Temporal and spatial variability in climate-growth response of mountain hemlock at treeline

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Abstract

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Climate-growth relationships in treeline forests are particularly informative because they represent the upper limit of a species range where growth is often especially sensitive to climatic variation. Radial growth response to climatic variables typically ranges from energy-limited to water-limited. In the Pacific Northwest (PNW) region of North America, treeline forests are typically energy-limited. Results from a recent study (Marcinkowski et al. 2015) indicate a change in climate-growth relationships over time in treeline mountain hemlock (*Tsuga mertensiana*) in northern Washington State. Here, we investigate whether these same changes occured across 700 km of the range of treeline mountain hemlock in Oregon and Washington. Using cores from trees >200 years old, we examined temporal and spatial variability of climate-growth relationships since the early 20th Century. Results indicate (1) a change in the climate variables influencing energy limitation in forest growth at treeline, (2) growth response to climate variables changes through time, (3) patterns of growth response to climate are similar between chronologies from similar latitudes, (4) and variable patterns of growth response to climate between chronologies from different topographic aspects. Correlations between radial growth and climate vary from significantly positively correlated to significantly negatively correlated for some variables. These results helped identify where changes in growth-limiting variables may be occurring, and suggest that the effects of a warmer climate on growth at treeline will be more complex temporally and spatially than has been suggested by previous analyses.

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Introduction

The growth response of coniferous tree species in the Pacific Northwest region of North America to changing climate can be characterized as a gradient from energy-limited to water-limited (Albright and Peterson 2013). However, pure energy limitation and pure water limitation represent the extremes, and most forests fall between the two. Growth in energy-limited forests is typically constrained by temperature and length of the growing season (Ettl and Peterson 1995, Gedalof and Smith 2001a), whereas growth in water-limited forests is typically constrained by climatic factors influencing soil water availability, such as solar radiation and precipitation (Case and Peterson 2005, Littell et al. 2008).

The subalpine treeline represents an ecotone across which trees gradually, or suddenly, become less dominant with increasingly unfavorable environmental conditions (Malanson et al. 2007). A balance between abiotic climatic factors and biotic tolerance factors determines the survival of individual trees and the upper limit of tree growth (Arris and Eagleson 1989, Körner and Paulsen 2004). Longer periods of below-freezing temperatures and snow cover truncate the growing season compared to lower-elevation forests. Exposure increases at treeline because of higher wind velocity, increased solar radiation, and decreased forest cover (Wieser and Tausz 2007). Individual trees close to this threshold between physiologically habitable and inhabitable environments are especially sensitive to the environment (Brubaker 1986, Kipfmueller and Salzer 2010), and even minor changes in climate factors can influence annual growth by altering the rate of physiological processes (Fritts 1976, Wieser 2007, Bunn et al. 2011, Salzer et al. 2014).

Microclimate is especially influential on plant growth in the subalpine environment, with no closed forest canopy to buffer the interaction between atmospheric processes and local site conditions (Wieser 2007). Differences in radiation inputs between north- and south-facing slopes affect soil and air temperatures, snow cover duration, soil moisture, and the resulting distribution of vegetation. For example, in the Pacific Northwest, the elevation of treeline is typically 150 m higher on southerly aspects than nearby northerly aspects (Franklin and Dyrness 1973). In the subalpine environment, even slight differences in topographic position may change growth responses to climate (Villalba et al. 1994, Bunn et al. 2011, Tran et al. 2017), including a shift from energy limitation to water limitation from northerly to southerly sites (respectively) within the same approximate elevation band (Leonelli et al. 2009).

Annual average temperatures in the Pacific Northwest have increased 0.8°C during the 20th century, and are expected to continue to increase an average of 0.3°C per decade during the 21st century (Abatzoglou et al. 2014). Additional changes in Pacific Northwest climate include reduced mountain precipitation (Luce et al. 2013), reduced snowpack (Mote 2006), a longer freeze-free season, and an increase in climatic water deficits (Abatzoglou et al. 2014). Seasonal projections include higher temperatures and less precipitation in the summer, and higher temperatures and slightly more precipitation, with more falling as rain, in the winter (Mote and Salathé 2010). These changes may affect climate-growth relationships to change in species found near treeline.

Mountain hemlock is a dominant subalpine tree species throughout the west side of the Cascade Range and Olympic Mountains and has been the subject of previous climate-growth investigations (Graumlich and Brubaker 1986; Taylor 1995; Smith and Laroque 1998; Gedalof and Smith 2001a, 2001b; Peterson and Peterson 2001; Laroque and Smith 2003, 2005; Marcinkowski 2012). Mountain hemlock growth has been shown to be sensitive to different phases of the Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO). Mountain hemlock climate-growth relationships also exemplify the gradient from energy limited to water limited (Peterson and Peterson 2001). At high-elevation sites, growth is correlated with variables that influence growing season length. Growth is negatively correlated with winter precipitation and snowpack and previous-year summer temperatures (Smith and Laroque 1998, Gedalof and Smith 2001a, Peterson and Peterson 2001). Growth is positively correlated with current-year summer temperatures (Smith and Laroque 1998, Gedalof and Smith 2001a, Peterson and Peterson 2001), and with winter PDO index (Gedalof and Smith 2001b, Peterson and Peterson 2001, Marcinkowski 2012) and spring ENSO index (Marcinkowski 2012). At low-elevation sites, growth is correlated with variables that influence water availability. Growth is negatively correlated with previous-year summer temperature and with winter PDO index (Peterson and Peterson 2001). Growth is positively correlated with previous-year summer precipitation (Smith and Laroque 1998, Gedalof and Smith 2001a, Peterson and Peterson 2001, Marcinkowski 2012).

Peterson and Peterson (2001) laid a foundation for investigating changes in growth response to climate throughout the range of mountain hemlock populations in the Pacific Northwest. Mountain hemlock in Washington and northern Oregon displayed a climate-growth relationship typical of an energy-limited system at high elevations and a water-limited system at low elevations. At lower-latitude sites in southern Oregon, climate-growth correlations suggested that a different set of climatic variables control growth. Growth was negatively correlated with spring snowpack depth, and previous-year summer temperature, but positively correlated with previous-year August precipitation. These results demonstrated that mountain hemlock growth was influenced by annual climatic factors, and growth responses to climate range from energy-limited to water-limited along elevation and latitudinal gradients.

In energy-limited subalpine forests, if climate change is manifest as warmer temperatures, decreased snowpack, and increased precipitation falling as rain, a longer growing season and increased productivity would be expected (Latta et al. 2010). Since the early 20th century, several coniferous species showed an increase in growth with increasing temperatures in the Northern Hemisphere:

- Washington: western hemlock *(Tsuga heterophylla* (Raf.) Sarg.), Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes), and mountain hemlock (Graumlich et al. 1989).
- California and Nevada: bristlecone pine (*Pinus longaeva* D.K. Bailey) (Salzer et al. 2014) and limber pine (*Pinus flexilis* E. James) (La Marche et al. 1984).
- California: lodgepole pine (*Pinus contorta* var. *murrayana* Douglas ex Loudon), whitebark pine (*Pinus albicaulis* Engelm.) (Peterson et al. 1990), and limber pine (*Pinus flexilis* E. James) (Millar et al. 2015).
- California: whitebark pine and western white pine (*Pinus monticola* Douglas ex D. Don) (Millar et al. 2004).
- Europe: Scots Pine (*Pinus sylvestris* L.), mugo pine (*Pinus mugo* Turra), Bosnian pine (*Pinus heldreichii* Christ), Austrian pine (*Pinus nigra* Arnold), Balkan pine (*Pinus peuce* Griseb.), silver fir (*Abies alba* Mill.), and Norway spruce (*Picea abies* (L.) Karst) (Briffa 1992).

In contrast, studies across the Northern Hemisphere, sampling different tree species, have documented a recent decrease in sensitivity to temperature.

- (D'Arrigo et al. 2008); review of many studies of various species at high latitude and high elevation.
- Alaska: white spruce (*Picea glauca* (Moench)Voss) at latitudinal and elevation treeline (Jacoby and D'Arrigo 1995).

- Italian Alps: European larch (*Larix decidua* Mill.) at elevation treeline (Coppola et al. 2012).
- Siberia: Dahurian larch (*Larix gmelini* (Rupr.) Rupr.) at latitudinal treeline (Jacoby et al. 2000)
- Kyrgyzstan: Juniper species (*Juniperus* spp. L.) at elevation treeline (Esper et al. 2003)
- California: Bristlecone pine (*Pinus artistata* Englem.) near elevation treeline (Salzer et al. 2014).

In a large-scale study averaging tree-ring measurements across sites representative of boreal forests in the Northern Hemisphere, a weakening in sensitivity to temperature was detected in chronologies since the early 1960s (Briffa et al. 1998). Tree growth increased with the high temperatures recorded for the 1930s and 1940s, and decreased during the cooler 1950s, but did not respond to the continuous increase in temperatures that began in the 1970s. Suggested causes of decreased sensitivity to increased temperature included summer drought, increased competition with other plants, increased insect herbivory, and changes in solar radiation.

Peterson and Peterson (2001) found a growth response typical of an energy-limited system at high-elevation sites in the Cascade Range of Washington and northern Oregon, where growth was positively correlated with summer temperature and negatively correlated with winter precipitation and April 1 snow-water equivalent (SWE). However, D’Arrigo et al. (2004) found a weakening in the energy-limited signal at high-latitude treeline sites. Most recently, in the Cascade Range of Washington state, Marcinkowski et al. (2015) found growth-climate results similar to those of D’Arrigo et al. (2004). Although the sites sampled by Marcinkowski et al. overlapped the study area of Peterson and Peterson (2001), the recent results at treeline were different. At these high-elevation, previously energy-limited areas, growth was no longer significantly correlated with winter precipitation or April 1 SWE, and was significantly correlated with spring temperature. Climate-growth relationships changed over time, and correlations were not consistently significant over time. These recent findings suggest a change in the limiting factors that influence climate-growth relationships over time.

Research on mountain hemlock growth response to climatic factors in the Pacific Northwest (Peterson and Peterson 2001), and recent insight into potential changes in limiting factors (Marcinkowski et al. 2015), need to be reconciled with a broader contemporary sample. Treeline forests are ideal for detecting climatic effects because of (1) climatic sensitivities of trees living at the highest elevation edges of their distribution, (2) changes in temperature and snowpack documented at high-elevation sites, (3) their ecological importance as ecotones (EDW 2015), and (4) the value of their climate-growth relationships as proxies for reconstructing past climates. Quantifying changes in these relationships will improve the accuracy of modeling the effects of climatic variability and change in forest growth.

