ORIGINAL ARTICLE

Analyses of intrinsic water-use efficiency indicate performance differences of ponderosa pine and Douglas-fir in response to CO_2 enrichment

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ABSTRACT

Aim Increasing intrinsic water-use efficiency (iWUE) in trees is a global-scale response to increasing levels of atmospheric carbon dioxide (C_a). Our primary goal was to determine whether significant differences in either iWUE or radial growth exist between locally co-occurring ponderosa pine (*Pinus ponderosa* var. *ponderosa*; PIPO) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*; PSME) trees growing in minimally disturbed environments and exposed to gradually increasing levels of C_a.

Location Northern Rocky Mountains, USA.

Methods We developed 14 tree-ring chronologies, calculated basal area increment (BAI) and examined stable carbon isotope ratios ($\delta^{13}C$) contained in the tree cores to determine: (1) the consistency of climate/BAI responses and iWUE between the two species and the magnitude of climate change for the primary drivers of BAI; (2) changes in iWUE and BAI values during AD 1850–present; and (3) the extent of pan-regional consistency in iWUE, BAI and climatic responses.

Results PIPO and PSME experienced exponentially increasing iWUE rates during AD 1850–present suggesting either increased net photosynthesis or decreased stomatal conductance, or both. There was pan-regional consistency, with similar temporal trends in iWUE and climate/growth relationships between species. Both species experienced above-average BAI in the latter half of the 20th century despite no favourable changes in climate. We found substantive differences between species as PIPO has experienced greater increases in iWUE and BAI relative to PSME. The trends in BAI and iWUE were significantly correlated for PIPO, but not for PSME.

Main conclusions Differential radial growth and iWUE responses exist among co-occurring species and are most pronounced during the period of highest C_a. As PIPO and PSME forests have extensive geographical ranges and are critical to North American forestry, any substantive change in forest dynamics related to water use and growth may have ecological and economic implications.

Keywords

Basal area increment, carbon dioxide enrichment, co-occurring species, differential response, intrinsic water-use efficiency, northern Rocky Mountains, *Pinus ponderosa* var. *ponderosa*, *Pseudotsuga menziesii* var. *glauca*, radial growth.

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INTRODUCTION

Atmospheric carbon dioxide (C_a) concentrations reached 400 ppmv in 2014, representing an approximately 80 ppmv increase since direct measurements began in 1958 (Keeling *et al.*, 2001) and the highest level during the past 800,000 years (Lüthi *et al.*, 2008). An influence of rising C_a on intrinsic water-use efficiency (iWUE; the ratio between

net photosynthesis and stomatal conductance) in trees is the narrowing of leaf stomatal apertures, thus reducing transpiration rates and increasing the efficiency of soil-moisture usage (Tognetti et al., 1998). In a meta-study synthesizing results from 20 different locations in four biomes and 19 tree different species, Peñuelas et al. (2011) found positive changes in iWUE, ranging from 5.6% to 36.2% from the 1960s to the 2000s. The effect of elevated C_a can either indirectly (Peñuelas et al., 2011) or directly affect radial growth of trees. Indirect effects of increased iWUE include an extension to the growing season where soil moisture is limiting in late summer (Tyson et al., 2002; Soulé & Knapp, 2013) and/or increased growth during drought periods (Wullschleger et al., 2002; Soulé & Knapp, 2011). The effects of increased iWUE can be age-specific, with older trees preferentially benefitting (Knapp & Soulé, 2011). The direct effects of elevated C_a occur through increased rates of net photosynthesis (Morgan et al., 2004).

Despite a positive relationship between radial tree growth and increasing C_a, not all species have experienced growth increases commensurate with increases in iWUE (Peñuelas et al., 2008, 2011; Gedalof & Berg, 2010; Silva et al., 2010; Wang et al., 2012), suggesting either a limited benefit or the primacy of factors masking an iWUE effect. Trees respond to multiple environmental stimuli (Fritts, 1976) and site-specific radial growth declines have been attributed to increasing temperature (Salzer et al., 2009; Silva et al., 2010), drought (Linares & Camarero, 2012; Wang et al., 2012), insect attacks (Speer et al., 2001; Speer & Holmes, 2004; Knapp et al., 2013), pathogens (Stanton, 2007) and atmospheric pollution (Adams et al., 1985).

