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

P.T. Soulé [a,*], P.A. Knapp [b]

[a] Appalachian Tree-Ring Laboratory, Department of Geography and Planning, Appalachian State University, Rankin Science West, Boone, NC 28608, USA
[b] Carolina Tree-Ring Science Laboratory, University of North Carolina Greensboro, Greensboro, NC 27401, USA

ABSTRACT

We examined radial growth rates of locally co-occurring Douglas-fir (PSME – *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 CO_2 enrichment, have affected these co-occurring species on a largely equal basis and positively.

© 2013 Elsevier Ltd. All rights reserved.

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 CO_2.

Water stress may enhance the *relative* effects of elevated CO_2 on woody plant growth (Huang et al., 2007; Idso and Idso, 1994; Wullschleger et al., 2002), thus the impacts of increasing CO_2 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 CO_2 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 CO_2 assimilation and transpiration through stomatal openings) for Ponderosa pine trees

(*Pinus ponderosa* var. *ponderosa* – hereafter PIPO) throughout semiarid sites in the western United Sates 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 CO_2 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*)
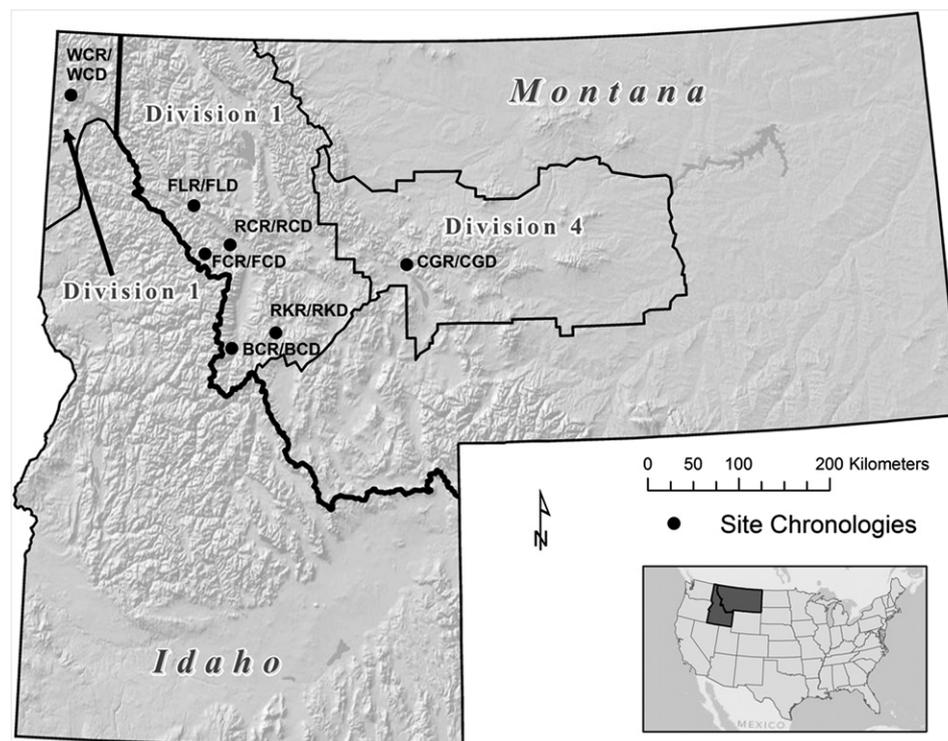
Fig. 1. Location of the seven matched pair study sites in Montana and Idaho, USA and boundaries of the climatic divisions from which climatic data were used. Study site names for the three letter site codes are found in Table 1.

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

Site	Interseries correlation	Mean sensitivity	Percent—absent rings	0.85 Rbar (AD)	# of samples series	
					In series	Dates (AD)
Boulder Creek Research Natural Area, Montana (BCR = Ponderosa pine chronology, BCD = Douglas-fir chronology)						
BCR	0.563	0.245	0.110	1734	48	1560—2008
BCD	0.549	0.212	0.014	1844	53	1307—2008
Rock Creek West, Montana						
RCR	0.655	0.295	0.278	1751	47	1602—2006
RCD	0.767	0.260	0.029	1776	68	1743—2006
Fish Creek, Montana						
FCR	0.576	0.252	0.269	1849	48	1575—2006
FCD	0.673	0.227	0.083	1785	54	1611—2006
Ferry Landing Research Natural Area, Montana						
FLR	0.637	0.261	0.028	1770	54	1560—2006
FLD	0.665	0.275	0.011	1797	60	1690—2006
Rock Creek East						
RKR	0.694	0.312	0.211	1718	61	1541—2008
RKD	0.744	0.310	0.016	1761	70	1665—2008
Cabin Gulch Research Natural Area, Montana						
CGR	0.690	0.355	1.056	1771	46	1542—2009
CGD	0.701	0.413	0.642	1810	44	1674—2009
Wellner Cliffs Research Natural Area, Idaho						
WCR	0.574	0.268	0.503	1677	42	1653—2009
WCD	0.611	0.244	0.314	1782	43	1673—2009

