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Divergent growth rates of alpine larch trees (*Larix lyallii* Parl.) in response to microenvironmental variability

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ABSTRACT

In this study we explore radial growth rates and climatic responses of alpine larch trees (*Larix lyallii* Parl.) growing in high elevations of the northern Rocky Mountains of Montana, USA. We examine responses between two stands of alpine larch that are separated by less than one kilometer and are growing at similar elevations, but with different aspects. Radial growth rates from trees sampled on the southern aspect of Trapper Peak (TPS) were largely controlled by January snow-water equivalent, while summer maximum temperature was the principal radial-growth driver for trees sampled on the northern aspect of Trapper Peak (TPN). Following the coldest summer (1993) in the century-long instrumental climate record, the radial growth at TPN became greater than at TPS and was the reverse of what occurred pre-1993. We posit that an upward trend in maximum summer temperature is preferentially benefitting the trees growing on the north-facing TPN site by extending the growing season and causing earlier snowmelt, and this has caused the growth rate divergence during the past two decades. As such, our study illustrates that the growth-divergence phenomenon noted in other high-elevation species, whereby macroenvironmental changes are eliciting responses at the microenvironmental level, occurs within stands of alpine larch growing in western Montana.

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Alpine larch; aspect; divergence problem; growth divergence; Montana

Introduction

Microenvironmental variations have emerged in recent decades concurrent with increasing temperature, resulting in differential stressors that are driving forces for tree growth (Wilmking et al. 2005). Büntgen et al. (2009, 212) describes this phenomenon as a “‘growth divergence’ . . . where formally homogeneous sites show emergent subpopulations of trees with diverging growth patterns during the late 20th century.” Growth divergence tangentially relates to the larger and more broadly examined issue commonly called the “divergence problem” (D’Arrigo et al. 2008), whereby northern hemisphere high-elevation trees experienced a temperature/growth response decline in recent decades. The causes of divergence are poorly understood because of the potentially large suite of interrelated variables affecting tree growth (D’Arrigo et al. 2008) and Büntgen et al. (2009) suggest that the divergence problem is not a response to a single mechanism but,

rather, should be examined at more localized scales before making broad conclusions.

Divergent tree growth does not pose a threat to ecosystem function or health, yet it becomes problematic when it is approached from a dendroclimatic perspective. The divergence problem arises when calibrating the instrumental climate record with tree growth. When tree-ring indices that contain recent decades are used in climate calibrations, the divergent tree growth does not allow for a precise fit, resulting in an underestimation of temperatures (D’Arrigo et al. 2008). Growth divergence and associated problems need to be critically considered as a limiting factor in the effectiveness of a given tree-ring chronology to accurately model and predict future temperatures, especially with the observed warming in the twenty-first century.

Our study is opportunistic in that we sampled alpine larch (*Larix lyallii* Parl.) from within a <0.5 km² region with the intent of incorporating all sampled trees into

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one chronology for a potential climate reconstruction of summer temperature in the northern Rocky Mountains. On examination of the climate-growth relationships from a chronology developed using all trees, we found that they were weaker than what we had found from nearby sites (Knapp and Soulé 2011) and thus decided to divide the chronology based on aspect. The discovery of a potential growth divergence based on aspect led us to the research question addressed in this study: What is the potential for differential responses in radial growth and climate/growth relationships over time between groupings of alpine larch trees exposed to identical macroenvironmental conditions but different microenvironmental conditions related to aspect? The leading drivers of microenvironmental differences in relation to aspect are solar radiation and associated soil moisture fluctuations (Kelsey et al. 2017). Southern aspects in the northern hemisphere and northern aspects in the southern hemisphere generally experience drier conditions because of longer and more intense exposure to incoming solar radiation. In the southwestern Colorado Rocky Mountains, Kelsey et al. (2017) identified negative trends in radial growth for subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) trees growing on southern, eastern, and western aspects and linked the declining growth to increasing minimum summer temperatures in the region. Conversely, on northern aspects, they found increasing radial growth trends. Similarly, Salzer et al. (2014) identified an aspect-related growth divergence for bristlecone pine (*Pinus longaeva* Bailey) trees growing in the White Mountains of California. Historically, trees on southern aspects outperformed those on northern aspects, but that relationship has switched since the mid-1990s concurrent with increasing temperature.