In this study, we investigated climate-growth correlations for treeline mountain hemlock on north- and south-facing aspects on the west side of the Cascade Range and Olympic mountains in Washington and Oregon. We used a 95–120 year analysis period to explore (1) variability throughout time in climate-growth correlations, (2) variability between aspects for climate-growth relationships, and (3) variability among populations on a latitudinal gradient.

Methods

Study Area

Sampling was conducted in subalpine forests on the west side of the Cascade Range in Washington state and Oregon, and in the Olympic Mountains of Washington (Figure 1). Subalpine forests are found at the highest elevations of these mountains with environmental conditions that support the physiological function of trees, characterized by the gradual decrease of continuous forest into tree islands, as environmental conditions become increasingly unfavorable with increasing elevation (Malanson et al. 2007). The Olympic Mountains and the west side of the Cascade Range in Washington and northern Oregon have a maritime climate that is strongly influenced by air circulation patterns from the Pacific Ocean. Winters are wet and cold, and summers are warm and dry. These subalpine areas are extensions of the maritime climate, however at these high elevation sites, the high amounts of precipitation fall as snow early in autumn, and low temperatures create a deep snowpack that can persist into the summer months.

Nine high-elevation locations were sampled in the summer of 2016. At each location, a dominant north and south aspect was sampled, for a total of 18 sites. Sites were chosen along a latitudinal transect to span the range of subalpine mountain hemlock populations in Washington and Oregon. The sites spanned from near Mt. Baker in northern Washington, to Crater Lake National Park in southern Oregon (Figure 1). All sites were above 1300 m in elevation.

At each site, sampling was conducted by hiking above the treeline, and then slowly dropping elevation until 20 suitable trees were located on the respective aspect, and cores were collected. This method ensured that the highest-elevation trees were sampled at each site. Suitable trees were defined as greater than 200 years old (to eliminate juvenile growth trends), dominant or codominant (to eliminate strong signals from competition), and with no obvious structural flaws (e.g., broken tops, insect or fire damage). The location of all sampled trees was recorded using a hand-held GPS, and the height and diameter at breast height were also recorded.

Chronology construction

Trees were cored at breast height (1.3 m), using an increment borer on the cross-slope position whenever possible to avoid compression wood. Tree cores were stored in paper straws for transport back to the lab, where they were mounted in grooved boards and sanded with progressively finer grades of sand paper. Tree rings were measured to the nearest 0.001 mm with a measuring stage (Velmex Inc., Bloomfield, New York), Measure J2x software (version V4.2 VoorTech consulting, Holderness, New Hampshire), and an Olympus DF PLAN 1.5x measuring scope. Tree rings were crossdated using standard dendrochronology techniques (Stokes and Smiley 1968), and crossdating was substantiated by creating time-shifted correlation coefficients for cores with mean chronologies for each site with the program COFECHA (Holmes 1983).

Each series was detrended with the the R package dplR (Bunn et al. 2017) to remove trends in growth from age-related biological processes. A cubic spline with a 50% cutoff of 150 years was used for detrending in order to isolate annual and decadal variability without washing out trends occurring over longer time spans. Other detrending techniques were investigated, but according to descriptive statistics, the results were not sensitive to the method (Fritts 1976).

The detrended series were standardized into a unitless index by dividing the ring-width measurement by the value of the fitted curve. In order to maximize the climate-growth signal, the individual series were prewhitened with an autoregressive model to remove autocorrelation and biological signals. Chronologies were generated for each site by averaging all of the residuals for trees in each site together using a Tukey’s biweight robust mean. A correlation matrix was created with the site chronologies using Pearson’s product moment correlation to investigate broad similarities in growth between sites (Appendix 1).

Climate data

A combination of results from monthly correlations and similar previous studies (Peterson and Peterson 2001, Marcinkowski et al. 2015) determined which climatic variables would be most appropriate for this analysis. The following climatic variables are included: spring (April – May) temperature, summer (June – August) temperature, winter (November – March) precipitation, summer precipitation, summer Palmer Drought Severity Index, winter El Niño Southern Oscillation Index (ENSO), winter Pacific Decadal Oscillation (PDO), previous growth year winter precipitation, previous growth year summer temperature, and previous growth year spring temperature.

Monthly climate data for temperature, precipitation, and PDSI spanning 1986 – 2015, and aggregated from weather stations in similar climatic regions to division, were obtained from the National Climate Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html, accessed February 2017). Divisional data were used because the compilation of individual station data within a climatic region represents the overall regional climate better, and has a longer record than most single stations. The 18 sites fell within the boundaries of 8 different climate divisions. Trees sampled at the north aspect site of Minotaur Lake fell between two divisions, so the one containing more samples was used. PDO index data for 1901–2015, were obtained from the University of Washington Joint Institute for the Study of the Atmosphere and Ocean climate data archives (available from http://research.jisao.washington.edu/pdo/PDO.latest, accessed March 2017). The Niño region 3.4 Index (ENSO) from 1870 – 2015 was obtained from the National Oceanic and Atmospheric Administration (available from https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Nino34/, accessed April 2017). Monthly climate variables were averaged to create seasonal climate variables for spring, summer and winter.

Correlations

Climatic variables used in this analysis were chosen based on correlations between monthly climate variables and site chronologies, and significant climate variables from similar previous studies (Marcinkowski et al. 2015, Peterson and Peterson 2001). Monthly Pearson product-moment correlations were calculated between site chronologies and current-year and previous-year values for precipitation, temperature, PDSI, PDO index, and ENSO index.

The chronologies were shortened to the length of the climate records, which varied from 120 to 145 years. Moving correlations were calculated between seasonal climatic variables and each site chronology. Moving correlation functions systematically move forward over a fixed amount of time, and significance is calculated for each year with a constant sample size (Biondi 2000), producing a time series of annual correlations between the two variables. This method employs multiple Pearson product-moment correlation tests that assess significance ($\alpha=0.05$) for each time step, as the window steadily shifts forward over the analysis period. Only window lengths less than 40 years were considered to ensure observation of decadal and annual trends that would be obscured by longer window lengths. A 25-year right-aligned window was chosen to mirror the analysis from the Marcinkowski et al. (2015) study, and all direct comparison of results. The many consecutive correlation tests performed in this analysis method could inflate the type I error rate, leading to spurious correlation values, and a misclassification of significant results. The interpretation of the analysis presented relies on both significant and non-significant results.

Results

Chronology Descriptions

Chronology statistics were calculated for the chronologies to infer appropriateness for use in climate-growth analysis (Table 1). Sample depth for all site chronologies was 20 cores. Mean interseries correlation measures the similarity of growth response between trees at a site. Values ranged from 0.497 to 0.684, which suggests a similar response to climatic variability among the chronologies. Expressed population signal (EPS) measures how similar a chronology is to an ideal hypothetical chronology. A general guide for acceptable EPS values is ≥ 0.85 (Wigley et al. 1984), and values in this study ranged from 0.80 to 0.91. Although the EPS value was below the common guide for three sites, we were comfortable continuing with our analysis because EPS values were close to 0.85, our sample depth was high for all sites, and the point of the study was to compare patterns across many populations.

Changes in mountain hemlock growth over time are illustrated through moving correlations for the 18 site chronologies and different climatic variables and indices. All site correlations are nonstationary over the analysis time period, with correlation values varying and moving in and out of significance.

The following sites change from significantly negatively correlated with winter precipitation (figure 2), to not significantly correlated during the most recent 25 years of the study: Baker-N, Olympic-N, Minotaur-N, Minotaur-S, Rainier-N, Rainier-S, Adams-N, Hood-N, Bachelor-N, Bachelor-S, Crater Lake-S. Correlations between growth chronologies and winter precipitation for all sites fluctuate throughout time, and are not significant during the early to mid 1920s. All sites visually trend toward more negatively correlated during the late 1920s to 1930s. Growth becomes more negatively correlated with winter precipitation in the late 1970s. The north and south aspect sites at Mt. Baker, the Olympic Peninsula, and Crater Lake are more distinctly different from each other throughout time than the paired aspect sites for other locations.

The following sites have changed from not significantly correlated, to a significant positive correlation with spring temperature (Figure 3) during the past 25 years: Baker-S, Olympic-S, Minotaur-N, Minotaur-S, Hood-N, Jefferson-N, Jefferson-S, Bachelor-N, Bachelor-S, Crater Lake-N, Crater Lake-S. Correlations between site growth chronologies and spring temperature are significant during the 1920s for all sites except Olympic-N, Olympic-S, Minotaur-N, and Adams-N. Correlations between growth and spring temperature for all sites are not significant for a period during the 1960s and 1970s. All sites except Olympic-N have been significantly positively correlated with spring temperature at least once throughout the analysis period.

Growth at Baker-S, Rainier-N, Jefferson-N, Jefferson-S, Bachelor-N, and Bachelor-S is significantly positively correlated with summer temperature (Figure 4) during the last 10 years of the analysis. Correlations between site growth chronologies and summer temperature fluctuate over time, with multiple sites varying from negatively to neutral to positively correlated. The north and south aspect sites of Mt. Baker appear independent of each other until recently, when the two aspects converge near a significant positive correlation. Olympic-N, Olympic-S, and Crater Lake-S are the only sites for which growth is significantly negatively correlated with summer temperature during the period of analysis.

Bachelor-N and Jefferson-S show a recent significant negative correlation between growth and summer precipitation (Figure 5), and are the only two sites for which growth is currently negatively significantly correlated with summer temperature. Correlations between growth and summer precipitation are non-significant for all sites except Hood-S until the 1930s. Growth is not significantly correlated with precipitation for any site from the 1980s until the early 2000s. Olympic-S is the only site that shows significant positive correlation with summer precipitation at any point in the analysis period. The Oregon sites follow a similar visual trend throughout the analysis period, whereas the Washington sites are in agreement for some periods and variable for others. The Oregon sites all share a distinct decrease in correlation around 1940, followed by an immediate upward trend. Olympic-S is significantly positively correlated with summer precipitation from the late 1950s to the mid 1970s.