(Speer et al., 2001) outbreaks; and 5) are geographically diverse to ensure that we sampled PSME and PIPO across a spectrum of environmental conditions including soils, slope and aspect. Thus, the impacts of climate and other exogenous factors such as changing atmospheric composition should be well expressed in the data. Additionally, we collected samples for both species from the same area at each location so as to minimize potential intrasite topoedaphic differences between species that might affect radial growth. Soil conditions varied between and within sites based on slope (0—40%), soil depth (25—50 cm) and parent material (pers. observation), but no detailed soil surveys exist for our sites (except for BCR). Absent this information, we accounted for edaphic conditions potentially affecting our analysis by consistently sampling equal numbers of trees from both species at the same locations and avoided collecting samples from one species where the other species did not locally co-occur (i.e., within 100 m). Approximately 50% of our samples were from PSME and PIPO growing within 15 m of each other.

We sampled a minimum of 30 PSME and 30 PIPO trees at each site using standard dendroecological field techniques (Phipps, 1985). We employed a selective process to ensure sampling of trees from a variety of age classes and to minimize any potential impacts on radial tree growth associated with fire, lightning strikes, or pathogens. We avoided individual trees with visual signs of infections (e.g., witches' broom associated with dwarf mistletoe [*Arceuthobium* spp].), mountain pine beetles (*Dendroctonus ponderosae*) and blue stain fungus (*Grosmannia clavigera*), visible scars from fire and lightning strikes, or broken or dead tops. We sampled only in open-canopy locations to minimize potential growth surges/declines associated with canopy loss/infilling. We collected two increment cores at approximately 1.4 m height from opposite sides of each tree and parallel to slope contours to avoid problems associated with reaction wood.

We processed and crossdated all core samples using standard laboratory procedures for dendroecological samples (Phipps, 1985). We used a linear encoder to measure annual ring widths to an accuracy of 0.01 mm and corrected crossdating errors using diagnostics provided by COFECHA (Holmes, 1983). We obtained standardized annual radial growth values by applying conservative

techniques (e.g., negative linear, negative exponential) available within the program ARSTAN (Cook and Holmes, 1997). The annual values are normalized to a mean of 1.0 to account for age-related declines in growth and represent average tree growth within a given site. After experimentation, we determined that the STANDARD chronology consistently had stronger relationships with climate than the ARSTAN chronology, so we used the STANDARD chronology index values for all analyses.

2.2. Growth/climate analyses

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 (e.g., Fye and Cleaveland, 2001; Grissino-Mayer, 1996; Pohl et al., 2002) 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 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 also compared radial growth between selected decades of the early and late 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 PIPO 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 CGR/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

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 $p < 0.02$.

Site	Drought relationship	Precipitation relationship	Temperature relationship
r-value (climate variable)			
BCR	0.57 (jaspd)	0.53 (mjjppt)	−0.37 (mjjtemp)
BCD	0.41 (julpd)	0.5 (mjjppt)	−0.3 (mjjtemp)
RCR	0.47 (julpd)	0.55 (mjjppt)	−0.3 (mjjtemp)
RCD	0.44 (julpd)	0.53 (mjjppt)	−0.34 (mjjtemp)
FCR	0.48 (l1octpd)	0.47 (mjjppt)	−0.3 (mjjtemp)
FCD	0.55 (junpd)	0.47 (l1n_appt)	−0.26 (jultemp)
FLR	0.54 (jaspd)	0.44 (l1o_sppt)	−0.41 (mjjtemp)
FLD	0.6 (junpd)	0.5 (mjjppt)	−0.32 (jultemp)
RKR	0.61 (julpd)	0.59 (mjjppt)	0.29 (mjjtemp)
CGR	0.54 (julpd)	0.51 (l1o_sppt)	−0.39 (jultemp)
CGD	0.6 (julpd)	0.52 (l1o_appt)	−0.41 (mjjtemp)
WCR	0.53 (julpd)	0.52 (mjjppt)	−0.35 (mjjtemp)
WCD	0.46 (l1seppd)	0.5 (mjjppt)	−0.35 (mjjtemp)

