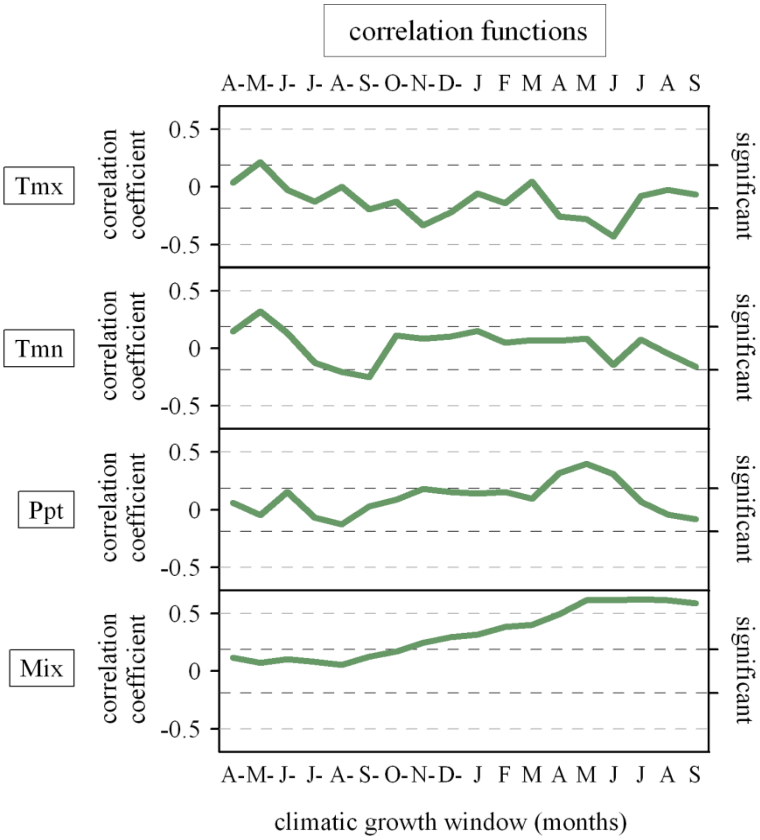

Figure A.32. Graph of correlation functions for the oak stand at Clark Creek.

Twin Rocks Ridge

Oregon white oaks on Twin Rocks Ridge in Mendocino National Forest grow in mixed-woodland (Figure A.33). California black oaks, live oaks (*Quercus agrifolia*), blue oaks (*Quercus douglasii*), manzanita (*Arbutus menziesii*), Douglas-fir, ponderosa pine, and gray pine (*Pinus sabiniana*) occur on or near the ridgetop. These trees grow at the highest elevation sampled in this study and are the furthest south. This stand experiences the warmest winters of sites included in this work and is relatively warm throughout much of the year. Its winters are very wet and summers very dry.

This stand in a remote area of northern California generally responds negatively to maximum temperatures and positively to minimum temperatures throughout most of the year. An even stronger positive growth-response occurs to precipitation and moisture availability in fall, winter, and especially in spring (Figure A.34). Changes in climate resulting in decreased moisture availability is likely to result in decreased radial-growth.

Figure A.33. Photograph of the Oregon white oak stand on Twin Rocks Ridge in California.