In this study, we chose to work with alpine larch, because summer temperature has been documented as a consistent driver of radial growth for this species in particular (Graumlich and Brubaker 1986; Kipfmueller 2008; Peterson and Peterson 1994) and larch in general (Büntgen et al. 2006, 2012; Coppola et al. 2012; Hafner et al. 2014). Alpine larch is one of only three deciduous conifers, in addition to tamarack (*Larix laricina* [Du Roi] K. Koch) and western larch (*Larix occidentalis* Nutt.), that are native to North America, and it is unique in being the only erect deciduous tree that inhabits the alpine timberline (Arno and Habeck 1972). Alpine larch occupies a small geographic range (45–51°N and 113–121°W) in southeastern British Columbia, southwestern Alberta, north-central Washington, northern Idaho, and western Montana. The altitudinal range of alpine larch is approximately 1,520–3,010 m, and it is the predominant tree above 2,300 m on northern exposures

throughout its range, but is scarce on southern aspects (Arno and Habeck 1972).

Alpine larch displays an affinity for cold, snowy, and rocky sites; temperatures are below freezing for more than half the year, and the growing season representing average temperatures of over 5.6°C lasts about ninety days (Arno and Habeck 1972). There is pronounced variation in growth rates among individuals in diverse habitats, and suppressed growth rates resulting from competition or the extremely harsh physical environment are common (Arno and Habeck 1972). The relationship between stem age and diameter is direct and relatively stable, with late-twentieth-century research suggesting longevity of more than 1,000 years based on growth/diameter relationships (Worrall 1990). Crossdated samples from the Canadian Rockies can exceed 700 years, and Colenutt and Luckman (1995) found a mean age from a large sample (115 trees) of approximately 350 years. While our oldest crossdated tree was 477 years old, at nearby sites within the northern Rockies Kipfmueller (2008) found alpine larch trees dating back to AD 12, and successfully crossdated samples ($EPS > 0.85$; Wigley, Briffa, and Jones 1984) over 1,950 years old for use in a summer temperature reconstruction. Also within the region, Knapp and Soulé (2011) used crossdated alpine larch to reconstruct annual area burned back to AD 1626.

For this study we developed two tree-ring chronologies from a contiguous grouping of alpine larch trees but separated by aspect and: (1) searched for the dominant climatic drivers of radial growth, (2) examined the climate/growth responses for long-term temporal continuity, (3) examined the long-term temporal patterns of standardized and raw radial growth rates to determine if and when growth divergence occurred between sites, and (4) hypothesized on environmental and climatic controls for radial-growth and climate/growth differences between sites.

Methods

Study area

We collected samples from alpine larch growing near the treeline (~2750 m) at Trapper Peak (TPS = south facing and TPN = north facing) in the Selway-Bitterroot Wilderness in the Bitterroot National Forest in western Montana (Figure 1). The two study sites were less than 1 km apart with an elevation difference of less than 30 m. Soil composition of the area is dominated by decomposed plant material in the upper 2.5 cm; bouldery, ashy loam in the subsequent 23 cm; followed by loamy sands and sandy loams until a