The variables are: jaspd = mean of July–September PDSI values; mjjppt = total precipitation in May–July; mjjtemp = mean temperature June–August; julpd = July PDSI value; l1octpdd = PDSI value of the prior year October; junpd = June PDSI value; l1n_appt = total precipitation prior year November to current year August; jultemp = July mean temperature; l1o_sppt = total precipitation prior October to current year September; l1o_appt = total precipitation prior year October to current year August; l1seppd = PDSI value of the prior year September.

during years of moisture stress may have changed temporally in relation to increasing iWUE by determining if radial growth rates during drought years of the *early* period were significantly different (via the Wilcoxon test and a null hypothesis of no significant differences between time periods) than during drought years of the *late* period. We also examined radial growth responses following drought to determine recovery rates between species and whether these rates have changed temporally in association with the ameliorative effects of increasing atmospheric CO_2. This effect is theorized to be related to an overall reduction in stress during recent drought periods because of increased iWUE (Knapp et al., 2001b). Within the pre- and post-1950 periods we identified moderate (mild) drought recovery years as any year having a PDSI value >0 that was preceded by at least one year with PDSI values <−2.0 (−1.0). We then used the Wilcoxon test and a null hypothesis

of no significant differences between time periods to determine if radial growth rates during drought recovery years differed between *early* and *late* periods.

We quantitatively assessed whether PSME and PIPO have experienced differential growth responses using matched pairs Wilcoxon tests to compare standardized radial growth rates of PSME and PIPO within a given sites (e.g., BCR compared to BCD). We did this for the 1905-end of record period and for the *early* and *late* periods with a null hypothesis of no significant differences in radial growth rates between the two species. In addition, we qualitatively assess the similarity in climate response between species and compare species-specific responses from all statistical tests.

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 ($p < 0.02$) relationships demonstrate 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
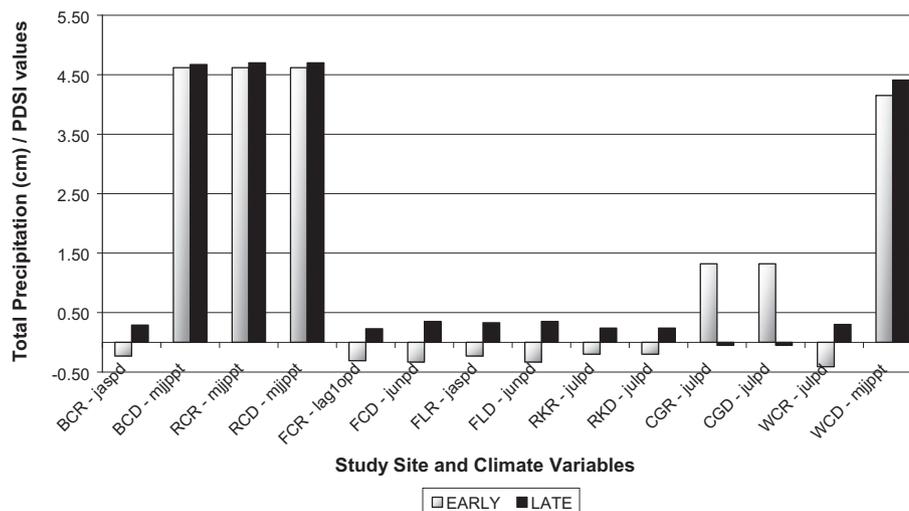
Fig. 2. A comparison of the climate variable most closely related to radial growth at each study site during the early (1905–1950) and late (1951–end of record) periods. There were no significant ($p < 0.05$) differences at any site based on Wilcoxon tests. The variables are: jaspd = mean of July–September PDSI values; mjjppt = 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.
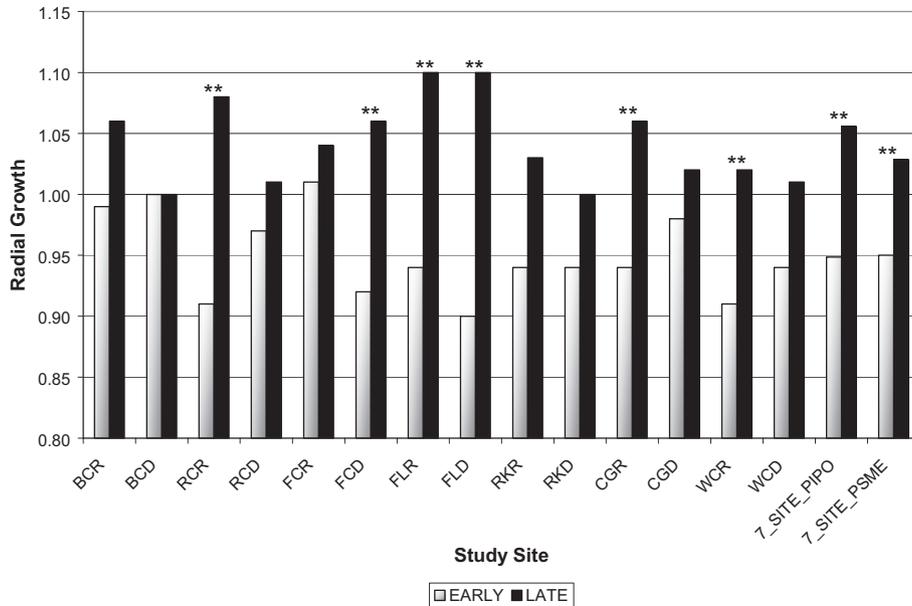
Fig. 3. A comparison of standardized radial growth rates during the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant ($p < 0.05$) differences based on Wilcoxon tests. Study site names for the three letter site codes are found in Table 1.