The following sites moved from not significantly correlated, to significantly negatively correlated with summer PDSI (Figure 6) during the last 25 years of the analysis: Baker-N, Baker-S, Olympic-N, Olympic-S, Rainier-N, Rainier-S, Adams-N, Adams-S, Hood-N, Hood-S, Jefferson-N, Jefferson-S, Bachelor-N, and Crater Lake-N. Correlations between growth and summer PDSI for Oregon sites show similar trends over the analysis period, whereas the Washington sites are more variable. Olympic-S is the only site significantly positively correlated with summer PDSI during the analysis period.

All sites share similar overall trends in correlations between growth and winter ENSO index (Figure 7). Correlations are positive (or neutral, e.g. Baker-N) around 1900, and steadily trend down to neutral or negative until the 1950s to 1970s, trend to positive around the 1980s, and then back down to neutral or negative until the end of the analysis period. Growth is not significantly correlated with winter ENSO index for any sites during the last 15 years of the analysis period.

Correlations between growth and winter PDO index (Figure 8) are variable in the direction and magnitude of correlation, and mostly not significant over time. All sites share a similar decrease in magnitude of correlation around 1940, followed by an increase over the next decade. There is a similar peak shared by all sites around 1980. Growth is not significantly correlated with winter PDO index for any site from the 1980s to 2015.

Correlations between growth and previous growth-year spring temperature (Figure 9) are mostly negative throughout the analysis, with the exception of Olympic-N and Olympic-S. Growth and previous growth-year summer temperature (Figure 10) are also mostly negatively correlated throughout the analysis. Previous growth-year winter precipitation (Figure 11) is largely positively correlated with growth throughout the analysis, with the exception of Baker-N and Baker-S.

Discussion

Previous studies have demonstrated that high-elevation mountain hemlock growth is controlled by climatic variables that influence length of the growing season (and therefore energy limitation) (Peterson and Peterson 2001, Albright and Peterson 2013), and these relationships change through time (Marcinkowski et al. 2015). The results of this study corroborate previous results for subalpine forests (Driscoll et al. 2005, Lloyd and Fastie 2002, Marcinkowski et al. 2015, Sherriff et al. 2017), by suggesting that climate-growth relationships vary by location. The results also indicate that relationships between climatic factors and mountain hemlock growth at high elevation are changing in Washington and Oregon.

Winter precipitation, a surrogate for growing season length, has longer periods of significant correlation, and for more sites, than other climate variables. However, correlations with growth at 7 of 10 Washington sites, and 3 of 8 Oregon sites recently decreased below significance (Figure 2). During this same recent time period, growth at 6 of 10 Washington sites and 7 of 8 Oregon sites became significantly positively correlated with spring temperature

(Figure 3). These recent changes are similar to results from Marcinkowski et al. (2015) who posited that these changes might suggest a change in the factors limiting growth, and a shift along the gradient from energy-limitation, to an intermediate response between energy-and water-limitation. Winter precipitation, or the length of the growing season, could be replaced by temperature variables as the growing season starts earlier.

However, a decrease in sensitivity to the length of the growing season, and an increase in sensitivity to spring temperature, is still an energy-limited response, but indicates a change in the variables driving the relationship. If a climate variable changes, so that it is no longer limiting, growth will theoretically continue until a variable becomes limiting again (Fritts 1976). As the snow melts out earlier, the growing season is initiated earlier, and these energy-limited populations are able to take advantage of energy inputs earlier. This relationship manifests as a decrease in the magnitude of correlation with winter precipitation, and an increase in correlation with spring temperature.

The increase in correlation with spring temperature indicates that these populations throughout Oregon and Washington are not showing a decrease in sensitivity to temperature similar to the higher latitude treeline populations summarized in D'Arrigo et al. (2008). Although the variables driving climate-growth relationships are shifting, the mountain hemlock populations sampled in this study are still sensitive to changes in temperature, and still within an energy-limited environment. The results presented here indicate that the decoupling from the temperature signal occurring in some higher-latitude treeline populations is not occurring at these lower-latitude treeline populations of mountain hemlock in Washington and Oregon.

Summer temperature is overall positively correlated with growth during the recent period of analysis (Figure 4), and summer precipitation is overall negatively correlated (Figure 5). For water-limited sites, the opposite response is characteristic, and growth is negatively correlated with summer temperature, and positively correlated with summer precipitation. This implies that these sites are not showing a climate-growth response of water-limited sites, and still within the energy-limited domain.

Although growth is positively correlated with summer temperature during the recent period of analysis, correlations are variable throughout time. For energy-limited, subalpine sites, higher summer temperatures would theoretically result in increased growth, or a positive correlation. Lower summer temperatures would theoretically result in less growth, which would also manifest as a positive correlation. Many combinations of climate variables can produce an annual growth ring. For example, a negative correlation with summer temperatures could occur from a summer with high temperatures, but frequent overcast skies, or conversely, lower than normal temperatures, but ample solar radiation. In addition, temperatures can fluctuate greatly between day and night in the subalpine environment, and determining whether the high or low temperatures are driving these correlations, is not possible with the analysis conducted in this study.

PDSI is a measure of dryness based on recent temperature and precipitation measurements (Palmer 1965). Lower PDSI values indicate more dryness. Growth is mostly negatively correlated with summer PDSI throughout the analysis period. Six out of 10 Washington sites, and 6 out of 8 Oregon sites show a recent, significant negative correlation with summer PDSI (Figure 6). This is similar to what Marcinkowski et al. (2015) found for treeline chronologies in northern Washington. A negative correlation with summer PDSI for subalpine locations probably means that increased dryness increases growth. Winter ENSO is variable in correlation with growth at all sites through time. Correlations fluctuate from positive to neutral to negative, and in and out of significance. Correlations for all sites are generally in agreement throughout the analysis period. The visual increase in correlation around 1977, and the decrease around 1999, may be explained by PDO phase changes during these years. Correlations with growth and winter PDO are similar for all sites, and variable throughout the analysis period. Correlations are only briefly significant for Baker-N, Minotaur-N, and Rainier-N in the 1980s.

Correlations between growth and previous-year climate variables were a secondary consideration for this study, because the physiological mechanisms between current-year growth and climate of the previous year are poorly understood. Correlations between growth and previous-year climate often display an inverse relationship with their current-year counterpart. In this study, growth is positively correlated with summer temperature during the last 25 years of the study, and negatively correlated with previous-year summer temperatures during the same time period. A similar inverse relationship exists for spring temperature and winter precipitation.

Different aspect sites at a location had different correlations for multiple climate variables (winter precipitation, summer temperature, summer precipitation) throughout the analysis period. This indicates that tree growth on different dominant topographic aspects is influenced differently by certain climate variables. Aspect is rarely considered as a mechanism controlling growth in the subalpine ecosystem, because the dominance of snow as a limiting factor is thought to diminish the importance of topographic position of trees (Peterson 1998). However, aspect and microsite conditions are significant drivers of growth for some treeline locations (Villalba et al. 1994, Bunn et al. 2011). Winter precipitation has similar correlations for the farthest north sites, with Baker-N and Olympic-N close to neutrally correlated and Baker-S and Olympic-S significantly negatively correlated. However, the Minotaur Lake and Mt. Rainier sites have a distinctly different pattern by aspect, and receive similar amounts of winter precipitation.

Overall, different aspect sites at the same location follow similar patterns throughout time. When aspects are distinctly different, they have periods of convergence, for example winter precipitation and summer temperature for the north and south aspect sites at Mt. Baker have distinctly different correlations throughout most of the analysis, but aspects for both variables converge to nearly identical correlations at various points. This mixed response for aspects could indicate that other factors still overwhelmingly influence growth in the subalpine ecosystem, and topographic aspect is less impactful to growth than other factors.

Conclusions

This study investigated a potential change in climate-growth correlations in mountain hemlock by using an extensive spatial extent and contemporary sample. This allowed investigation of changes throughout time for a large portion of the range of mountain hemlock. Results of this study indicate that mountain hemlock climate-growth relationships at treeline are variable throughout a large portion of the range of the species. Recent changes in correlations between growth and winter precipitation and spring temperature suggest that the variables driving energy limitation in these populations are changing, and climatic factors that were previously limiting, no longer are. Correlation patterns are typically grouped by latitude, where the highest latitude sites share a similar signal over time, the lowest latitude sites share a similar signal over time, and the responses of the mid-latitude sites are less consistent.

Although the economic value of subalpine forests is generally low (e.g., for timber), as a dominant species across montane regions of the Pacific Northwest, mountain hemlock is ecologically significant, and accurate quantification of its growth and productivity are important for understanding ecosystem function (Blanco et al. 2017). Empirical results from this study can be used to project productivity and carbon storage for mountain hemlock in response to a warmer climate (Laroque and Smith 2003, 2005). The results can also inform resource managers about current conditions in subalpine forests, which is relevant for local resource planning and project management. The variability in results over time provide evidence to resource managers that climate-growth relationships will probably continue to change in the future, and a monitoring program is important for tracking these changes.

Variability of mountain hemlock populations in radial growth response to climate can provide fine-scale input for risk management and prioritization of monitoring activities. For example, a long-term program to quantify climate-growth relationships for a subset of sites from this study would provide a parsimonious, meaningful, and feasible monitoring design for land managers with limited resources. In addition, the portion of mountain hemlock geographic distribution not included in this study could be sampled to determine if results from this study are consistent across the entire species range. Finally, this study could be conducted again in 20-30 years to determine how growth has continued to respond to climatic variability and change.

It is tempting to make generalizations from limited data on climate-growth relationships about how a species will respond to future changes in climate. Indeed, vegetation models often simulate responses for individual species across large land areas without regard to significant sources of variability (Gustafson et al. 2016). The variable temporal response observed across the geographic domain of this analysis indicates that simple generalizations may be inaccurate. Assuming that growth is a component of fitness (Clark et al. 2011), flexible climate-growth relationships in mountain hemlock will probably ensure the persistence of this species in subalpine ecosystems in a warmer climate, at least in the absence of severe disturbances (e.g., crown fire; Dickman and Cook 1989) and large-scale regeneration failure.