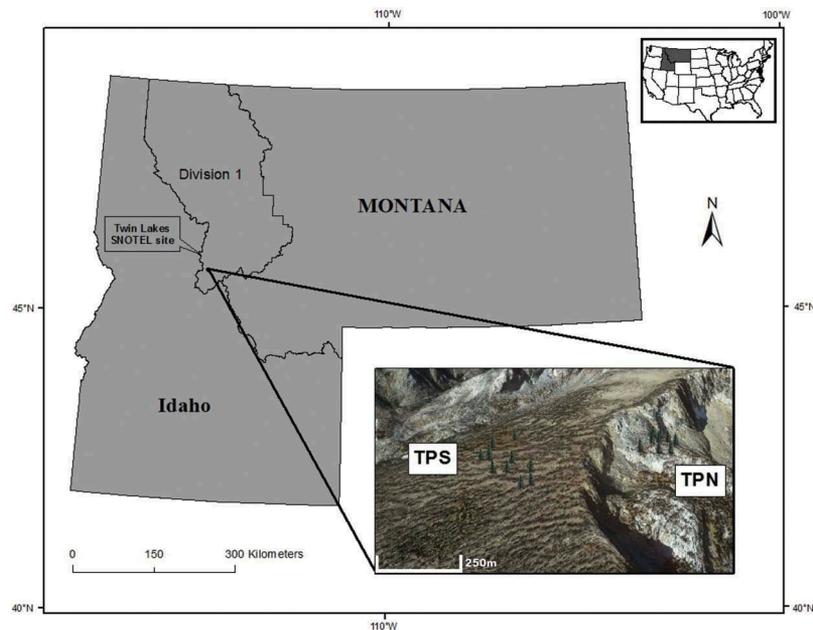


Figure 1. Study site location in western Montana within Climatic Division One. We sampled trees at Trapper Peak in the Selway-Bitterroot Wilderness in the Bitterroot National Forest. The Twin Lakes SNOTEL site is located approximately 30 km north of TPN and TPS.

restrictive layer (Natural Resource Conservation Service 2014). Because of glaciation of the area as recently as 10,000 years BP, soils are young (National Climatic Data Center 2014). Macroclimatic conditions at the site have mean temperatures ranging from -6.4°C in January to 16.3°C in July (National Climatic Data Center 2016). July is the warmest and driest month, with mean maximum temperatures of 24.7°C and average precipitation of 3.3 cm. January is the wettest and coldest month, with mean maximum temperatures of -2.4°C and average precipitation of 9.7 cm (National Climatic Data Center 2016). The sites are exposed and experience high winds in winter, which leads to significant and spatially variable drifting of snow, especially at TPS (personal observation, J. Stephen Shelly). April is the peak month for snow-water equivalent (SWE; mean value during 1968–2015 = 98.5 cm) and is measured at the Twin Lakes SNOTEL site (Natural Resource Conservation Service 2016), which is approximately 30 km away and 800 m lower than our study sites (Figure 1). Considerable interannual variability in SWE occurs, yet snowpack persists into June most (90%) years.

Sampling

We obtained two core samples from trees at a height of approximately 1.4 m using 5.15 mm diameter

increment borers. We sampled exclusively mature trees and avoided trees with visible damage, such as fire and lightning scars and excessive upper bole damage. We restricted our sampling to open-canopy trees to avoid temporal changes in radial growth rates associated with canopy infilling or nearby tree senescence.

Laboratory and statistical methodology

We processed the cores using standard techniques by first gluing the cores to wooden mounts and then sanding with progressively finer grit sandpaper to reveal the cellular structure of the wood. We crossdated and measured the samples to 0.001 mm using the program WINDENDRO (Regent Instruments Inc. 2011) and verified crossdating accuracy using the diagnostic program COFECHA (Grissino-Mayer 2001; Holmes 1983). We used the program ARSTAN (Cook 1985) for standardization and developed separate tree-ring chronologies for TPS and TPN. We standardized trees using both conservative techniques (e.g., negative exponential, negative linear; hereafter CT) and a Friedman Super Smoother (Friedman 1984).

We examined climate-radial-growth relationships for TPS and TPN using the Standard, Residual, and ARSTAN chronologies and monthly and seasonal (e.g., JJA for summer) climatic division-level temperature, precipitation, and Palmer Drought Severity Index