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 ($r = -0.35$, $p = 0.000$ 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 *early* and *late* decades. Radial growth was greater in the late
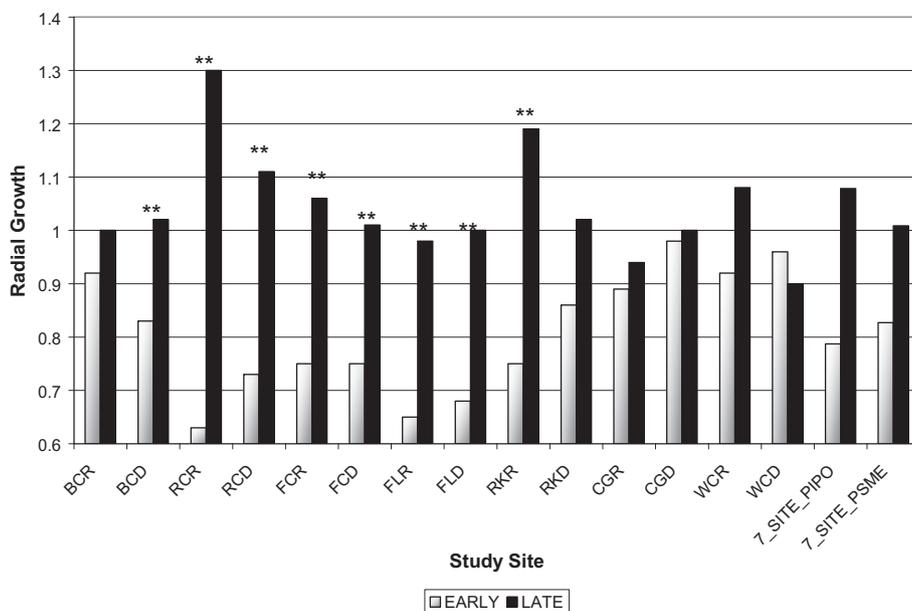
Fig. 4. A comparison of standardized radial growth rates between selected decades during the early (1905–1950) and late (1951–end of record) period for each study and the seven site means for PIPO and PSME. ** = significant ($p < 0.05$) differences based on Wilcoxon tests. A statistical test for the 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.
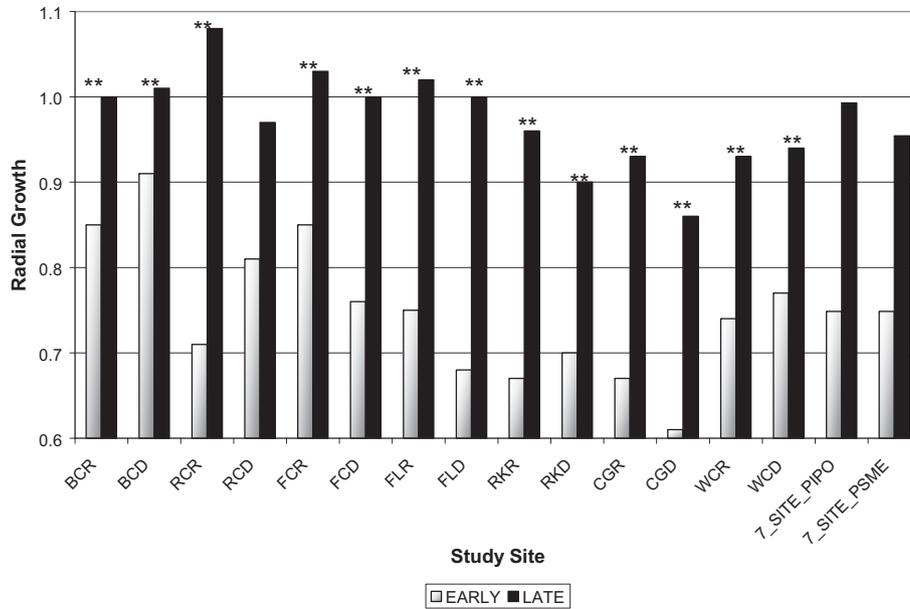
Fig. 5. A comparison of standardized radial growth rates during mild (PDSI values < −1.0) drought years between the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant (*p* < 0.05) differences based on Wilcoxon tests. 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.