Responses to both water stress (Piñol & Sala, 2000; Stout & Sala, 2003; Marshall & Monserud, 2006) and C_a enrichment vary among tree species (Gedalof & Berg, 2010; Andreu-Hayles et al., 2011; Dawes et al., 2011). C_a enrichment can ameliorate moisture stress in woody plants (e.g. Idso & Idso, 1994; Wullschleger et al., 2002; Huang et al., 2007; Soulé & Knapp, 2011, 2013; Koutavas, 2013), thus the question arises of whether co-occurring tree species experiencing near-identical climatic and topoedaphic conditions respond differently. In the northern Rockies, two dominant tree species, ponderosa pine (Pinus ponderosa var. ponderosa; PIPO) and Douglas-fir (Pseudotsuga menziesii var. glauca; PSME), have similar ranges (Earle, 2013), frequently co-occur (Fig. 1) and have great ecological and economic value (WWPA, 2013). However, interspecific comparison of the responses of PIPO and PSME to water stress in the northern Rockies has shown that while PIPO is more vulnerable to xylem cavitation, PIPO has higher xylem conductance because of higher stomatal control (Piñol & Sala, 2000; Stout & Sala, 2003). The few studies of long-term responses of PSME and PIPO to elevated C_a exhibit mixed results (e.g. Marshall & Monserud, 1996; Feng, 1999) and require further investigation. Here, we posit that PIPO may preferentially benefit from increasing iWUE because of its inherent physiological characteristics.

Our work represents a previously unexplored aspect of the relationship between iWUE and tree growth. We confine our analyses to trees growing in areas that have been subjected to minimal human interference and exposed to gradual increases in C_a. By sampling locally co-occurring tree species, we minimized the effects of exogenous factors including microclimate and topoedaphic conditions that might mask otherwise significant growth differences between species. Thus, examining radial-growth rates and iWUE temporal trends of co-occurring PSME and PIPO may offer insights regarding species-specific responses to increasing C_a levels. Our primary goal was to determine whether significant differences existed in either iWUE or radial growth (measured via basal area increment, BAI) between locally co-occurring

Figure 1 Common conditions for co-occurring ponderosa pine (Pinus ponderosa var. ponderosa; PIPO); and Douglas-fir (Pseudotsuga menziesii var. glauca; PSME) trees at 14 study sites in the northern Rocky Mountains, USA. The two nearest trees are PSME (left) and PIPO (right centre). They are growing within an open canopy ecosystem at Ferry Landing Research Natural Area (FLR/FLD).

ponderosa pine (PIPO) and Douglas-fir (PSME) trees growing in minimally disturbed environments and exposed to gradually increasing levels of C_a. Our specific objectives were: (1) to examine the consistency of climate/BAI responses and iWUE between species and the magnitude of climate change for the primary drivers of BAI; (2) to determine the magnitude of changes in iWUE and BAI values during AD 1850–present; and (3) to determine the extent of pan-regional consistency in iWUE, BAI and climatic responses.

MATERIALS AND METHODS

Fieldwork

We collected tree-ring data from seven sites within the boundaries of the United States Forest Service Northern Rockies Region (FSNRR) (Fig. 2, Table 1). Each collection site has stands with co-occurring PIPO and PSME. We selected study sites that minimized potential anthropogenic influences on radial growth. Three of the sites have a Research Natural Area (RNA) designation [BCR/BCD, FLR/FLD and WCR/WCD (where R = ponderosa pine chronology and D = Douglas-fir)] and are noted for their ecological significance and minimal anthropogenic impacts (Evenden et al., 2001). The remaining four sites were chosen based on a history of minimal human influence associated with factors such as topographic isolation and land-use history. All sites are in either northern interior Idaho or western Montana: locations where the potential radial growth impacts of either ozone or nitrogen are minimized because of low exposure (Lee & Hogsett, 2001).

