Radial growth rates of two co-occurring coniferous trees in the Northern Rockies during the past century

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ABSTRACT

We examined radial growth rates of locally co-occurring Douglas-fir (PSE – Pseudotsuga menziesii var. glauca) and ponderosa pine (PIPO – Pinus ponderosa var. ponderosa) trees growing within the Northern Rockies to determine if there are differential growth and climatic responses between these species and whether these responses are consistent among topographically and climatologically diverse sites. We developed standardized tree-ring chronologies from seven sites, with each site a matched pair of PSME and PIPO. For each chronology we examined the climate response of radial growth by comparing the standardized ring widths to a suite of climatic variables. We examined temporal changes by comparing 1905–1950 and post-1950 growth rates and climatic conditions. Both conifers experience increased radial growth post-1950. A combination of spring/summer moisture conditions related positively to radial growth and the primary climatic drivers were consistent both between species and within the region. The primary climatic drivers of radial growth remain unchanged during the last century or have trended toward drier conditions unfavorable for growth. We conclude that increases in standardized radial growth rates are unlikely climatically-driven. Other potential vectors of radial growth change, such as atmospheric CO2 enrichment, have affected these co-occurring species on a largely equal basis and positively.

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1. Introduction

Global circulation models for the Northern Rockies – an area that encompasses the natural range of some of the most commercially viable U.S. tree species and includes extensive tracts of semiarid woodlands – predict warmer and drier conditions the next several decades (Christensen et al., 2007; Littell et al., 2011). In North America west of the Mississippi river, summer temperatures are predicted to rise by as much as 4 °C coupled with precipitation declines up to 20% below current normals by late century (Christensen et al., 2007). Similar predictions for warmer, drier summers occur for other areas containing arid and semiarid lands, including the Mediterranean region and central Asia (Christensen et al., 2007).

The predicted climatic conditions create an impetus to examine the historical responses of trees to changing climate and atmospheric composition to improve our understanding of how the dominant conifers in the region have responded during and after warmer and drier periods throughout the past century. If climatic change in the Northern Rockies occurs as predicted (Christensen et al., 2007; Hamlet et al., 2007; Littell et al., 2011; Westerling et al., 2006), forests in this region will experience more frequent drought conditions that should impact forest productivity. But to what degree and which species will be most affected? Complicating this understanding is that the limiting impacts of drought may be offset by one possible cause of the climatic change – increasing atmospheric CO2.

Water stress may enhance the relative effects of elevated CO2 on woody plant growth (Huang et al., 2007; Idso and Idso, 1994; Wullschleger et al., 2002), thus the impacts of increasing CO2 can be ameliorative for drought stress in semiarid environments (Knapp and Soulé, 2011; Soulé and Knapp, 2006, 2011) and older trees (i.e., >250 years) may benefit the most (Knapp and Soulé, 2011). Under higher atmospheric CO2 concentrations, stomatal openings for tree leaves contract during photosynthesis (e.g., Tognetti et al., 1998), reducing transpiration rates and resulting in increased water-use efficiency (WUE). Soulé and Knapp (2011) examined changing rates of intrinsic water-use efficiency (iWUE – a measure of the relationship between the rate of CO2 assimilation and transpiration through stomatal openings) for Ponderosa pine trees.

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(Pinus ponderosa var. ponderosa—hereafter PIPO) throughout semiarid sites in the western United States and found significant upward trends at all locations, including three of the sites examined in this study. With increasing iWUE, radial growth may continue later through the summer in environments where soil moisture becomes limiting by July or August such as the Pacific Northwest and Northern Rockies, or may continue at higher rates during a drought period.

In this paper we examine relationships between climatic conditions and radial growth rates of locally co-occurring Douglas-fir (Pseudotsuga menziesii var. glauca—hereafter PSME) and PIPO trees within USFS Region 1 of the Northern Rockies and determine if differential responses to changing environmental conditions exist between these two conifers. By working in natural settings where gradual increases in atmospheric CO₂ have occurred during the last 100+ years, by sampling from sites with minimal historic human agency where the trees locally co-occur, and by carefully selecting trees so as to minimize potentially confounding factors for radial growth, we gain insight into how these two species are responding to climate and changing atmospheric conditions. Specifically, we hypothesize that: 1) radial growth rates of PSME and PIPO have changed significantly during the past century; 2) changes in observed radial growth rates are climatically driven; 3) radial growth responses of PSME and PIPO during and after drought have temporally changed; and 4) differential responses between the two co-occurring tree species exist and are spatially consistent. Herein we follow methodologies developed from earlier studies (Knapp and Soulé, 2011; Soulé and Knapp, 2011) in the same region that focused on PIPO, and use similar evaluative metrics (Knapp et al., 2001a, 2001b) to compare PSME and PIPO responses to changing environmental conditions.