(Palmer 1965) data from Montana Climatic Division 1 (National Climatic Data Center 2016) during 1895 to 2015. We also examined relationships between monthly SWE and radial growth using SNOTEL data from Twin Lakes (Natural Resource Conservation Service 2016) from 1968 to 2015. Our initial findings produced the strongest climate-radial growth relationship using the CT standardization with the ARSTAN chronology, so we used this combination for our analyses. After identification of the primary climatic drivers of radial growth, we examined their temporal consistency via moving interval analyses on monthly (seasonal) data and twenty-four-year windows using the computer program DENDROCLIM (Biondi and Waikul 2004). We also examined the temporal pattern of raw and standardized radial tree growth graphically and by subtracting annual growth values at TPN from TPS and graphing the difference. We conducted formal tests for regime shifts of both mean tree growth and climatic parameters using a sequential algorithm technique (Rodionov 2004; Rodionov and Overland 2005) and a ten-year cut-off length. Shorter cut-off lengths are more restrictive (i.e., a greater change is needed to cause a shift), and a ten-year cut-off length can detect regime shifts as short as five years in length as long as the magnitude of change between regimes is large (i.e., >2 standard deviations; Rodionov 2004).

Results and discussion

For TPS the chronology includes twenty-three samples (twelve trees) with an interseries correlation of 0.674 and a mean sensitivity of 0.298; for TPN the interseries correlation and mean sensitivity from nineteen samples (ten trees) were 0.658 and 0.365, respectively. We obtained the Expressed Population Signal (Wigley, Briffa, and Jones 1984) of 0.85 at TPS beginning in 1717 with three samples and 1751 for TPN with four samples.

Table 1. Relationships (Pearson) between standardized radial growth and climate at TPN and TPS. For PDSI, the month with the strongest relationship is shown in parentheses.

	TPN Arstan	TPS Arstan
Palmer Drought Severity Index		
<i>r</i> value	-.282 (Sep.)	-.235 (Jul.)
<i>p</i> value	.002	.009
Number of samples	121	121
Summer (JJA) Maximum Temperature		
<i>r</i> value	.435	.224
<i>p</i> value	.000	.014
Number of samples	121	121
January Snow-Water Equivalent		
<i>r</i> value	-.346	-.344
<i>p</i> value	.016	.017
Number of samples	48	48

Radial growth at both TPS and TPN responded most positively to maximum summer (JJA) temperature and negatively to January SWE (Table 1), but the strongest relationships differed between sites (TPN max summer temperature, TPS January SWE). Positive relationships with June temperature were found for alpine larch growing in the southern Canadian Rockies (Colenutt and Luckman 1991, 1995) and at multiple sites in the northern Rocky Mountains (Kipfmüller 2008). Kipfmüller (2008) also found weak negative relationships between radial growth and precipitation in June, July, or August. For alpine larch growing in the Washington Cascades, Graumlich and Brubaker (1986) found that spring snowpack and summer temperatures were synergistically related to alpine larch radial growth.

We examined the temporal pattern of standardized radial growth at TPS and TPN from 1751 to 2015 and found that the long-term covariance was similar ($r = 0.629$, $P = 0.000$, $n = 265$), although growth at TPS was greater in 60.4 percent of the years (Figure 2A), and the number of significant ($P < 0.05$) regime shifts in growth was greater at TPS (ten for raw growth and eleven for standardized) compared to TPN (eight for both raw and standardized) over a common growth period of 1751–2015 (Figure 2A). The radial growth patterns diverge in the early 1990s, with every year since 1993 recording greater standardized values at TPN compared to TPS (Figure 2B). Prior to 1994 TPS growth exceeded TPN growth 65.8 percent of the years. The post-1993 growth divergence was less dramatic for raw growth, but follows a similar pattern (Figure 2C). While raw growth at TPN only exceeded TPS 30.6 percent of the years, in the past twenty-one years (post 1994), growth at TPN exceeded TPS 90.5 percent of the years (Figure 2D). A significant regime shift was detected at TPS beginning in 1993 for both raw and standardized growth, but not at TPN (Figure 2A, C).