Our criteria for tree selection were designed to further reduce confounding influences on growth. We selected trees in open-canopy environments to minimize potential growth changes from canopy infilling and neighbouring tree senescence. We avoided sampling trees with visible signs of damage from fire or lightning, abnormal growth forms, or with visible signs of pathogens [e.g. pitch tubes associated with mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, and dwarf mistletoe (*Arceuthobium* spp.)]. At each site we non-destructively obtained two or more core samples at approximately 1.4 m height from 30–40 mature PIPO and PSME trees using standard dendrochronological techniques (Phipps, 1985).

Tree-ring data processing and basal area increment

We sanded each core sample until the cellular structure of the rings was visible and cross-dated the samples using the list method (Yamaguchi, 1991). We used linear encoders to measure ring widths to 0.001 mm precision and examined the measured data using COFECHA (Holmes, 1983; Grissino-Mayer, 2001) to ensure the dating accuracy. For analysis, we selected a subsample of 12 cores per species per site from our original sample of 30–40 cores/species/site. Each subsample was based on the criteria (Soulé & Knapp, 2011) of selecting two cores from each of six trees that had well-defined ring structure, strong correlations with the full chronology and multi-century longevity (mean age > 225 years; Table 1).

For each core we calculated annual basal area increment (BAI) values via Silva et al. (2010):
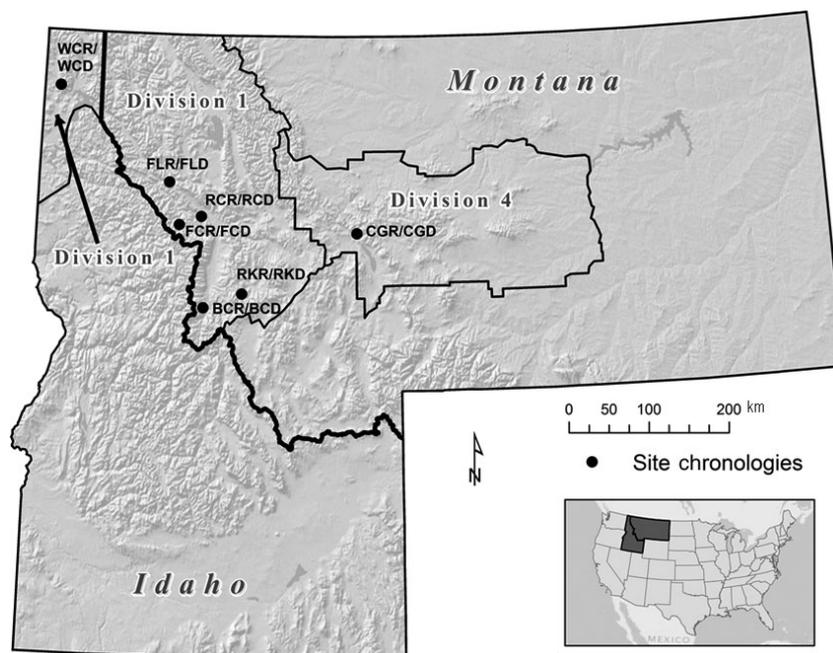
Figure 2 Location of the 14 study sites in the northern Rocky Mountains (Montana and Idaho), USA, including climate division boundaries. Reprinted from Soulé & Knapp (2013) with permission from Elsevier.

Table 1 Details for tree-ring chronologies ($n = 12$ samples in each chronology) collected from co-occurring ponderosa pine (*Pinus ponderosa* var. *ponderosa*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees in the northern Rocky Mountains, USA.