Both PSME and PIPO are ecologically important tree species throughout the American West, have similar and extensive geographical ranges, and often grow at the same locations (Earle, 2007). PSME and PIPO are also major species for US forestry, representing the first- and third-most harvested trees by volume, respectively (WWPA, 2012). Changing atmospheric and climatic conditions may create a scenario where growth rates of PSME or PIPO are differentially affected, either positively or negatively, thus potentially affecting the structure and composition of these forests/woodlands. Globally, climate change can impact semiarid forests directly through water use and net primary productivity changes, and via “cascading” disturbances whereby a change in one climatic vector such as drought can cause subsequent changes in fire regimes and the frequency and intensity of insect and pathogen outbreaks (Dale et al., 2001). These cascading perturbations can result in radical changes in forest dynamics (Dale et al., 2001; Paine et al., 1998), and this has a direct bearing on current and future management decisions and practices (Peterson et al., 2011).

2. Methods

2.1. Tree-ring data collection and processing

We collected samples and developed fourteen standardized tree-ring chronologies from seven matched-paired sites (PSME and PIPO) in Idaho and Montana (Fig. 1, Table 1). Each chronology is identified using a three letter alphabetic code common in tree-ring science (Table 1). We selected all sites based on criteria designed to limit the number of potential confounding influences that could affect radial growth. Specifically, our selected sites: 1) were open stands of co-occurring PSME and PIPO trees available in both older (establishing prior to AD 1800) and younger (interior dates post-1875) age classes; 2) had a history of minimal anthropogenic disturbance; 3) are located in interior Idaho and western Montana to negate or minimize potential impacts on radial growth by ozone (Lee and Hogsett, 2001) or nitrogen deposition (Fenn et al., 2003); 4) have no known histories of pandora moth (Coloradia Pandora).

Fig. 1. Location of the seven matched pair study sites in Montana and Idaho, USA and boundaries of the climatic divisions from which climatic data were used. Study site names for the three letter site codes are found in Table 1.
surges/declines associated with canopy loss/in only in open-canopy locations to minimize potential growth
fi
Speer et al., 2001) outbreaks; and 5) are geographically diverse to
chronology meeting the 0.85 threshold ensuring adequate sample size.

Table 1
Chronology information. Rbar values represent the earliest date (year) for each chronology meeting the 0.85 threshold ensuring adequate sample size.

<table>
<thead>
<tr>
<th>Site Interseries correlation</th>
<th>Mean sensitivity</th>
<th>Percent–absent rings</th>
<th>0.85 Rbar (AD)</th>
<th># of samples series</th>
<th>In Dates (AD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boulder Creek Research Natural Area, Montana (BCR – Ponderosa pine chronology, BCD – Douglas-fir chronology)</td>
<td>0.863  0.245  0.110</td>
<td>1734  48</td>
<td>1560–2008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock Creek West, Montana</td>
<td>0.895  0.260  0.178</td>
<td>1752  48</td>
<td>1560–2008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RCR 0.767  0.200  0.229</td>
<td>1776  68</td>
<td>1743–2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish Creek, Montana</td>
<td>0.576  0.252  0.269</td>
<td>1849  48</td>
<td>1575–2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FCD 0.673  0.227  0.083</td>
<td>1785  54</td>
<td>1611–2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ferry Landing Research Natural Area, Montana</td>
<td>FLR 0.637  0.261  0.028</td>
<td>1770  54</td>
<td>1580–2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FLD 0.665  0.275  0.011</td>
<td>1797  50</td>
<td>1690–2006</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock Creek East</td>
<td>RKR 0.694  0.312  0.211</td>
<td>1718  61</td>
<td>1541–2008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RKD 0.744  0.310  0.016</td>
<td>1761  70</td>
<td>1665–2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cabin Gulch Research Natural Area, Montana</td>
<td>CCR 0.690  0.355  1.956</td>
<td>1771  46</td>
<td>1542–2009</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCD 0.701  0.413  0.642</td>
<td>1810  44</td>
<td>1674–2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wellner Cliffs Research Natural Area, Idaho</td>
<td>WCR 0.574  0.268  0.503</td>
<td>1677  42</td>
<td>1653–2009</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WCD 0.611  0.244  0.314</td>
<td>1782  43</td>
<td>1673–2009</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