Given the growth divergence during the past two decades, we examined the temporal stability of the climate-growth relationships. Moving-interval analysis results suggest that summer maximum temperatures, especially in July and August, have become more consistent drivers of radial growth at TPN since the mid-1950s (Figure 3A, B). At TPS, June maximum temperatures were consistent drivers of radial growth both early in the record (through the twenty-four-year windows ending in the early 1940s) and since the mid-1970s. The strongest relationship between standardized radial growth and SWE at both sites occurred in January (Table 1), but this relationship became nonsignificant ($P < 0.05$) at TPS with the moving

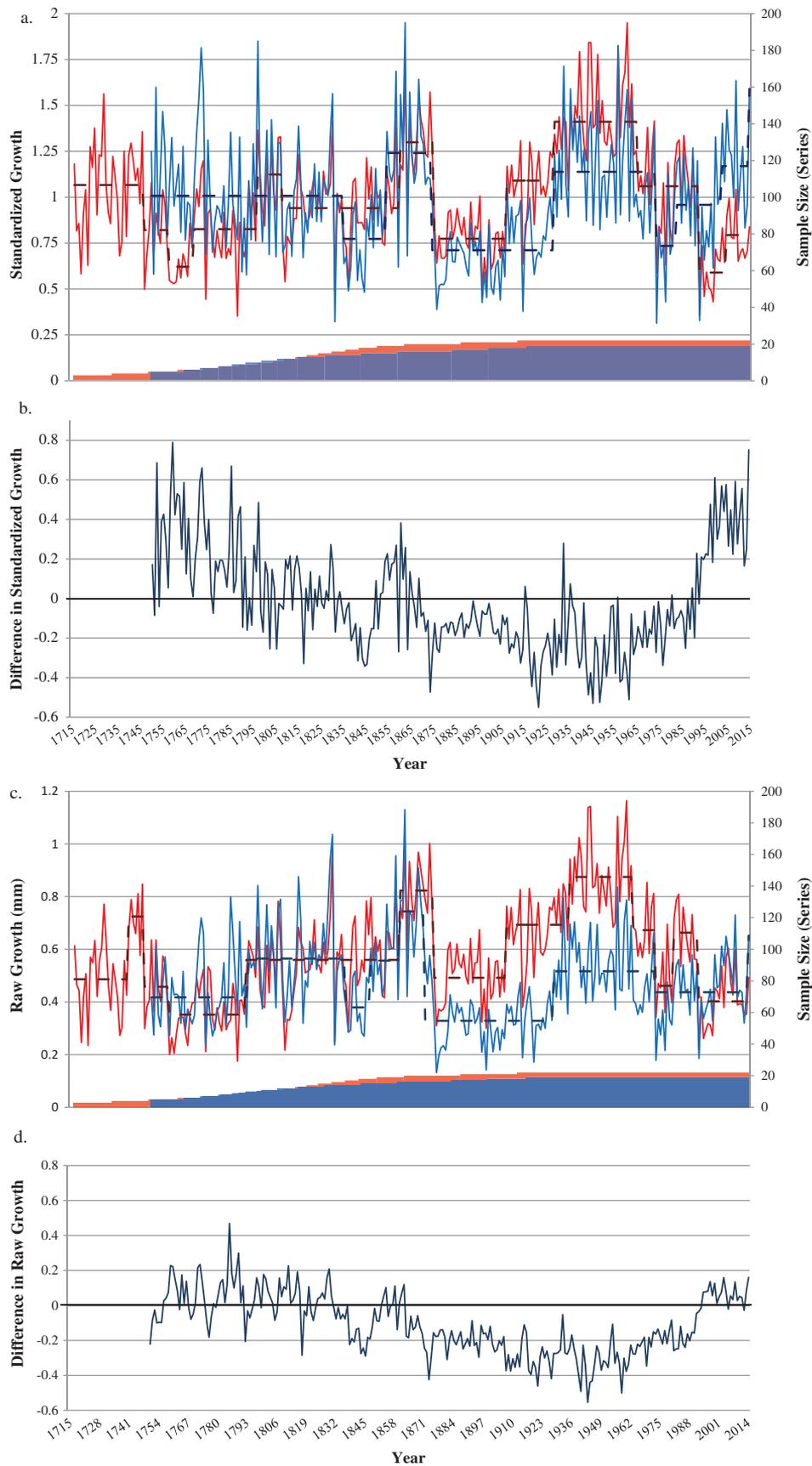


Figure 2. Radial growth patterns at the study sites. (A) Raw radial growth (1 = average) for alpine larch from TPS (red line) and TPN (blue line). Weighted mean radial growth within temporal regimes and significant ($P < 0.05$) regime shifts (TPS = dashed brown line; TPN = dashed dark blue line). Sample depth (TPS = vertical red bars; TPN = vertical blue bars). (B) Difference in raw radial growth: TPN minus TPS. (C) As in Figure 2, part A, except for standardized radial growth. (D) As in Figure 2, part B, except for standardized radial growth.