Site	Interseries correlation[a]	Mean sensitivity[b]	AR1 correlation[c]	% absent rings[d]	Complete dates (AD)[e]	Mean age of trees (years)[f]
Wellner Cliffs Research Natural Area, Idaho						
WCR[g]	0.557	0.249	0.73	0.441	1653–2009	335
WCD	0.572	0.231	0.642	0.498	1673–2009	283
Ferry Landing Research Natural Area, Montana						
FLR	0.607	0.257	0.542	0.052	1560–2004	318
FLD	0.678	0.266	0.515	0	1690–2006	240
Rock Creek West, Montana						
RCR	0.650	0.281	0.647	0.062	1602–2006	266
RCD	0.734	0.251	0.516	0.037	1757–2006	227
Fish Creek, Montana						
FCR	0.534	0.246	0.503	0.189	1710–2006	220
FCD	0.707	0.227	0.452	0.060	1611–2006	277
Rock Creek East						
RKR	0.669	0.286	0.496	0.055	1541–2008	301
RKD	0.744	0.302	0.454	0	1672–2008	269
Boulder Creek Research Natural Area, Montana						
BCR	0.618	0.261	0.523	0.088	1650–2004	282
BCD	0.538	0.218	0.485	0.022	1307–2008	374
Cabin Gulch Research Natural Area, Montana						
CGR	0.675	0.367	0.472	1.241	1634–2009	301
CGD	0.667	0.437	0.447	0.708	1674–2009	247

[a]Interseries correlation is a measure of signal strength among all samples. Values range from 0 (no relationship) to 1.0 (perfect agreement).
[b]Mean sensitivity is a measure of interannual variation in ring-widths. Higher values represent greater year-to-year variation.
[c]Autoregression coefficient for time = -1 from ARSTAN with no detrending.
[d]% (0–100) absent rings is a measure of the frequency of years in which trees did not produce an annual ring. It is a surrogate measure of environmental stress.
[e]The calendar year for the oldest core in the sample and the common ending year for the BAI sample.
[f]Mean age of the $n = 12$ cores in each sample.
[g]xxR = ponderosa pine chronology, xxD = Douglas-fir chronology.

$$BAI = \pi(R_n^2 - R_{n-1}^2)$$

where R is tree radius and n is year. To match with iWUE values, we then calculated pentadal means for BAI. We excluded from our analyses all data prior to 1850 to avoid the 'juvenile effect' (McCarroll & Loader, 2004) associated with iWUE calculations. The first pentad includes data from 1850 to 1854, the last complete pentad for all sites was 2000–2004, and the final pentad (2005) has means based on a varying number of years of radial growth per site (Table 1). As our sampling was focused on older trees that often produce narrow (< 0.5 mm) annual rings that can bias results when radial growth rates are standardized (Cook & Peters, 1997), we based our analyses on BAI, an absolute measure of radial growth.

Isotopic analysis and determination of iWUE

We examined stable carbon isotope ratios ($\delta^{13}C$) contained in the tree cores to determine the extent of physiological changes incurred by PSME and PIPO since 1850 during rising C_a conditions. All tree species have C_3 photosynthetic pathways that discriminate against the heavier ^{13}C isotope as they preferentially assimilate $^{12}C_a$ during photosynthesis (i.e.

photosynthetic discrimination); thus, $\delta^{13}C$ values are lower in tree tissue compared to ambient air. Correcting for changes in $\delta^{13}C$ of the atmosphere provides a better measure of photosynthetic discrimination (Δ) and is linearly related to the ratio of intercellular to ambient C_a concentrations (Farquhar et al., 1989), which are variables required to determine iWUE. Photosynthetic discrimination is also affected by soil moisture availability as stomata narrow during drought periods thereby decreasing Δ and, in turn, increasing iWUE (e.g. Zhang & Marshall, 1994). Thus, changes in iWUE for each species should reflect centennial-length increases associated with rising C_a coupled with shorter-term fluctuations caused by above/below-average soil moisture conditions.

Isotopic analysis from wood cellulose of complete rings was performed by the Environmental Isotope Laboratory (EIL) of the Department of Geosciences at the University of Arizona. The EIL used standard procedures (Sternberg, 1989; Leavitt & Danzer, 1993; Coplen, 1996) to process the samples, and returned to us pentadal values of carbon isotope composition ($\delta^{13}C$), which we then used to calculate pentadal values of iWUE via (Ehleringer & Cerling, 1995):

$$iWUE = A/g = (c_i/c_a)0.625$$

where iWUE (µmol/mol) measures the CO_2 assimilation of the tree (A) relative to stomatal conductance through the

leaf (g); c_i is intercellular CO_2; and c_a is CO_2 in the atmosphere. Details on the exact procedures employed to obtain end values of iWUE are outlined by Knapp & Soulé (2011).