We examined climate/growth relationships using regionally derived climatic division-level data from 1905–end of record (2006–2009). Divisional data are high quality and bias corrected (Karl et al., 1986) monthly records of temperature, precipitation, and Palmer Drought Severity Index (PDSI) values (Palmer, 1965). Divisional data are commonly used in dendroecological studies (P. T. Soulé, P. A. Knapp, 2006) and have been successfully used in studies of semiarid tree species (Knapp et al., 2001a; Soulé and Knapp, 2006). Using Pearson correlation, we examined monthly precipitation, temperature, and drought severity influences including lagged influences up to one year and various composite variables derived from the monthly variables to represent seasonal (e.g., total summer precipitation) conditions. We identified the primary climate driver for radial growth at each site and determined if there was consistency in the response to multiple thermal and moisture variables to determine if there are differential climate responses between species.

For consistency, we used the 1905–end of record (Table 1) period to determine if radial growth rates have changed temporally. We identified the presence or absence of long-term trends using Pearson correlation between radial growth and time and a null hypothesis of no trends in radial growth through time. Throughout, we use \( p < 0.05 \) to establish statistical significance. Because increases in atmospheric \( \text{CO}_2 \) levels become pronounced from the mid 20th century onward, AD 1950 is used as a divide in vegetation-change studies (e.g., Graumlich, 1991; Knapp et al., 2001a, 2001b; Soulé and Knapp, 2006). We compared radial growth rates from early (1905–1950) and late (1951–end of record) periods using a Wilcoxon Signed Ranks Test and a null hypothesis of no significant differences in radial growth between time periods. We used similar tests to determine the degree of radial growth-related climate change. For each site we identified the primary variable for radial growth and then tested this variable for long-term linear trends and for significant differences between the early and late time periods. We chose a decade from the early period that matched the late period in terms of mean drought severity (as defined by July PDSI values) and number of years with above and below-normal moisture conditions. We used July PDSI as it was the most common climatic driver for radial growth across the 14 chronologies from the seven study sites (i.e., one matched PSME and one PIP0 chronology from each of seven sites). For sites in Montana Climatic Division 1 (Fig. 1) we compared 1921–1930 (mean July PDSI = 0.52, 6/10 years <0) with 1996–2005 (July PDSI = 0.55, 6/10 years <0), for CCR/CGD we used 1925–1934 (July PDSI = 1.26, 7/10 years <0) and 1995–2004 (July PDSI = 1.24, 7/10 years <0), and for WCR/WCD we used 1915–1924 (July PDSI = 0.13, 6/10 years <0) and 2000–2009 (July PDSI = 0.21, 5/10 years <0).

We tested for changing responses in radial growth to drought conditions several ways. First, we identified all years when July PDSI values exceeded –1.0 (mild drought) and –2.0 (moderate drought). We then tested the theory that radial growth responses
Precipitation in May is correlated with July temperature (jultemp) and the PDSI value of the prior year September. The variables are: jaspd = mean of July–September PDSI values; mjtppt = total precipitation in May–July; mjtemp = mean temperature June–August; julpd = July PDSI value; julpd = PDSI value of the prior year October; junpd = June PDSI value; julpppt = total precipitation prior year November to current year August; jultemp = July mean temperature; julppt = total precipitation prior October to current year September; julpd = total precipitation prior October to current year August; julpppt = PDSI value of the prior year September.

Fig. 2. A comparison of the climate variable most closely related to radial growth at each study site during the early (1905–1950) and late (1951–end of record) periods. There were no significant differences between time periods to determine if radial growth rates during drought recovery years differed between early and late periods.