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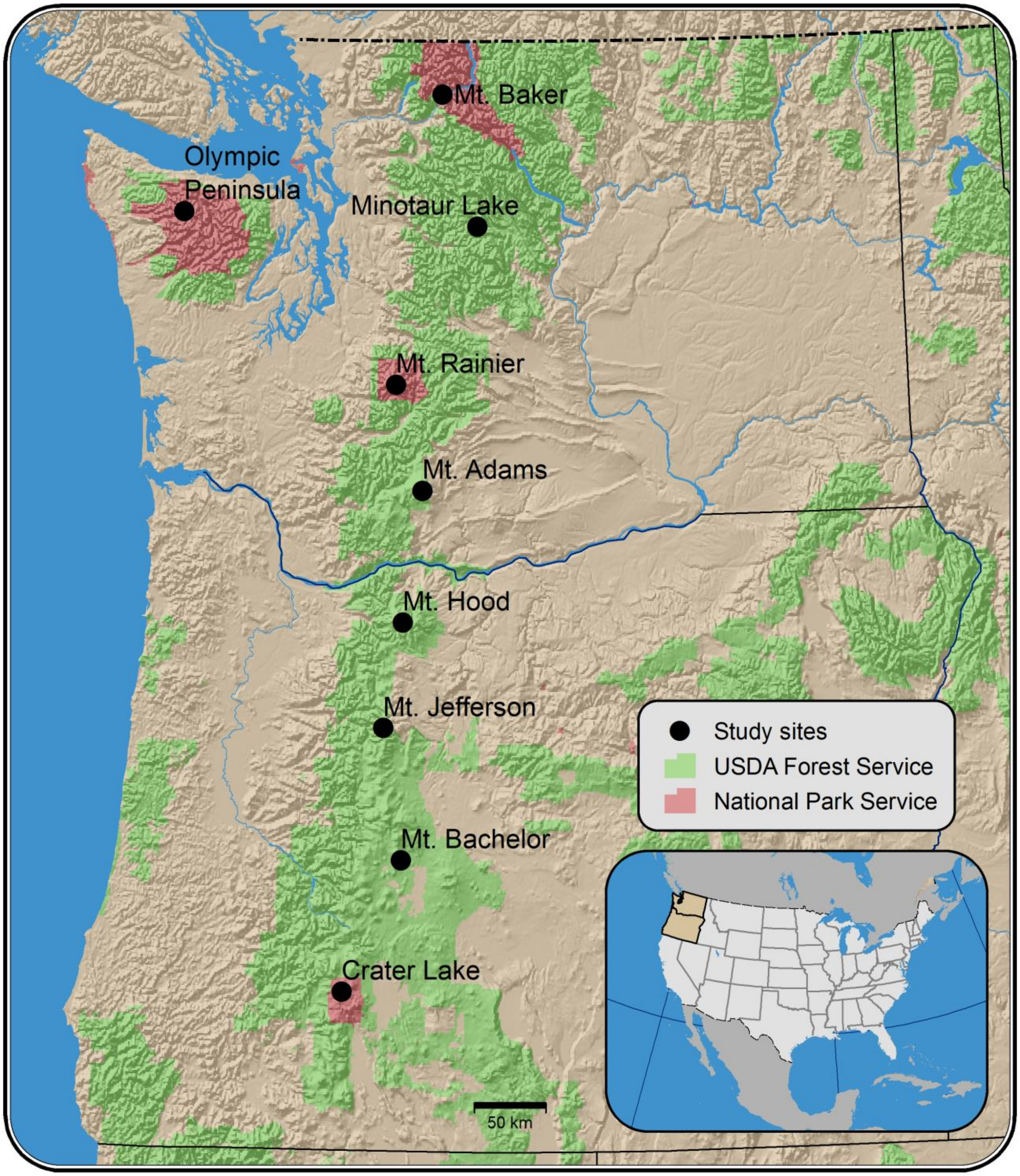


Figure 1. Region where mountain hemlock was sampled.

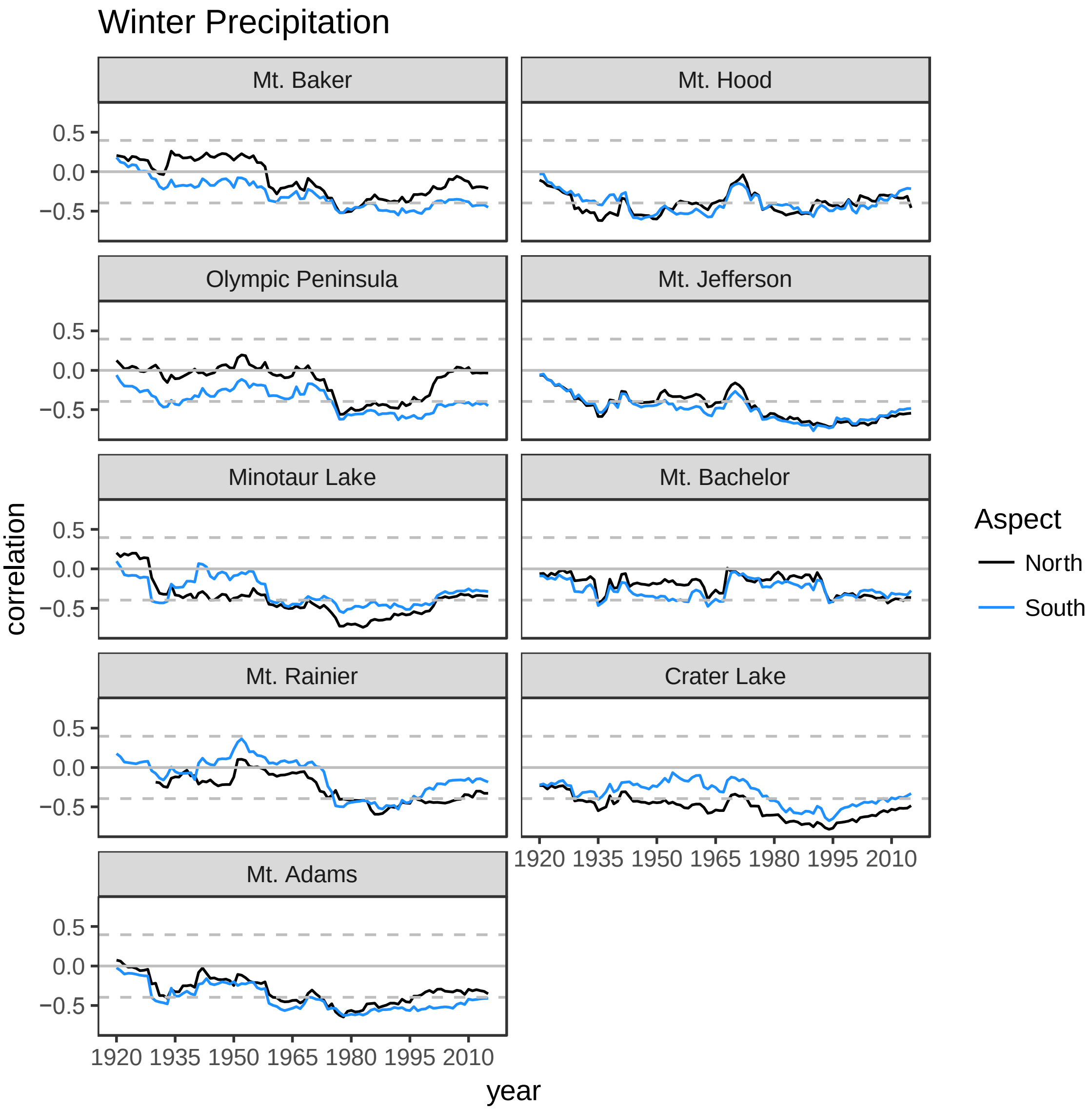


Figure 2. Moving correlations over a 25-year window between mountain hemlock radial growth and winter precipitation at each site. Dashed lines indicate a significance (*p*<0.05) cutoff of ±0.396.

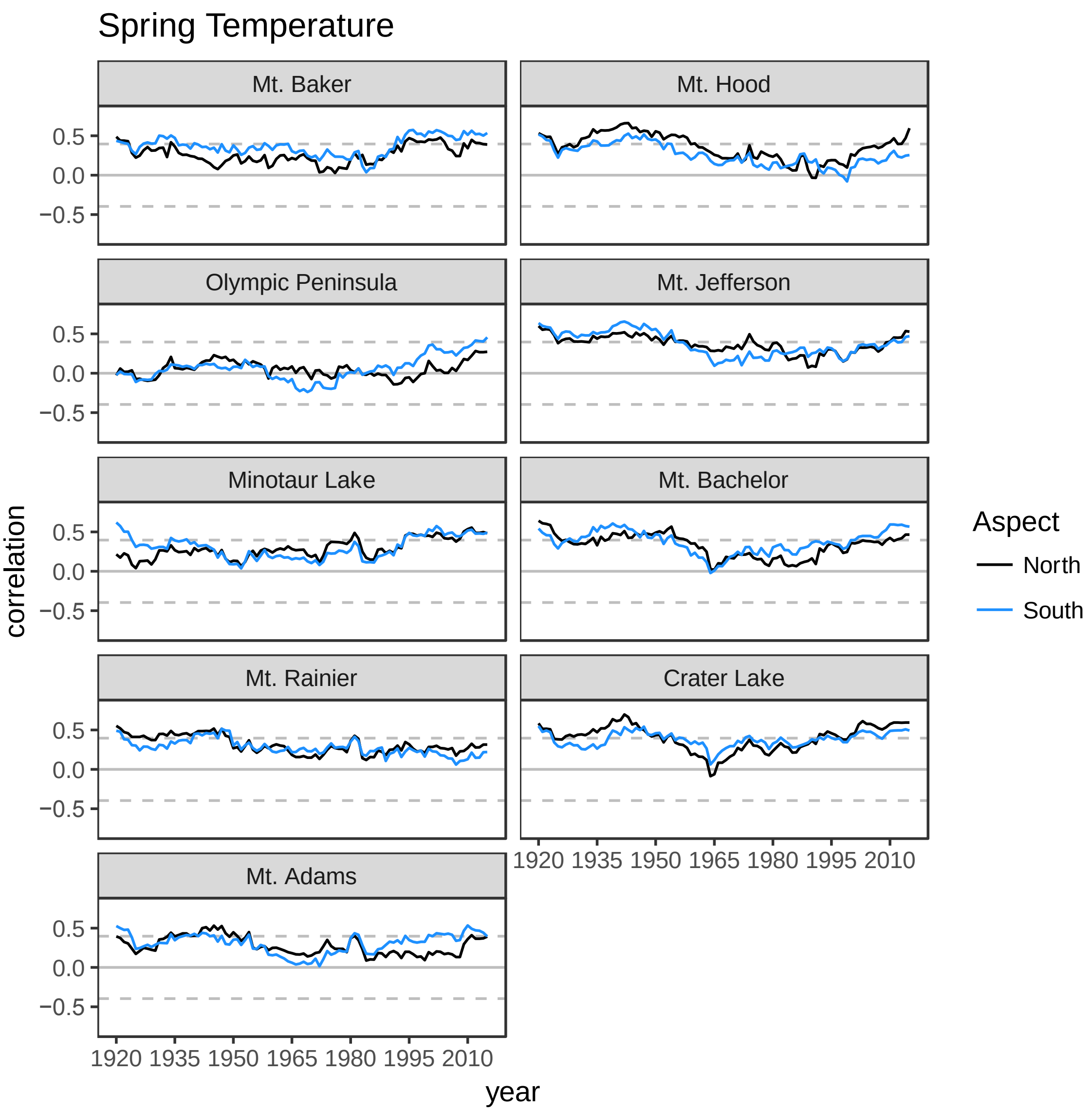


Figure 3: Moving correlations over a 25-year window between mountain hemlock radial growth and spring temperature at each site. Dashed lines indicate a significance (*p*<0.05) cutoff of ±0.396.