Statistical analysis

For BAI, we began with the $n = 12$ sample of cores and calculated annual values. Per established procedures in dendrochronological research (Fritts, 1976), we used two cores/tree as this minimizes within-tree variance. We then averaged values for 5-year periods to obtain pentadal measurements (e.g. 1850 pentad = 1850–1854) and averaged the pentadal values across all sites to obtain the seven-site means. We then obtained standardized scores (z-scores) from the pentadal averages and used the standardized values in further testing, as our goal was to determine relative differences in radial growth between species and through time as opposed to absolute differences. Similarly, for iWUE we averaged the pentadal values across all sites to obtain the seven-site means. We used matched-pairs Wilcoxon tests on standardized pentadal BAI values for the seven study sites and for the seven-site means to determine whether significant differences in radial growth exist between PIPO and PSME at each site and for regional averages. We used SPSS version 20 for all statistical analyses. For iWUE, we assessed between-species similarities via Spearman correlation, as both the raw data and transformed data (e.g. $\log_{10}$, natural log) were not normally distributed. We used Spearman correlation between BAI/iWUE values and pentad to determine whether temporal trends existed and to determine the degree of association between BAI and iWUE. As not all variables examined were normally distributed or had linear relationships (i.e. iWUE and time), we used nonparametric techniques for consistency. To determine whether differences between species had changed through time we used the seven-site mean and calculated the pentadal ratio of standardized PIPO BAI to standardized PSME BAI. For iWUE we did the same using the raw values for the seven-site means. We examined the pentadal patterns graphically and determined whether temporal trends in the ratios existed using Spearman correlation.

We examined the climatic response of radial growth using Spearman correlation between a suite of monthly, seasonal and annual measures of temperature, precipitation, and drought severity as measured by the Palmer drought severity index (PDSI; Palmer, 1965) compared to annual BAI data. We used climate-division data from 1905 to the end of the BAI record (Table 1, Fig. 2). After identifying the primary climatic driver of radial growth for PIPO and PSME at each study site (e.g. July drought severity), we determined whether long-term (1905–end of record; Table 1) temporal trends were present using Spearman correlation. We also addressed potential changes in climate that might impact radial tree growth by determining whether conditions have become significantly wetter/drier in the post-1950 period relative to

pre-1950s by testing the primary climatic drivers of radial growth for significant differences pre- and post-1950 using Wilcoxon tests.

RESULTS

Radial growth of both PIPO and PSME is positively associated with moisture availability, either directly through supply (e.g. May–July precipitation) or through supply and demand as measured by the PDSI (Table 2). None of the monthly/seasonal/lagged temperature variables were the most significant climatic factors for radial growth, but the strongest associations (r_s value range -0.2 to -0.47 with $n = 101–104$) all involved some aspect of summer temperature and were negatively and significantly ($P < 0.05$) related to radial growth. The only significant ($P < 0.05$) long-term temporal trend for any of the primary climatic drivers for radial growth (Table 2) occurred in Montana Climate Division 4 (CGR and CGD study sites; Fig. 2), where negative trends in PDSI values of the previous-year November to the current-year August indicate a shift towards increasing aridity. The primary climatic driver of radial growth at WCR (previous-September PDSI) was significantly different in the post-1950 period, with wetter conditions experienced. All other comparisons of pre- to post-1950 conditions revealed there were no significant changes in the climatic conditions most closely associated with radial growth. The lack of meaningful long-term climate change for radial tree growth in the region is demonstrated by plots showing mean May to July values of temperature and precipitation for the three climate divisions (Fig. 3).