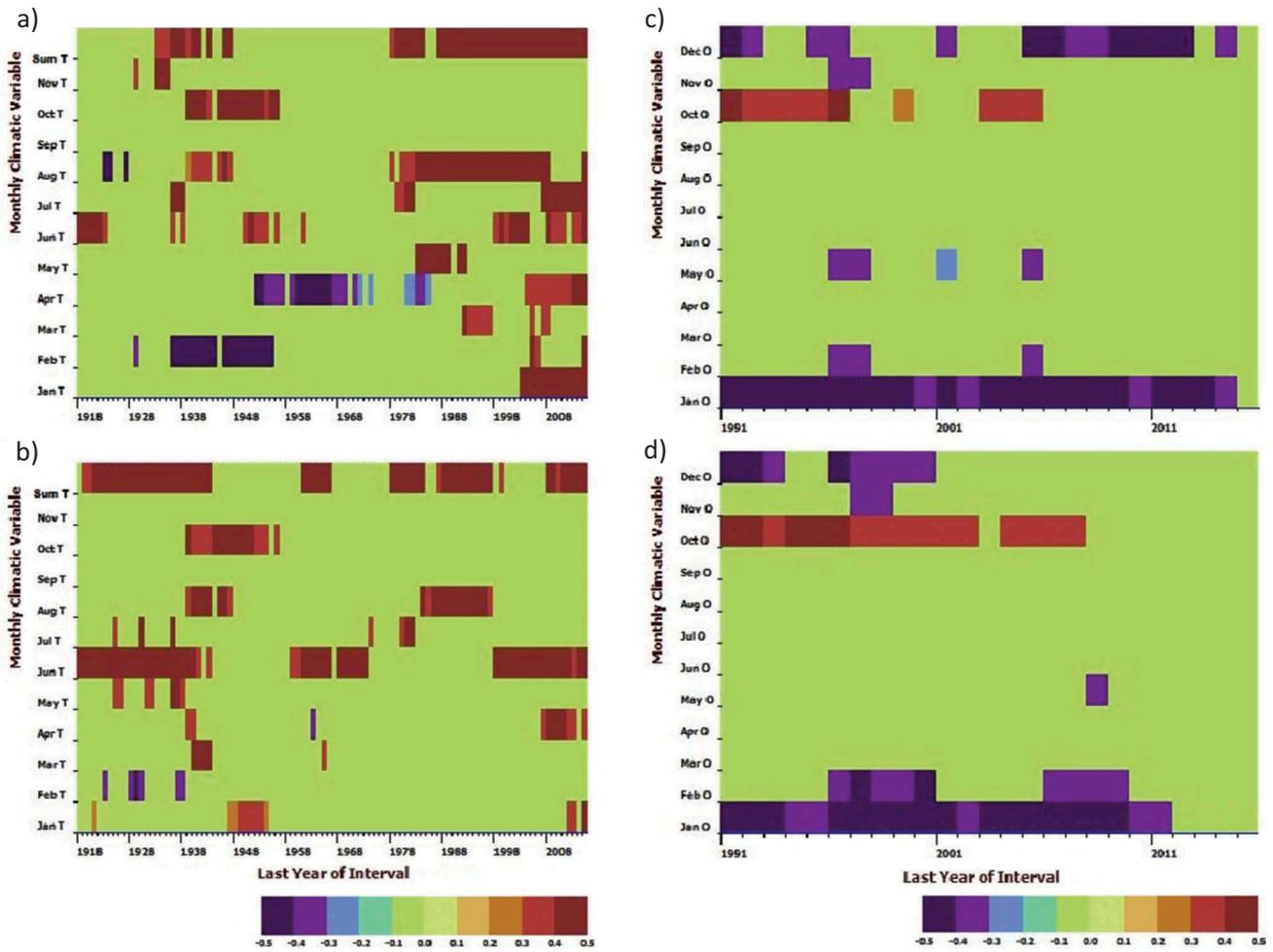


Figure 3. Moving correlation analysis. (A) TPN and (B) TPL, significant ($P < 0.05$) correlations with monthly (current year January–November) and summer (JJA) maximum temperatures within moving twenty-four-year windows. Colors (blue to purple = negative relationships; orange to red = positive relationships) represent strength of relationship (r values). (C) TPN and (D) TPL, significant ($P < 0.05$) correlations with monthly snow-water equivalent within moving twenty-four-year windows. Colors (blue to purple = negative relationships; orange to red = positive relationships) represent strength of relationship (r values).