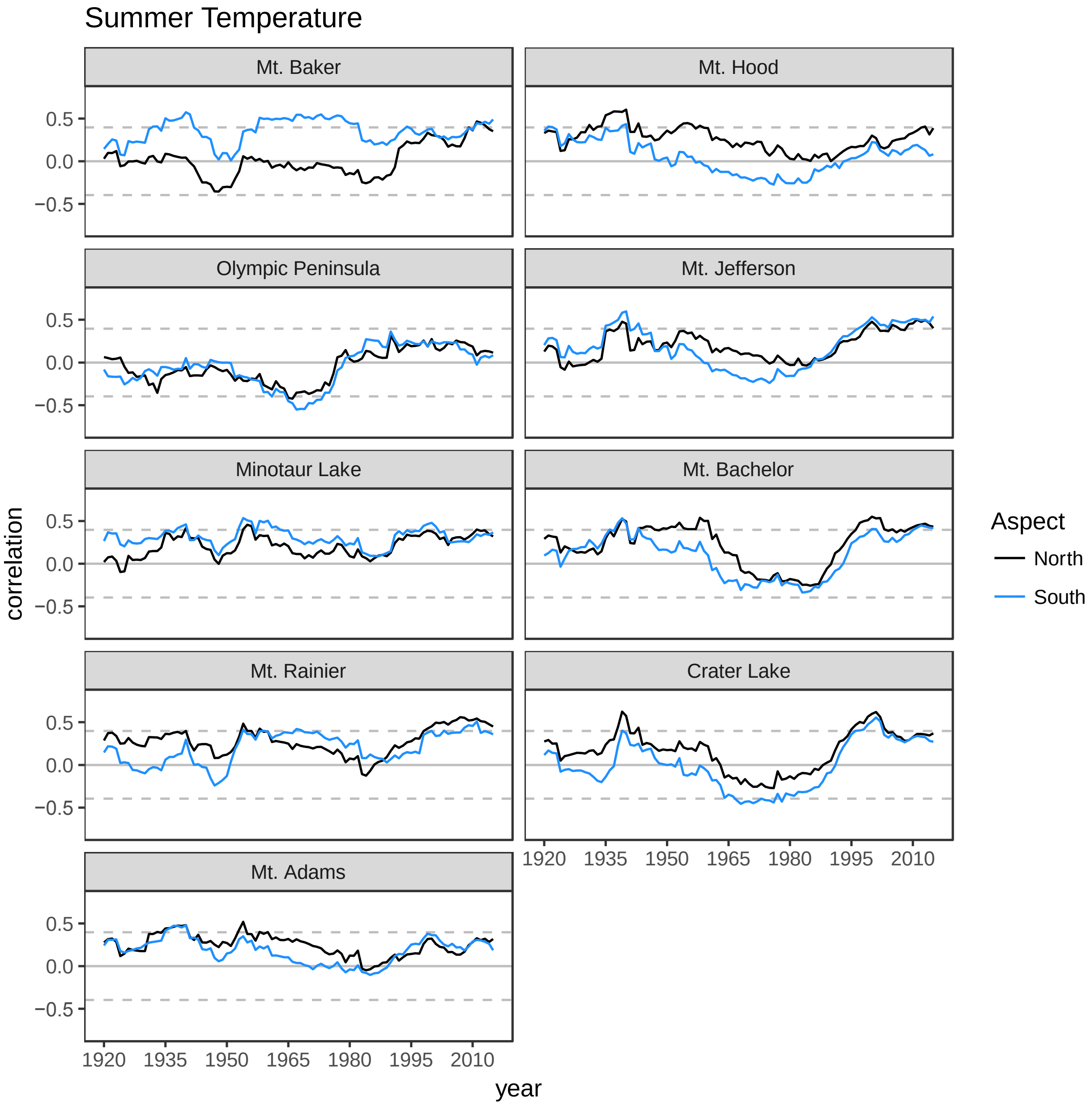


Figure 4: Moving correlations over a 25-year window between mountain hemlock radial growth and summer temperature at each site. Dashed lines indicate a significance (*p*<0.05) cutoff of ±0.396.

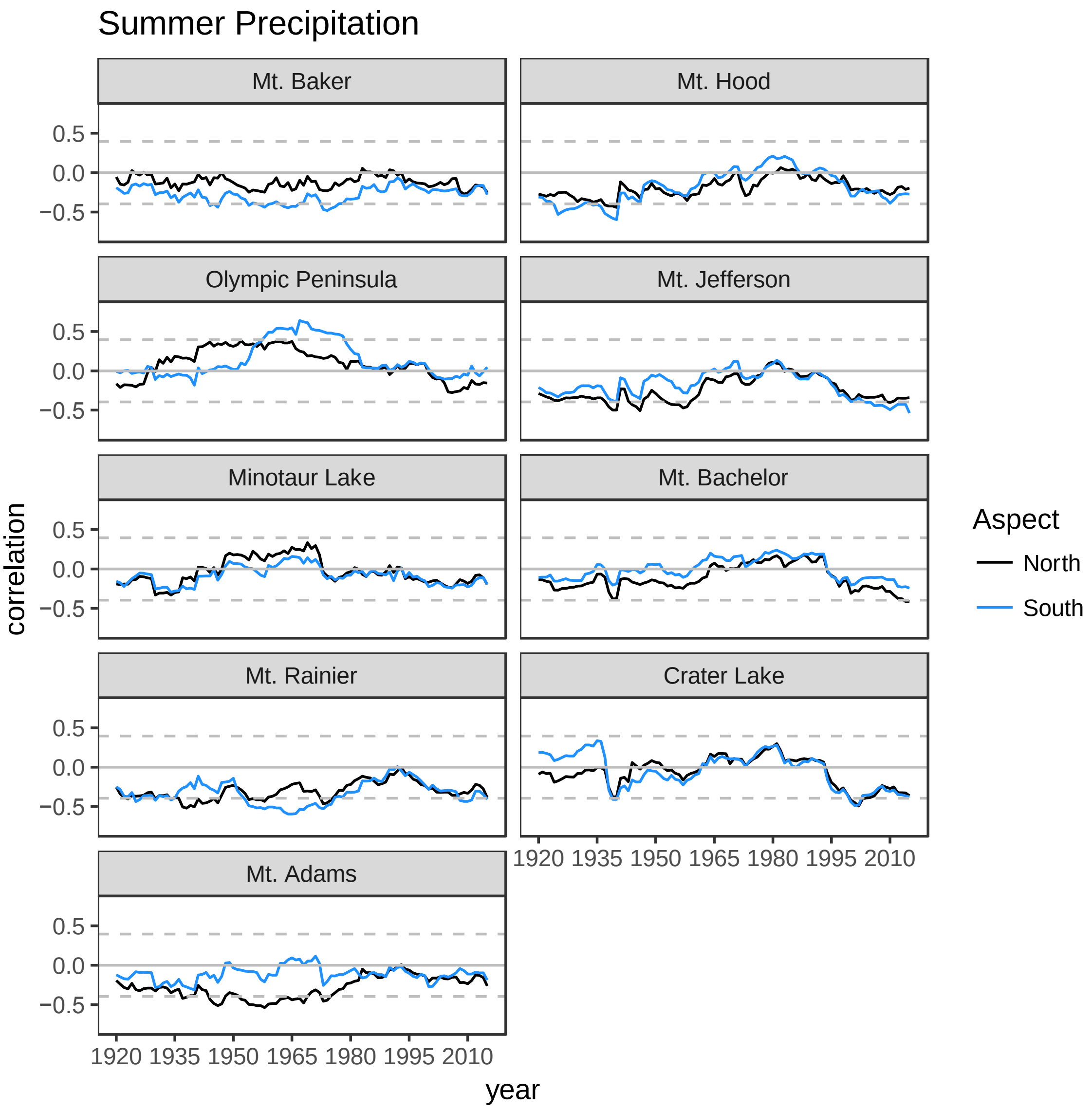


Figure 5: Moving correlations over a 25-year window between mountain hemlock radial growth and summer precipitation at each site. Dashed lines indicate a significance (*p*<0.05) cutoff of ±0.396.