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
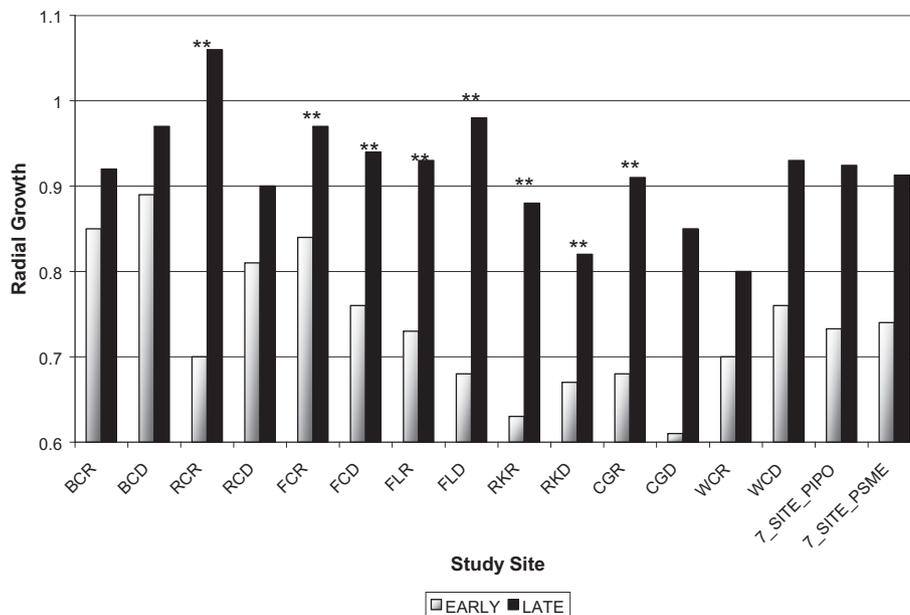
Fig. 6. A comparison of standardized radial growth rates during moderate (PDSI values < −2.0) drought years between the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant (*p* < 0.05) differences based on Wilcoxon tests. 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.
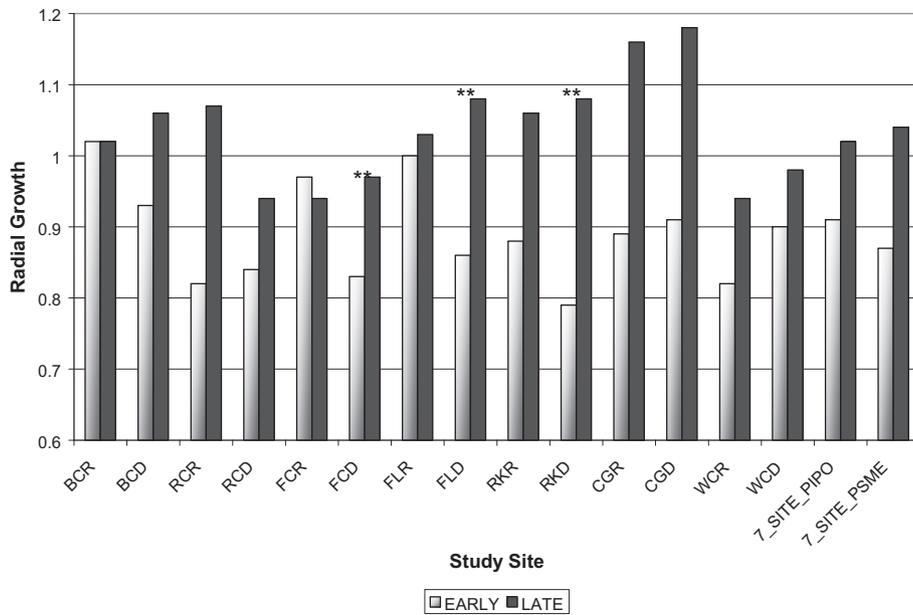
Fig. 7. A comparison of standardized radial growth rates during recovery years from moderate drought during the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant ($p < 0.05$) differences based on Wilcoxon tests. Due to a varying mix of drought recovery 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 CO_2