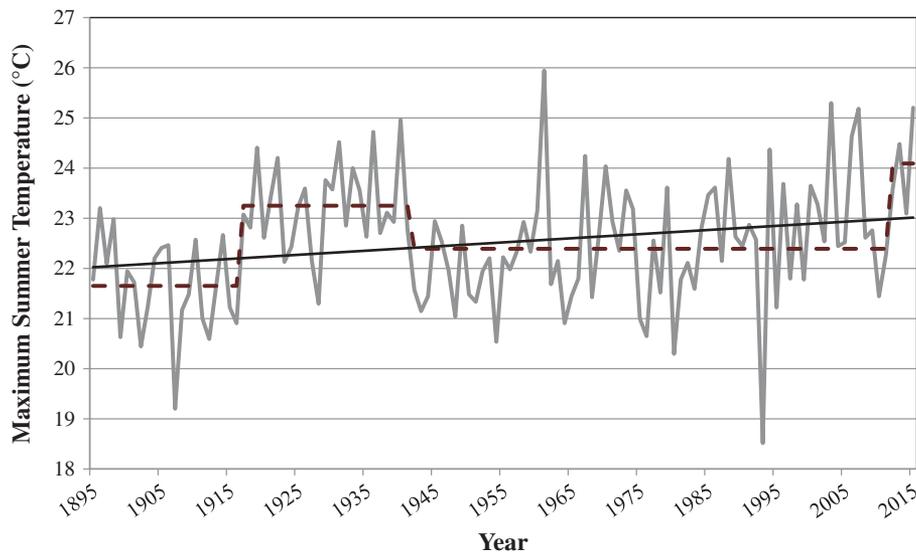


Figure 4. Mean summer (JJA) maximum temperature ($^{\circ}\text{C}$), 1895–2015 (data from Montana climatic division one = gray line), linear trend (black line), and regime shift (dashed red line).

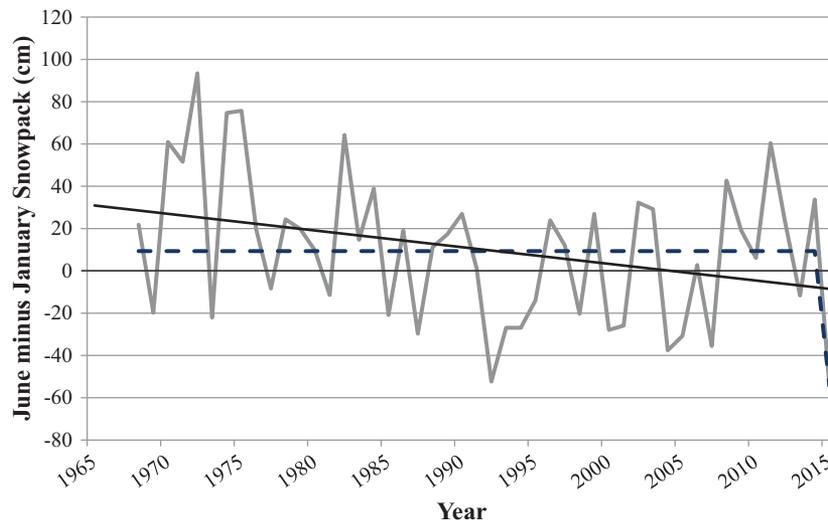


Figure 5. Difference in snow-water equivalent (cm), June minus January, 1968–2015 (data from Twin Lakes SNOTEL site, Montana = gray line), linear trend (black line), and regime shift (dashed blue line).

window ending in 2011 and in the 2014 window at TPN (Figure 3C, D).