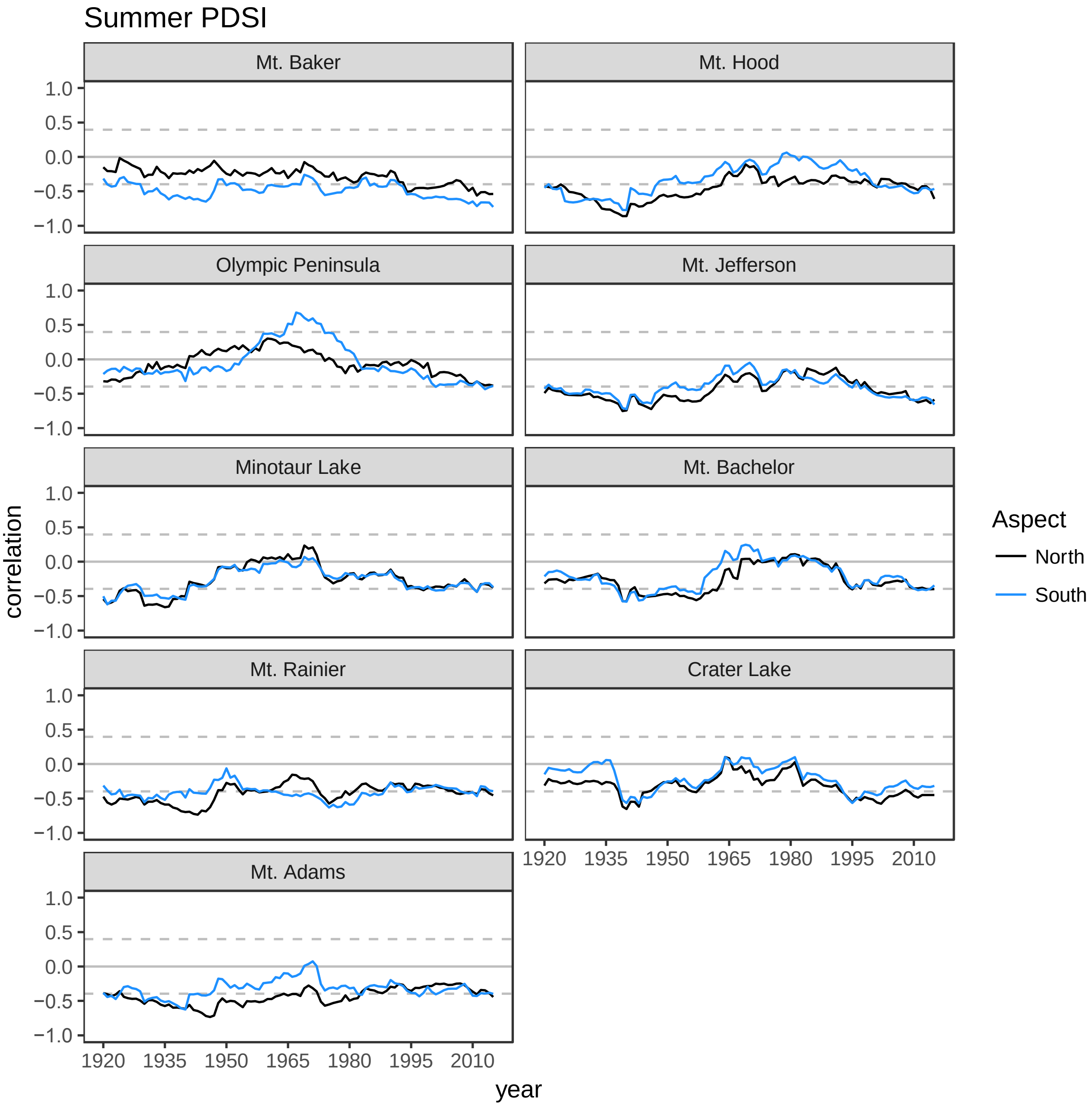


Figure 6: Moving correlations over a 25-year window between mountain hemlock radial growth and summer PDSI at each site. Dashed lines indicate a significance ($p<0.05$) cutoff of ±0.396.

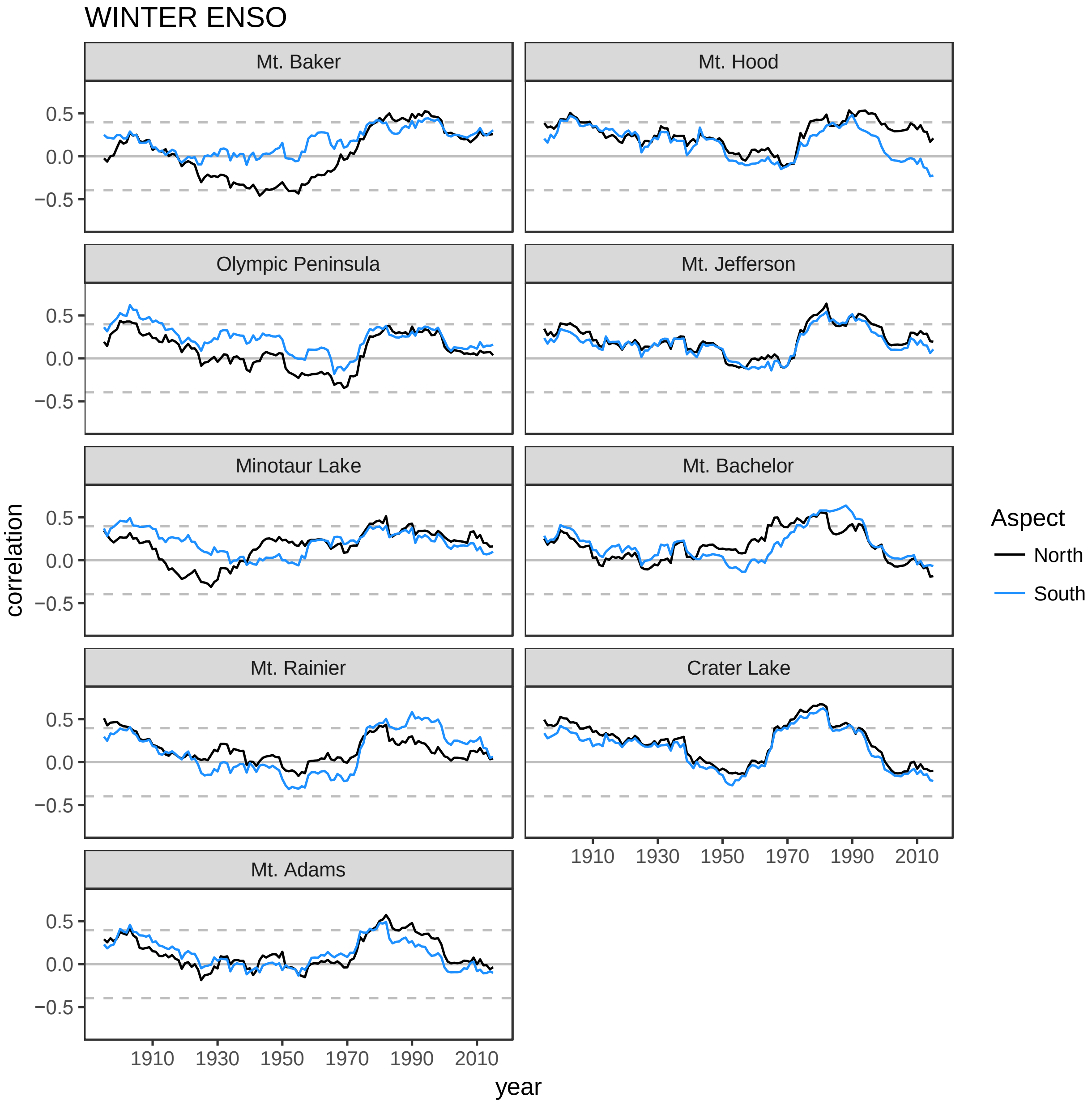


Figure 7: Moving correlations over a 25-year window between mountain hemlock radial growth and winter ENSO index at each site. Dashed lines indicate a significance (p<0.05) cutoff of ±0.396.

Figure 8: Moving correlations over a 25-year window between mountain hemlock radial growth and winter PDO index at each site. Dashed lines indicate a significance ($p<0.05$) cutoff of ±0.396.

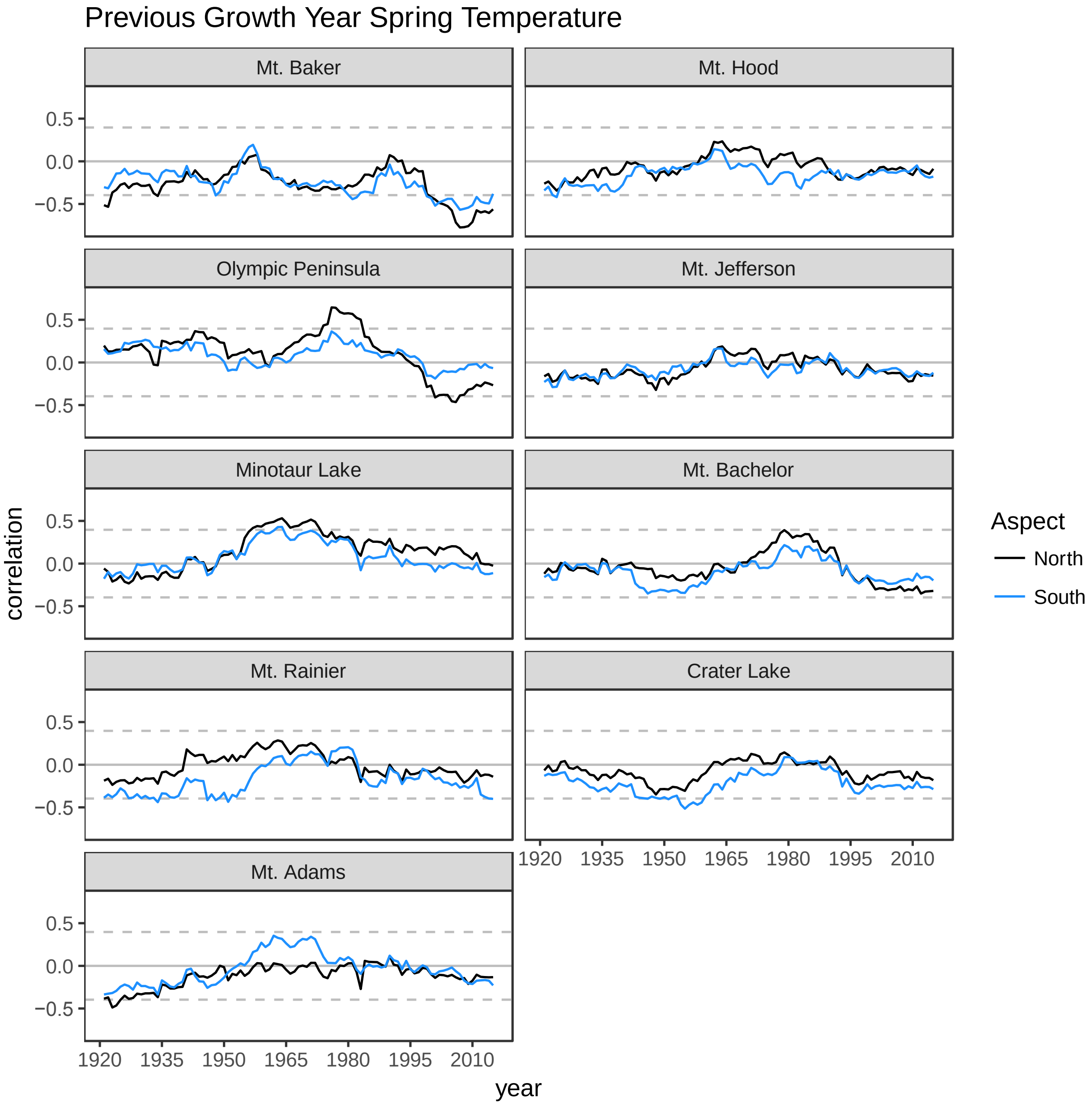


Figure 9: Moving correlations over a 25-year window between mountain hemlock radial growth and previous growth-year spring temperature at each site. Dashed lines indicate a significance ($p<0.05$) cutoff of ±0.396.