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 CO_2 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 CO_2 enrichment is a likely driving force. During the *early* period, average atmospheric CO_2 levels were 305 ppmv, and from 1951 to 2006 the average increased 11% to 339
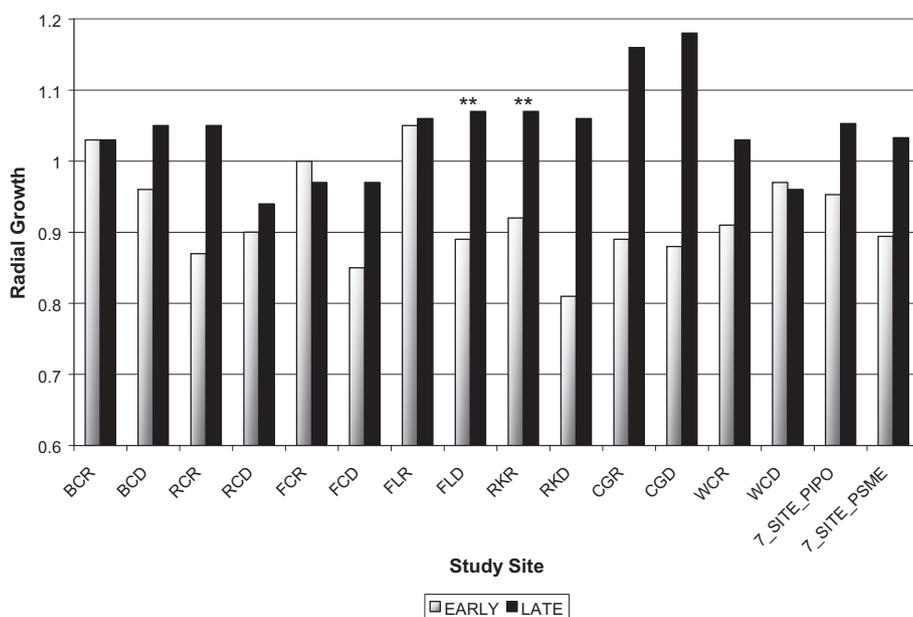
Fig. 8. A comparison of standardized radial growth rates during recovery years from mild (PDSI < -1.0) drought during the early (1905–1950) and late (1951–end of record) periods for each study site and the seven site means for PIPO and PSME. ** = significant ($p < 0.05$) differences based on Wilcoxon tests. Due to a varying mix of drought recovery 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.

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 CO_2 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 CO_2 enrichment than PIPO. While Gedalof and Berg (2010) relate increasing radial growth associated with atmospheric CO_2 enrichment to enhanced photosynthesis, the alternative explanation of growth responses through increasing iWUE 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 CO_2 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 during the first half of the 20th century. Several studies have documented that increased WUE associated with elevated atmospheric CO_2 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 Grissino-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 conditions, 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 CO_2 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).