3. Results

3.1. Growth/climate relationships

Radial growth of both PSME and PIPO is largely controlled by available moisture during the growing season (Table 2). Among all variables, July drought severity had the most consistent relationship to radial growth, with the strongest relationship at 5/14 sites and second to fourth strongest at the remaining sites. As PDSI accounts for antecedent moisture conditions, the positive and significant relationship demonstrates that PSME and PIPO radial growth is principally affected by moisture conditions of the late spring to early summer. A further confirmation of this relationship is the consistent response of the dominant precipitation variable, total May to July precipitation, which has the strongest climate response at 4/14 sites and is the dominant precipitation variable at 10/14 sites. The response of radial tree growth to temperature is consistently negative and is also maximized in the late spring-early summer period (Table 2).

3.2. Radial growth rates during entire record

Differential growth responses between PSME and PIPO were unsupported by our results. From 1905 until the end of the record (i.e., long-term) there were no significant differences between any of the seven matched pairs, and the seven site mean for PIPO was 1.01 compared to 1.00 for PSME. Although the yearly ring-width values are standardized to a mean of 1.00, the tree-ring record

<table>
<thead>
<tr>
<th>Site</th>
<th>Drought relationship</th>
<th>Precipitation relationship</th>
<th>Temperature relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCR</td>
<td>0.57 (jaspd)</td>
<td>0.53 (mjtppt)</td>
<td>−0.37 (mjtemp)</td>
</tr>
<tr>
<td>BCD</td>
<td>0.41 (julpd)</td>
<td>0.5 (mjtppt)</td>
<td>−0.3 (mjtemp)</td>
</tr>
<tr>
<td>RCR</td>
<td>0.47 (julpd)</td>
<td>0.55 (mjtppt)</td>
<td>−0.3 (mjtemp)</td>
</tr>
<tr>
<td>RCD</td>
<td>0.44 (julpd)</td>
<td>0.53 (mjtppt)</td>
<td>−0.34 (mjtemp)</td>
</tr>
<tr>
<td>FCR</td>
<td>0.48 (julpd)</td>
<td>0.47 (mjtppt)</td>
<td>−0.3 (mjtemp)</td>
</tr>
<tr>
<td>FCD</td>
<td>0.55 (julpd)</td>
<td>0.47 (mjtppt)</td>
<td>−0.26 (jultemp)</td>
</tr>
<tr>
<td>FLR</td>
<td>0.54 (jaspd)</td>
<td>0.44 (julp)</td>
<td>−0.41 (jultemp)</td>
</tr>
<tr>
<td>FLD</td>
<td>0.6 (julpd)</td>
<td>0.5 (mjtppt)</td>
<td>−0.32 (jultemp)</td>
</tr>
<tr>
<td>RKR</td>
<td>0.61 (julpd)</td>
<td>0.59 (mjtppt)</td>
<td>0.29 (mjtemp)</td>
</tr>
<tr>
<td>CCR</td>
<td>0.54 (julpd)</td>
<td>0.51 (julp)</td>
<td>−0.3 (jultemp)</td>
</tr>
<tr>
<td>CGD</td>
<td>0.6 (julpd)</td>
<td>0.52 (julp)</td>
<td>−0.41 (jultemp)</td>
</tr>
<tr>
<td>WCR</td>
<td>0.53 (julpd)</td>
<td>0.52 (mjtppt)</td>
<td>−0.35 (mjtemp)</td>
</tr>
<tr>
<td>WCD</td>
<td>0.46 (julp)</td>
<td>0.5 (mjtppt)</td>
<td>−0.35 (jultemp)</td>
</tr>
</tbody>
</table>

Table 2: The strongest relationships (1905-end of record) between standardized annual radial growth and climate variables representing drought severity (PDSI), precipitation, and temperature at each study site based on Pearson correlation. All r-values are significant with p < 0.02.

The variables are: jaspd = mean of July–September PDSI values; mjtppt = total precipitation in May–July; lag1opd = PDSI value of the prior year October; junpd = June PDSI value; julpd = July PDSI value. Study site names for the three letter site codes are found in Table 1.
extends back to at least AD 1743 at each site (Table 1), allowing for variance around the mean post-AD 1905. For the early period we found significant differences between RCR/RCD (0.91/0.97 radial growth) and FCR/FCD (1.01/0.92) and for the late period we found no significant differences.