The temporal pattern of summer maximum temperature is weakly but significantly upward through time ($r = 0.231$, $P = 0.011$, $n = 121$; Figure 4), and if we remove the outlier year of 1993 the relationship improves slightly ($r = 0.273$, $P = 0.003$, $n = 120$). Only three significant regime shifts in maximum summer temperature were detected, the last being an upward shift beginning in 2012 (Figure 4). For January SWE there are no temporal trends ($r = -0.004$, $P = 0.980$, $n = 48$), and for June SWE there are significant negative trends ($r = -0.311$, $P = 0.031$). Using June minus January SWE as a proxy measure of snowpack decline through the snowpack season, a significant negative trend exists ($r = -0.331$, $P = 0.021$, $n = 48$; Figure 5), but only one downward regime shift was detected beginning in 2013.

Several possibilities exist for the post-1993 radial-growth divergence between TPS and TPN. First, warmer summer temperatures and longer growing seasons would be more beneficial to TPN, which would typically begin growing later in the season and end growth earlier. During the past twenty-two years (after the anomalously cool summer of 1993; Figure 4), 73 percent of the years had mean temperatures above the long-term average (1895–2015 = 22.5°C), with four years experiencing deviations of more than 2°C. Second, the divergent growth patterns may relate to an earlier snowmelt, leading to a faster reduction in soil moisture during the summer growing season in the south-facing stand of alpine larch that comprise the TPS chronology, a microenvironment prone to substantial drifting of snow in linear patterns during most

winters (personal observation, J. Stephen Shelly). This is supported by SWE data from the nearby Twin Lakes SNOTEL site, which indicates that January SWE values remained stable, but June SWE data significantly decreased, as did the difference between January and June SWE (Figure 5). Third, higher soil-moisture retention on the north-facing TPN site may favor increased growth relative to the increasingly drier TPS site. Fourth, alpine larch on droughty microsites have been observed to turn color and shed their needles up to one month early during drought periods; while this earlier deciduous behavior may reduce drought-caused mortality (Arno and Habeck 1972), it might also limit growth rates because the TPS site is affected by drier conditions.

Conclusions

Our findings suggest that the “growth divergence” (Büntgen et al. 2009, 212) phenomenon detected in other high-elevation species (Wilmking et al. 2005; Pisaric et al. 2007; Zhang, Wilmking, and Gou 2009) is occurring at our study sites in western Montana. Our examination of alpine larch radial growth at two study sites separated by less than 1 km and located at similar elevations revealed that: (1) tree growth at TPS (south-facing) outperforms tree growth at TPN (north-facing) for the majority of the instrumental record until the coldest year on record (1993); (2) post-1993, standardized radial growth at TPN exceeded that at TPS; and (3) growth responses to maximum summer temperature on the TPN site have become stronger and more

consistent in recent decades. With warming temperatures, winter snowpack is melting earlier in the spring and the growing-season length is increasing. These conditions appear to be preferentially benefiting trees on northern aspects and illustrate how macroscale environmental changes, such as increasing growing-season temperature and more rapid snowmelt, can differentially impact ecosystem processes at the microscale, a key aspect of the growth-divergence phenomenon. For tree-ring science, our findings include the following implications: (1) microenvironmental conditions can cause the primary climatic drivers of radial growth to vary between subpopulations of trees across short distances; (2) divergence in the radial growth rates of trees can occur at fine spatial scales (i.e., between subpopulations of trees); and (3) site-specific environmental factors with the ability to influence radial growth rates of trees should be considered when selecting the spatial parameters of a study site, particularly the combination of dominant aspect and distance separating trees that ultimately are being combined into a single tree-ring chronology.

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