References

Andreu-Hayles, L., Planells, O., Gutierrez, E., Muntan, E., Helle, G., Anchukaitis, K.I., Schleser, G.H., 2011. Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of tree growth at five Iberian pine forests. Global Change Biology 17, 2095–2112.
Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.T., Laprise, R., Magana Rueda, V., Mearns, L., Menendez, C.G., Raisanen, J., Rinke, A., Sarr, A., Whetton, P., 2007. Regional climate predictions. In: Solomon, S. (Ed.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, New York, USA.
Clifford, M.J., Cobb, N.S., Buenemann, M., 2011. Long-term tree cover dynamics in a pinyon-juniper woodland: climate-change-type drought resets successional clock. Ecosystems 14, 949–962.
Cook, E.R., Holmes, R.L., 1997. ARSTAN: chronology development. In: Grissino-Mayer, H.D., et al. (Eds.), The International Tree-ring Data Bank Program Library, Version 21 User's Manual. University of Arizona Laboratory of Tree-Ring Research, Tucson, AZ, pp. 75–92.
Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. BioScience 51, 723–734.
Dawes, M.A., Hattenschwiler, S., Bebi, P., Hagedorn, F., Handa, I.T., Korner, C., Rixen, C., 2011. Species-specific tree growth responses to 9 years of CO_2 enrichment at the alpine treeline. Journal of Ecology 99, 383–394.
Earle, C.J., 2007. The Gymnosperm Database. http://www.conifers.org.
Etheridge, D., Steele, L., Langenfelds, R., Francey, R., Barnola, J.-M., 1998. Historical CO_2 records from the LawDomeDE08, DE08-2, and DSS ice cores. In: Trends: a Compendium of Data on Global Change. Oak Ridge, TN: Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory, U.S. Department of Energy.
Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P., 2003. Ecological effects of nitrogen deposition in the western United States. BioScience 53, 404–420.
Fye, F.K., Cleaveland, M.K., 2001. Paleoclimatic analyses of tree-ring reconstructed summer drought in the United States, 1700-1978. Tree-Ring Research 57, 31–44.
Gedalof, Z., Berg, A.A., 2010. Tree ring evidence for limited CO_2 fertilization of forests over the 20th century. Global Biogeochemical Cycles 24. http://dx.doi.org/10.1029/2009GB003699.

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

Graybill, D.A., 1987. A network of high elevation conifers in the western United States for detection of tree-ring growth response to increasing atmospheric carbon dioxide. In: Jacoby, G.C., Hornbeck, J.W. (Eds.), Proceedings, the International Symposium on Ecological Aspects of Tree-ring Analysis. United States Department of Energy Report DOE/CONF-8608144, pp. 463–474.

Graybill, D.A., Idso, S.B., 1993. Detecting the aerial fertilization of atmospheric CO_2 enrichment in tree-ring chronologies. Global Biogeochemical Cycles 7, 81–95.

Grissino-Mayer, H.D., 1996. A 2129-year reconstruction of precipitation for northwestern New Mexico, U.S.A. In: Dean, J.S., Meko, D.M., Swetnam, T.W. (Eds.), Tree Rings, Environment, and Humanity. Radiocarbon, pp. 191–204.

Grissino-Mayer, H.D., Woodhouse, C.A., Carnine, S.I., Colbert, J.J., Diaz, S., Desta, F., Dougherty, P., Ford, C.R., Foster, T.E., Gross, W.S., Groven, R., Malmquist, D.L., Nunes, E., Sherriff, R.L., Solberg, B., 1998. Dendroclimatic Analysis of Ponderosa Pine and Douglas-fir in the Central Colorado Front Range. Final Report, 9th Annual North American Dendroecological Fieldweek. Mountain Research Station, Colorado, USA, 13 pp.

Hamlet, A.F., Mote, P.W., Clark, M.P., Lettenmaier, D.P., 2007. Twentieth century trends in runoff, evapotranspiration, and soil moisture in the western United States. Journal of Climate 20, 1468–1486.

Hättenschwiler, S., Miglietta, F., Raschi, A., Korner, C., 1997. Thirty years of in situ tree growth under elevated CO_2: a model for future forest responses. Global Change Biology 3, 464–471.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69–78.

Huang, J.-G., Bergeron, Y., Denneler, B., Berninger, F., Tardif, J., 2007. Response of forest trees to increased atmospheric CO_2. Critical Reviews in Plant Science 26, 265–283.

Idso, K.E., Idso, S.B., 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. Agricultural and Forest Meteorology 69, 153–203.

Karl, T.R., Williams Jr., C.N., Young, P.J., Wendland, W.M., 1986. A model to estimate the time of observation bias associated with monthly mean maximum, minimum, and mean temperatures for the United States. Journal of Climate and Applied Meteorology 25, 145–160.

Keeling, C., Whorf, T., 2005. Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: Acompendium of Data on Global Change. Oak Ridge, TN: Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory, U.S. Department of Energy.

Knapp, P.A., Soulé, P.T., Grissino-Mayer, H.D., 2001a. Detecting the potential regional effects of increased atmospheric CO_2 on growth rates of western juniper. Global Change Biology 7, 903–917.