Our analysis of long-term trends of the primary climatic determinants of radial growth for each study site revealed no linear trend for 12/14 sites, and a trend toward drier conditions that would be unfavorable for radial growth at CGR and CGD \( (r = 0.35, p = 0.000 \text{ for July PDSI}) \). Further, our comparison of climatic conditions between the pre-and post-1950 period showed no significant changes in any variable (Fig. 2). We found long term upward trends in radial growth only at RCR \( (r = 0.25, p = 0.012) \) and FLD \( (r = 0.21, p = 0.033) \). However, the comparison of radial growth differences between the early and late time periods illustrates that mean radial growth in the post-1950 period was greater at all sites, significantly greater at six sites, and significantly greater for the seven site averages by species (Fig. 3).

Our analysis of radial growth rate differences between the early and late periods using selected decades of similar drought severity also reveals increasing radial growth in the later years of the record (Fig. 4). For all three comparisons (i.e., three climatic divisions) there were no significant differences in drought severity between the pre-and post-1950 period. Radial growth was greater in the late

**Fig. 3.** A comparison of standardized radial growth rates during the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** – significant \( (p < 0.05) \) differences based on Wilcoxon tests. Study site names for the three letter site codes are found in Table 1.

**Fig. 4.** A comparison of standardized radial growth rates between selected decades during the early (1905–1950) and late (1951–end of record) period for each study and the seven site means for PIPO and PSME. ** – significant \( (p < 0.05) \) differences based on Wilcoxon tests. A statistical test for the seven site means was not conducted as the selected decades varied between climatic divisions. Study site names for the three letter site codes are found in Table 1.
period at 13/14 sites and for the two 7-site means, and significantly greater at 8/14 sites.

### 3.3 Radial growth rates during and after stress periods

Comparison of radial growth rates during drought years of the early and late periods shows a consistent response across the region and between species, as radial growth rates are greater in the late period at all sites for both mild (PDSI < -1.0) and moderate (PDSI < -2.0) drought years, with the differences statistically significant at 13/14 sites during mild droughts (Fig. 5) and at 8/14 sites during moderate droughts (Fig. 6). While mean drought conditions were generally worse in the early period relative to the late period (i.e., more negative mean July PDSI values), these differences were not statistically significant. During recovery years from moderate drought, radial growth rates were greater in the late period at 12/14 sites and significantly greater at 3/14 sites (despite having a low sample size) (Fig. 7). The recovery years for mild drought also had greater growth in the late period at 12/14 sites (Fig. 8). The species response to drought conditions and drought recovery were strong post-1950. Mean radial growth increased 0.20 during the late period relative to the early period for PSME for mild and moderate droughts, respectively, and increased 0.24 and 0.16 for PIPO. For moderate drought-recovery years the differences were greater for

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**Fig. 5.** A comparison of standardized radial growth rates during mild (PDSI values < -1.0) drought years between the early (1905-1950) and late (1951-end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant (p < 0.05) differences based on Wilcoxon tests. Due to a varying mix of drought years between the three climatic divisions, a statistical test for the seven site means was not conducted. Study site names for the three letter site codes are found in Table 1.

**Fig. 6.** A comparison of standardized radial growth rates during moderate (PDSI values < -2.0) drought years between the early (1905-1950) and late (1951-end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant (p < 0.05) differences based on Wilcoxon tests. Due to a varying mix of drought years between the three climatic divisions, a statistical test for the seven site means was not conducted. Study site names for the three letter site codes are found in Table 1.
PSME (0.18 increase) than for PIPO (0.10 increase), and the three sites with significant increases were PSME. For moderate drought-recovery years PSME again had the greater increase, 0.14 compared to 0.10.

4. Discussion

4.1. Changes in radial growth rates and rising atmospheric CO₂

The results support our first hypothesis that radial growth rates of PSME and PIPO have changed significantly during the past century. Specifically, the results show that radial growth rates have increased post-1950 absent changes in climate that would favor enhanced growth. Elevated atmospheric CO₂ can have a positive effect on radial growth rates of naturally-occurring trees in semi-arid environments (Graybill, 1987; Graybill and Idso, 1993; Hättenschwiler et al., 1997; Knapp and Soulé, 2011; Knapp et al., 2001a, 2001b; LaMarche et al., 1984; Martínez-Vilalta et al., 2008; Soulé and Knapp, 2006), thus providing a possible non-climatic explanation for the increased growth. In the absence of alternative explanations for the observed increases in radial growth, we posit that CO₂ enrichment is a likely driving force. During the early period, average atmospheric CO₂ levels were 305 ppmv, and from 1951 to 2006 the average increased 11% to 339 ppmv.
ppmv (Etheridge et al., 1998; Keeling and Whorf, 2005), with a total increase of approximately 83 ppmv from 1905 to 2006. Similarly, radial growth averages for all seven sites were 11.5% (PIPO) and 8.4% (PSME) higher during the late period compared to the early period. The majority of these differences occurred during and following drought-stress periods.