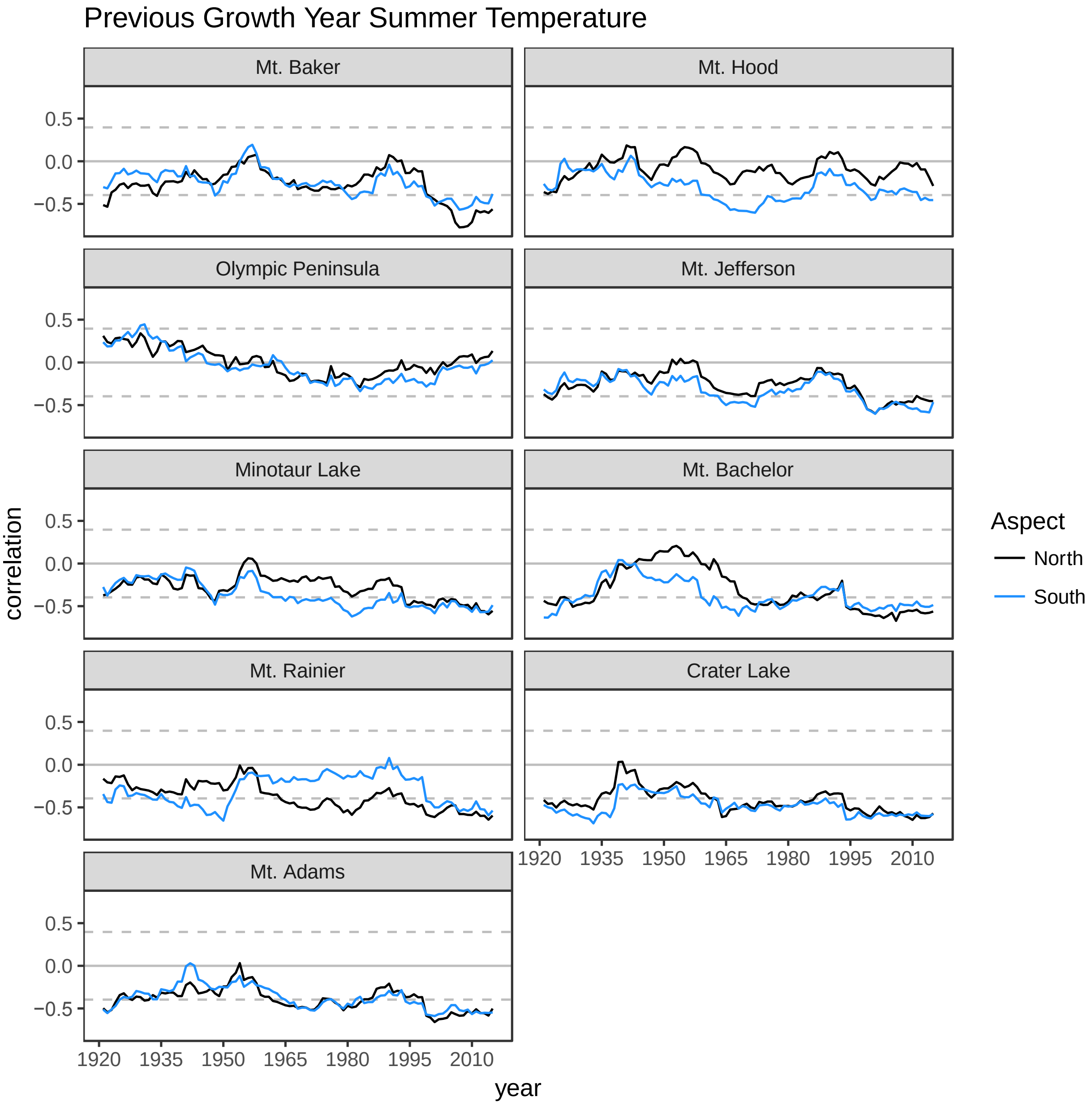


Figure 10: Moving correlations over a 25-year window between mountain hemlock radial growth and previous growth-year summer temperature at each site. Dashed lines indicate a significance (*p*<0.05) cutoff of ±0.396.

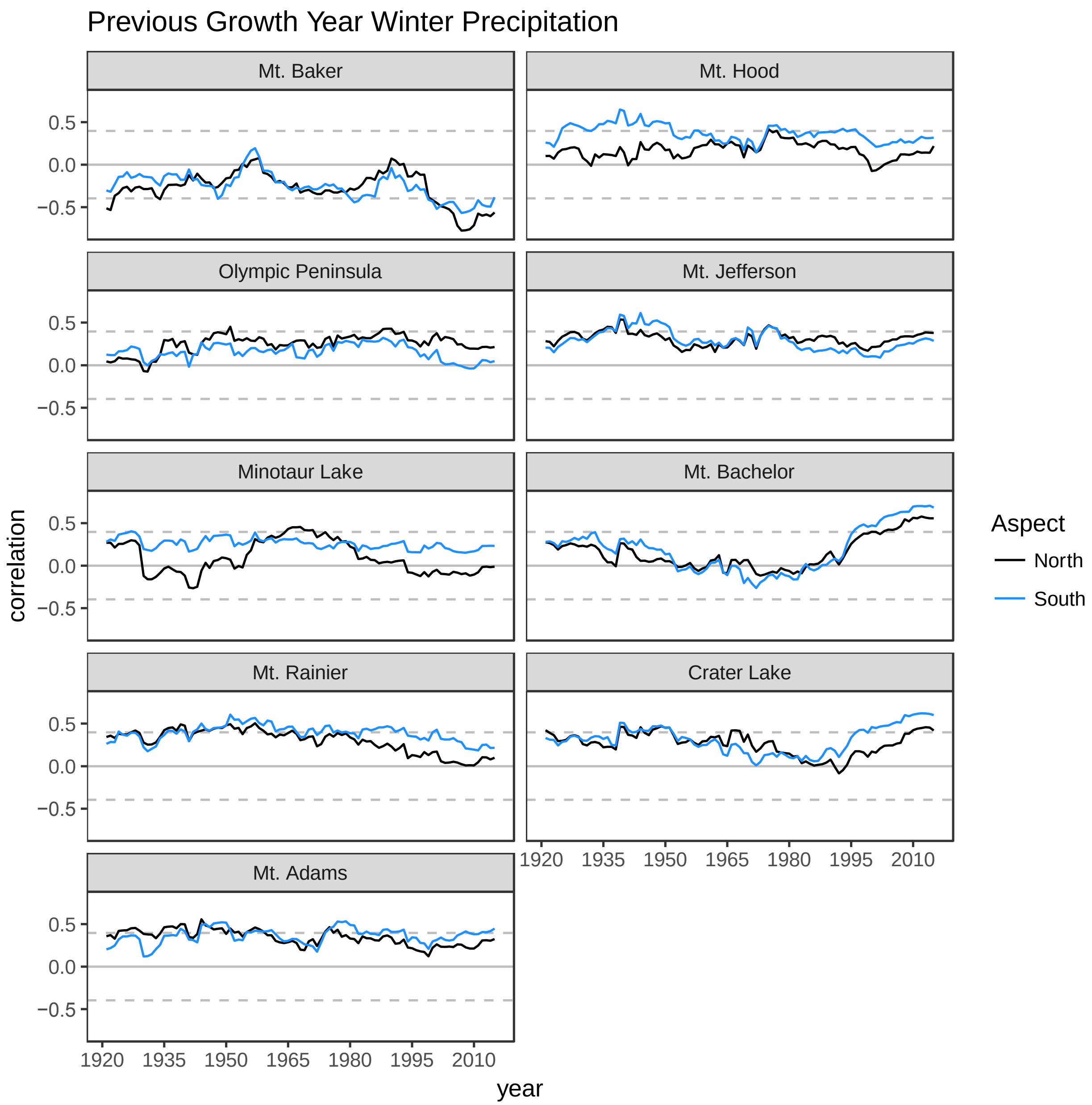


Figure 11: Moving correlations over a 25-year window between mountain hemlock radial growth and previous growth-year winter precipitation at each site. Dashed lines indicate a significance (p<0.05) cutoff of ±0.396.