Knapp, P.A., Soulé, P.T., Grissino-Mayer, H.D., 2001b. Post-drought growth responses of western juniper (*Juniperus occidentalis* var. *occidentalis*) in central Oregon. Geophysical Research Letters 28, 2657–2660.

Knapp, P.A., Soulé, P.T., 2011. Reconstructing annual area burned in the Northern Rockies, USA: AD 1626–2008. Geophysical Research Letters 38. http://dx.doi.org/10.1029/2011GL048119. L17402.

LaMarche, V.C., Graybill, D.A., Fritts, H.C., Rose, M.R., 1984. Increasing atmospheric carbon dioxide: tree-ring evidence for growth enhancement in natural vegetation. Science 225, 1019–1021.

Lee, E.H., Hogsett, W.E., 2001. Interpolation of temperature and non-urban ozone exposure at high spatial resolution over the western United States. Climate Research 18, 163–179.

Linares, J.C., Camarero, J.J., 2012. From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. Global Change Biology 18, 1000–1015.

Littell, J.S., Elsner, M.M., Mauger, G.S., Lutz, E., Hamlet, A.F., Salathe, E., 2011. Regional Climate and Hydrologic Change in the Northern US Rockies and Pacific Northwest: Internally Consistent Projections of Future Climate for Resource Management. Via: http://cses.washington.edu/picea/USFS/pub/Littell_etal_2010/. on July 1, 2012.

Little Jr., E.L., 1971. Atlas of United States Trees. In: Conifers and Important Hardwoods, vol. 1. USDA, Miscellaneous Publication 1146. Via: http://esp.cr.usgs.gov/data/atlas/little. on June 1, 2012.

Marshall, J.D., Monserud, R.A., 2006. Co-occurring species differ in tree ring $\delta^{18}O$ trends. Tree Physiology 26, 1055–1066.

Martínez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., Ninyerola, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. Global Change Biology 14, 2868–2881.

Miller, R.F., Wigan, P.E., 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44, 465–474.

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545.

Palmer, W., 1965. Meteorological Drought. US Government Printing Office, Washington, DC.

Peñuelas, J., Hunt, J.M., Ogaya, R., Jump, A.S., 2008. Twentieth century changes of tree-ring $\delta^{13}C$ at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. Global Change Biology 14, 1076–1088.

Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Global Ecology and Biogeography 20, 597–608.

Peterson, D.L., Millar, C.I., Joyce, L.A., Furniss, M.J., Halofsky, J.E., Neilson, R.P., Morelli, T.L., 2011. Responding to Climate Change in National Forests: a Guidebook for Developing Adaption Options. Gen. Tech. Rep. PNW-GTR-855. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Or, 109 pp.

Phipps, R.L., 1985. Collecting, preparing, crossdating, and measuring tree increment cores. US Geologic Survey Water-Resources Investigations Report, 85–4148.

Piñol, J., Sala, A., 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. Functional Ecology 14, 538–545.

Pohl, K.A., Hadley, K.S., Arabas, K.B., 2002. A 545-year drought reconstruction for central Oregon. Physical Geography 23, 302–320.

Soulé, P.T., Knapp, P.A., 2006. Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO_2 fertilization effect? New Phytologist 171, 379–390.

Soulé, P.T., Knapp, P.A., 2011. Radial growth and increased water-use efficiency for Ponderosa pine tree in three regions in the western United States. Professional Geographer 63, 1–13.

Speer, J.H., Swetnam, T.W., Wickman, B.E., Youngblood, A., 2001. Changes in pandora moth outbreak dynamics during the past 622 years. Ecology 82, 669–697.

Stout, D.L., Sala, A., 2003. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. Tree Physiology 23, 43–50.

Tognetti, R., Longobucco, A., Miglietta, F., Raschi, A., 1998. Transpiration and stomatal behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon dioxide spring. Plant, Cell and Environment 21, 613–622.

Watson, E., Luckman, B.H., 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research 32, 1858–1874.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science 313, 940. http://dx.doi.org/10.1126/science.1128834.

Wullschleger, S.D., Tschaplinski, T.J., Norby, R.J., 2002. Plant water relations at elevated CO_2 – implications for water limited environments. Plant, Cell, and Environment 25, 319–331.

WWPA – Western Wood Products Association, 2012. Ponderosa Pine Species Facts. Via: http://www2.wwpa.org/WESTERNSPECIES/PonderosaPine/tabid/298/Default.aspx. on July 1, 2012.