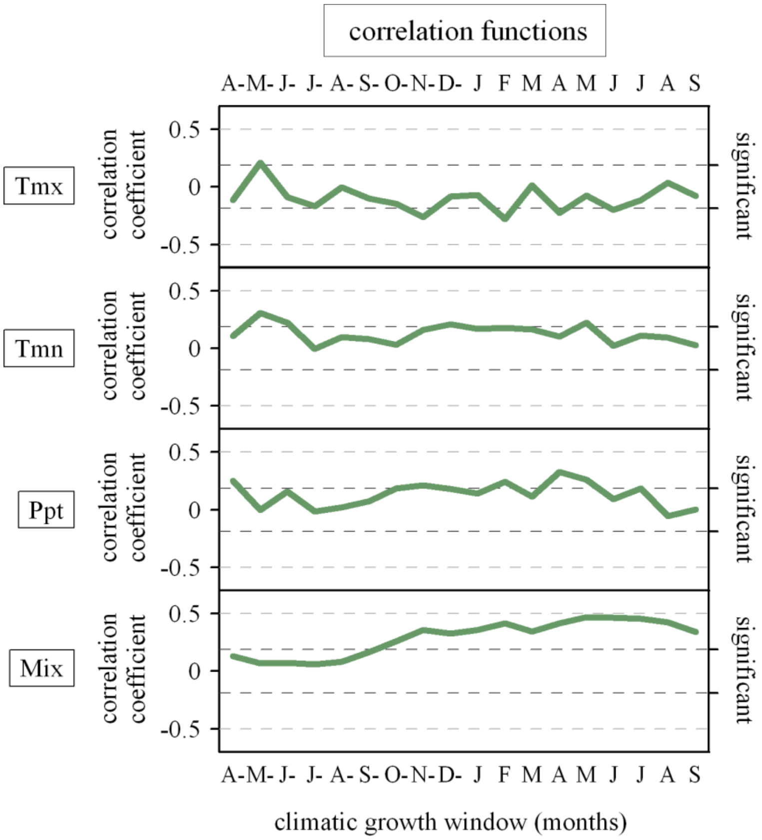

Figure A.34. Graph of correlation functions for the oak stand at Twin Rocks Ridge.

Bald Hills

Some Oregon white oak trees grow on the Bald Hills in Redwoods National Park in California. Moderately spaced clumps of oak trees grow among a diverse herb layer; no other woody tree species or shrubs were present (Figure A.35). Advanced fungal heartrot is common in the larger trees. The stand assessed here is on a south-facing convex slope bordered by ephemeral streams.

This stand near the coast experiences moderate temperatures throughout the year, including the highest minimum temperatures in winter, but has the wettest winters and some of the driest summers. The area is burned every few years to limit conifer encroachment, minimize the establishment of invasive species, and so maintain fire-adapted ecosystems (Sugihara et al 1987; park personnel 2007).

Unlike most other Oregon white oak stands, the trees at Bald Hills tend to respond positively to temperatures in May during the growing season, possibly reflecting the lack of irradiance available during this time. Foggy conditions may also be responsible for the lack of response to the moisture index during the growing season: this stand does not seem to be limited by water availability to the same degree as Oregon white oak stands experiencing drier conditions (Figure A.36).

Figure A.31. Photograph of the Oregon white oak stand on the Bald Hills in Redwoods National Park, California.

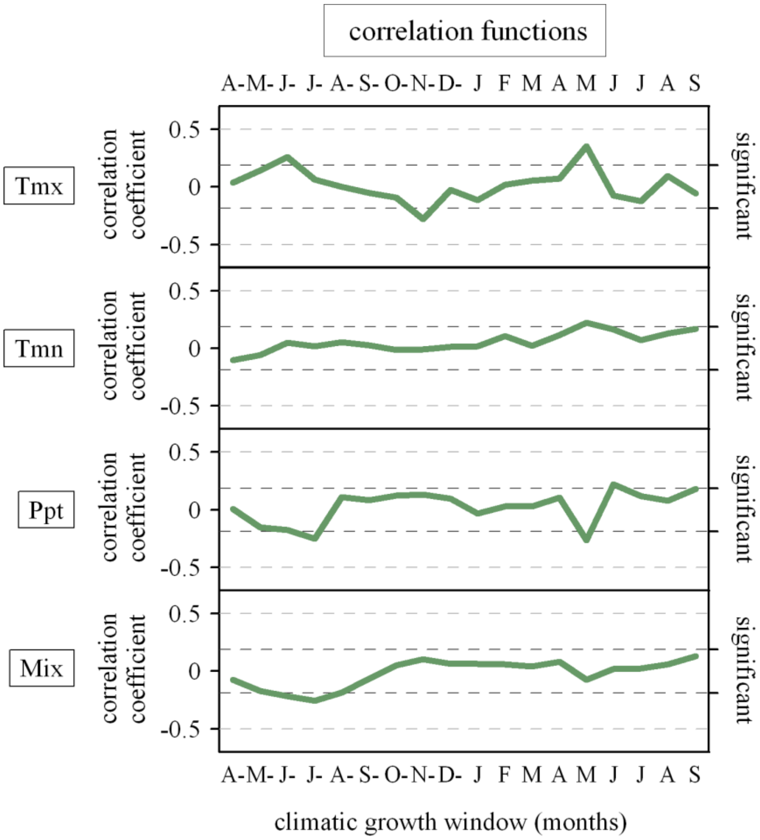

Figure A.32. Graph of correlation functions for an Oregon white oak stand on the Bald Hills.