Table 1. Summary of site characteristics

Site	Mean Elevation (m)	Longitude	Latitude	Mean DBH (cm) (SD)	Year Range	Median Age (years)	Mean Age (years)
Mt. Baker North (Baker-N)	1256	-121.675667	48.862467	86.1 (15.5)	1473-2015	370	365
Mt. Baker South (Baker-S)	1507	-121.825800	48.850767	73.3 (19.0)	1542-2015	317	329
Olympic Peninsula North (Olympic-N)	1348	-123.783817	47.920100	61.8 (18.4)	1445-2015	284	309
Olympic Peninsula South (Olympic-S)	1580	-123.771317	47.905700	49.7 (9.7)	1602-2015	296	312
Minotaur Lake North (Minotaur-N)	1663	-121.038167	47.855467	59.3 (13.5)	1547-2015	267	293
Minotaur Lake South (Minotaur-S)	1719	-121.036533	47.839350	64.1 (9.3)	1698-2015	223	236
Mt. Rainier North (Rainier-N)	1746	-121.581433	46.920533	77.0 (12.1)	1639-2015	252	260
Mt. Rainier South (Rainier-S)	1539	-121.728750	46.774883	75.0 (12.4)	1609-2015	243	258
Mt. Adams North (Adams-S)	1852	-121.544917	46.236733	75.0 (12.7)	1631-2015	254	263
Mt. Adams South (Adams-S)	1904	-121.494800	46.151117	70.6 (10.9)	1607-2015	253	265
Mt. Hood North (Hood-N)	1843	-121.705567	45.410233	61.2 (14.5)	1595-2015	293	300
Mt. Hood South (Hood-S)	1841	-121.722100	45.334983	66.0 (11.0)	1609-2015	317	313
Mt. Jefferson North (Jefferson-N)	1842	-121.807967	44.701017	79.5 (18.2)	1593-2015	273	295
Mt. Jefferson South (Jefferson-S)	1823	-121.825800	44.617417	84.2 (13.2)	1563-2015	285	299
Mt. Bachelor North (Bachelor-N)	2068	-121.686733	44.001917	85.4 (12.1)	1636-2015	300	304
Mt. Bachelor South (Bachelor-S)	2226	-121.968967	43.968967	80.1 (13.9)	1633-2015	311	309
Crater Lake North (Crater Lake-N)	2121	-122.117233	42.980950	105.2 (16.8)	1554-2015	308	326
Crater Lake South (Crater Lake-S)	2049	-122.118067	42.846733	95.3 (19.5)	1601-2015	280	290

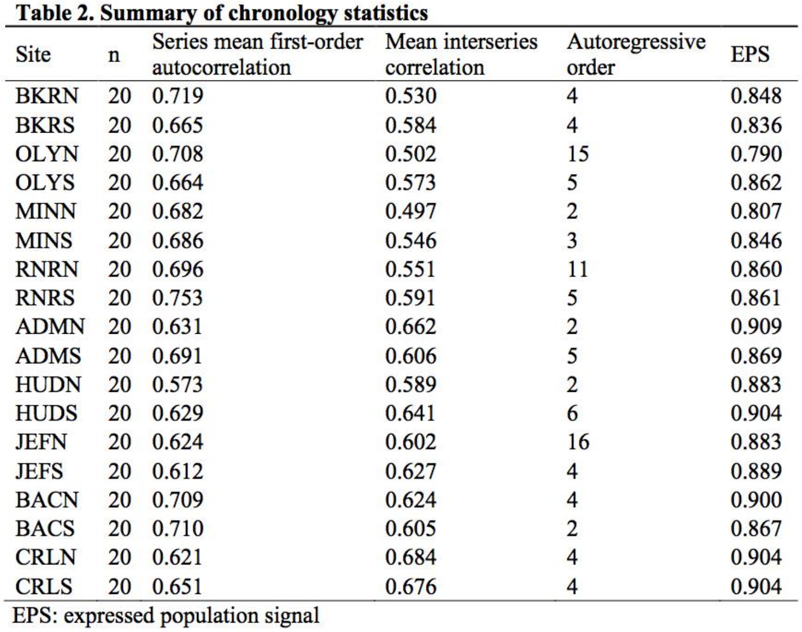


Table 2. Summary of chronology statistics

Site	n	Series mean first-order autocorrelation	Mean interseries correlation	Autoregressive order	EPS
BKRN	20	0.719	0.530	4	0.848
BKRS	20	0.665	0.584	4	0.836
OLYN	20	0.708	0.502	15	0.790
OLYS	20	0.664	0.573	5	0.862
MINN	20	0.682	0.497	2	0.807
MINS	20	0.686	0.546	3	0.846
RNRN	20	0.696	0.551	11	0.860
RNRS	20	0.753	0.591	5	0.861
ADMN	20	0.631	0.662	2	0.909
ADMS	20	0.691	0.606	5	0.869
HUDN	20	0.573	0.589	2	0.883
HUDS	20	0.629	0.641	6	0.904
JEFN	20	0.624	0.602	16	0.883
JEFS	20	0.612	0.627	4	0.889
BACN	20	0.709	0.624	4	0.900
BACS	20	0.710	0.605	2	0.867
CRLN	20	0.621	0.684	4	0.904
CRLS	20	0.651	0.676	4	0.904

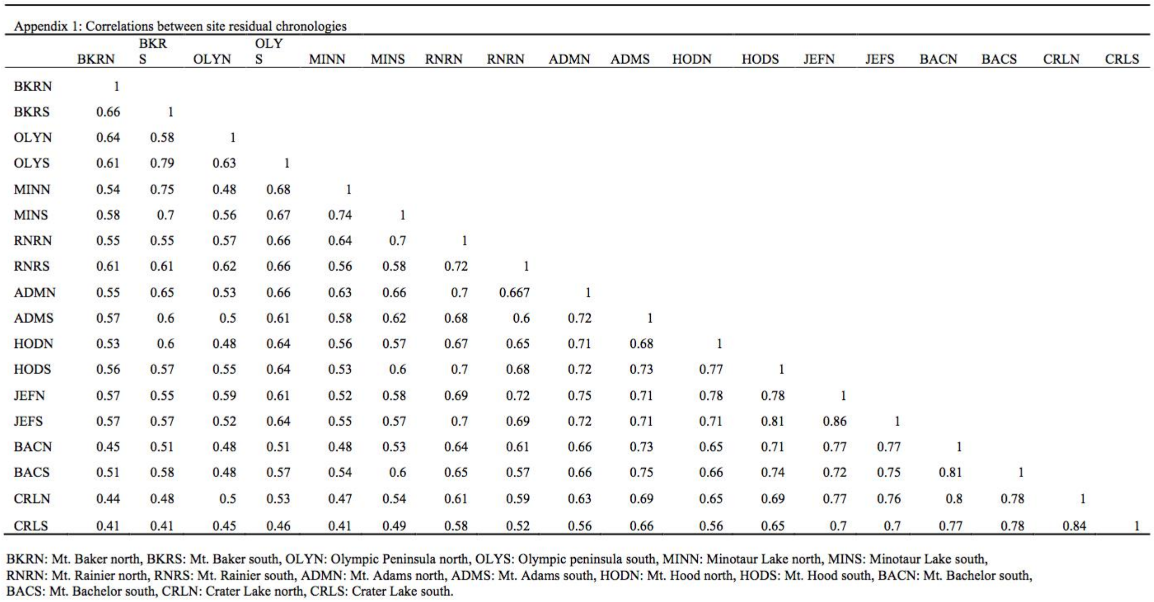
EPS: expressed population signal

Table 3. Cross correlations between climate variables

	Winter PDO index	Spring temperature	PY spring temperature	Summer temperature	PY summer temperature	Winter precipitation	PY winter precipitation	Summer precipitation	Summer PDSI	Winter ENSO index
Winter PDO index	1									
Spring temperature	-0.03	1								
PY spring temperature	-0.10	0.02	1							
Summer temperature	0.08	**0.27**	0.14	1						
PY summer temperature	-0.15	0.17	**0.26**	0.26	1					
Winter precipitation	**-0.22**	**-0.18**	**-0.26**	**-0.11**	0.02	1				
PY winter precipitation	0.12	-0.05	-0.18	0	-0.11	-0.06	1			
Summer precipitation	-0.02	-0.09	0.04	**-0.36**	0.05	0	0	1		
Summer PDSI	-0.13	**-0.46**	0.05	**-0.4**	-0.04	**0.31**	-0.06	**0.63**	1	
Winter ENSO index	-0.04	**0.25**	**0.23**	0.17	0.15	**-0.41**	-0.04	0.14	-0.06	1

Bold font indicates significance ($p<0.05$). PY, previous year; PDSI, Palmer Drought Severity Index; PDO, Pacific Decadal Oscillation Index; ENSO, El Niño Southern Oscillation Index

Appendix 1:



Appendix 1: Correlations between site residual chronologies

	BKRN	BKR S	OLYN	OLY S	MINN	MINS	RNRN	RNRN	ADMN	ADMS	HODN	HODS	JEFN	JEFS	BACN	BACS	CRLN	CRLS
BKRN	1																	
BKRS	0.66	1																
OLYN	0.64	0.58	1															
OLYS	0.61	0.79	0.63	1														
MINN	0.54	0.75	0.48	0.68	1													
MINS	0.58	0.7	0.56	0.67	0.74	1												
RNRN	0.55	0.55	0.57	0.66	0.64	0.7	1											
RNRS	0.61	0.61	0.62	0.66	0.56	0.58	0.72	1										
ADMN	0.55	0.65	0.53	0.66	0.63	0.66	0.7	0.667	1									
ADMS	0.57	0.6	0.5	0.61	0.58	0.62	0.68	0.6	0.72	1								
HODN	0.53	0.6	0.48	0.64	0.56	0.57	0.67	0.65	0.71	0.68	1							
HODS	0.56	0.57	0.55	0.64	0.53	0.6	0.7	0.68	0.72	0.73	0.77	1						
JEFN	0.57	0.55	0.59	0.61	0.52	0.58	0.69	0.72	0.75	0.71	0.78	0.78	1					
JEFS	0.57	0.57	0.52	0.64	0.55	0.57	0.7	0.69	0.72	0.71	0.71	0.81	0.86	1				
BACN	0.45	0.51	0.48	0.51	0.48	0.53	0.64	0.61	0.66	0.73	0.65	0.71	0.77	0.77	1			
BACS	0.51	0.58	0.48	0.57	0.54	0.6	0.65	0.57	0.66	0.75	0.66	0.74	0.72	0.75	0.81	1		
CRLN	0.44	0.48	0.5	0.53	0.47	0.54	0.61	0.59	0.63	0.69	0.65	0.69	0.77	0.76	0.8	0.78	1	
CRLS	0.41	0.41	0.45	0.46	0.41	0.49	0.58	0.52	0.56	0.66	0.56	0.65	0.7	0.7	0.77	0.78	0.84	1

BKRN: Mt. Baker north, BKRS: Mt. Baker south, OLYN: Olympic Peninsula north, OLYS: Olympic peninsula south, MINN: Minotaur Lake north, MINS: Minotaur Lake south, RNRN: Mt. Rainier north, RNRS: Mt. Rainier south, ADMN: Mt. Adams north, ADMS: Mt. Adams south, HODN: Mt. Hood north, HODS: Mt. Hood south, BACN: Mt. Bachelor south, BACS: Mt. Bachelor south, CRLN: Crater Lake north, CRLS: Crater Lake south.