Increasing levels of atmospheric CO2 can lead to reductions in moisture stress, although species-specific responses vary (Dawes et al., 2011; Gedalof and Berg, 2010). In comparing responses across multiple study sites, Gedalof and Berg (2010) found that PSME experienced greater radial growth responses to atmospheric CO2 enrichment than PIPO. While Gedalof and Berg (2010) relate increasing radial growth associated with atmospheric CO2 enrichment to enhanced photosynthesis, the alternative explanation of growth responses through increasing WUE has been demonstrated for PIPO growing in the northern Rocky Mountain region (Knapp and Soulé, 2011; Soulé and Knapp, 2011). If PSME and PIPO are sensitive to rising atmospheric CO2 levels, then their drought tolerance should increase over time. Our finding of greater radial growth during drought years and post-drought recovery years post-1950 compared to the 1905–1950 period supports our third hypothesis and the contention that these species cope better with drought than they did in the first half of the 20th century. Several studies have documented that increased WUE associated with elevated atmospheric CO2 levels cannot sufficiently compensate for decreases in water availability caused by warmer and/or drier conditions (Andreu-Hayles et al., 2011; Linares and Camarero, 2012; Peñuelas et al., 2008, 2011). Our findings suggest an ameliorative effect during stressful periods and an overall increase in radial growth during the latter 20th to early 21st century, despite considerably drier conditions during the past decade.

4.2. Climatic drivers of radial growth

In terms of the climatic responses to radial growth between species, our finding reveals there are minimal differences between PSME and PIPO, thus our hypothesis four was not supported. Radial growth of both species responds to the same climate drivers and the responses are of similar magnitude. Both Grisino-Mayer et al. (1998) and Watson and Luckman (2002) found similar climatic responses for PIPO and PSME growing in close proximity, PIPO and PSME overlap in their broad-scale geographic ranges (Little, 1971) and within a given site are exposed to similar topoedaphic and climatic conditions, and disturbance history. At all our sites the trees were spatially intermingled, with mature PSME and PIPO often growing within close proximity and thus in competition for resources. We conclude that changes in observed radial growth are not climatically driven, thus our second hypothesis is not supported. We did find significant increases in growth for both PSME and PIPO post-1950 (Fig. 3), but these changes were not concurrent with any significant changes in the primary climatic drivers of radial growth.

5. Conclusion

Although others have found differential physiologic (Stout and Sala, 2003) or growth responses between PSME and PIPO (Gedalof and Berg, 2010), our findings show that no meaningful interspecific differences in long-term growth rates or changing growth rates since the early 20th century occurred at seven sites located throughout the Northern Rockies. Specifically, we found that: 1) both conifers have experienced increased radial growth in the post-1950 period relative to the pre-1950 period; 2) PSME and PIPO respond similarly to climate; 3) the primary climatic drivers of radial growth remain unchanged during the last century or have trended toward drier conditions unfavorable for growth; and 4) any changes in standardized radial growth rates associated with CO2 enrichment have affected these co-occurring species positively and on a largely equal basis.

The consistency of responses at multiple sites under a variety of topoedaphic and climatic conditions and after controlling for a variety of growth-altering factors suggests that, at a regional scale, these trees have thrived under the environmental conditions of the latter half of the 20th century and early 21st century. That said, we caution that radial growth is only one measure of species health, and that we cannot extrapolate our findings to what would occur under continued warmer and drier conditions. Competition for resources may elicit species-specific physiologic responses as a coping mechanism for water stress (Marshall and Monserud, 2006; Piñol and Sala, 2000; Stout and Sala, 2003), and these responses can change through time (Marshall and Monserud, 2006), with potential implications under changing climatic conditions. Given the predictions of global circulation models for warmer and drier summers within multiple regions supporting semiarid forests and woodlands, our results may be applicable to regions such as central Asia, the Mediterranean, and throughout the American West that have undergone extensive changes during the past century (e.g., Clifford et al., 2011; Miller and Wigan, 1994).

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References