The Wilcoxon tests indicated that no significant ($P > 0.05$) differences existed in radial growth as measured by standardized BAI between PIPO and PSME for each of the seven study-site pairs. However, differences in BAI among sites exist, with six chronologies showing strong positive temporal trends, five no trends and three with a negative trend (Table 3, Fig. 4a–g). Only one clear match exists between long-term trends in radial growth and changing climatic conditions. The long-term and significant ($P < 0.001$) trend of reduced radial growth at CGD (negative but non-significant at CGR) matches the long-term trend for drier conditions within Montana Climate Division 4 (Table 3, Fig. 4b). At WCR/WCD in Idaho Climate Division 1 the climatic drivers of radial growth have no long-term trend, but there has been a shift towards wetter conditions post-1950 (significant for WCR) that would be conducive to increased tree growth (Table 2). Long-term trends of BAI are positive at WCR and significantly upward at WCD (Table 3).

For the seven-site means by species, PIPO growth increased significantly, while PSME growth was non-significant (Table 3). The seven-site means for PIPO BAI and PSME BAI are similar ($r_s = 0.701$, $P < 0.001$, $n = 32$; Fig. 4h), but there is a strong trend in the multi-site PIPO/PSME ratio ($r_s = 0.531$, $P < 0.01$, $n = 32$; Fig. 5) suggesting that, for the region as a whole, PIPO trees have grown at greater rates since the mid-20th century. During 1950 until

Table 2 The strongest relationships (1905–end of record) between annual basal area increment (BAI) from ponderosa pine (*Pinus ponderosa* var. *ponderosa*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees and a climate variable representing drought severity (Palmer drought severity index, PDSI) and precipitation at each study site (northern Rocky Mountains, USA) based on Spearman correlation; test for temporal trends for the main climate driver of radial tree growth via Spearman correlation; and Wilcoxon test for difference in the main climate driver of radial tree growth for years pre- and post-1950 (see Table 1 for complete study site names and chronology details).

Study sites	Relationship between BAI w/climate [r_s, variable (n; P-value)]	Temporal trend for main climate driver of radial tree growth (climate w/time) [r_s (n; P-value)]	Wilcoxon test for difference in main climate driver of tree growth (pre- vs. post 1950) [P-value (n early, n late)]
Sites in Idaho Climate Division 1			
WCR	**0.49**[a] sep^{-1}[b] (103; 0)[c]	0.11 (104; 0.25)	**0.028** (44, 54)
WCD	**0.44** jun (104; 0)	0.16 (104; 0.112)	0.074 (45, 54)
Sites in Montana Climate Division 1			
FLR	**0.49** oct^{-1}–aug (99; 0)	−0.1 (103[d]; 0.302)	0.258 (45, 58[e])
FLD	**0.41** jun (101; 0)	−0.09 (103; 0.393)	0.264 (45, 58)
RCR	**0.54** jul (101; 0)	−0.09 (103; 0.373)	0.393 (45, 58)
RCD	**0.49** mjjPPT (101; 0)	0 (103; 0.976)	0.525 (45, 58)
FCR	**0.21** oct^{-1} (101; 0.032)	−0.07 (103; 0.516)	0.378 (45, 58)
FCD	**0.44** sep^{-1} (101; 0)	−0.05 (103; 0.645)	0.347 (45, 58)
RKR	**0.62** jul (103; 0)	−0.09 (103; 0.373)	0.393 (45, 58)
RKD	**0.54** jun (103; 0)	−0.09 (103; 0.393)	0.264 (45, 58)
BCR	**0.49** mjjPPT (99; 0)	0 (103; 0.976)	0.525 (45, 58)
BCD	**0.46** mjjPPT (103; 0)	0 (103; 0.976)	0.525 (45, 58)
Sites in Montana Climate Division 4			
CGR	**0.53** nov^{-1}–aug (103; 0)	**−0.36** (103; 0)	0.68 (44, 59)
CGD	**0.69** nov^{-1}–aug (103; 0)	**−0.36** (103;0)	0.68 (44, 59)

[a]Boldfaced correlations are significant with $P < 0.05$.
[b]Variable acronyms (sep = September, jun = June, etc.; superscript −1 indicates variable is lagged by one year; mjj = average of May to July; PPT indicates monthly precipitation, all other variables represent drought severity as measured by PDSI values).
[c]P-values out to three decimal places.
[d,e]For consistency, we used the climate record through 2008 for all sites for the test of climate trends and differences for sites in Montana Climate Division 1.

the end of the record – a period when C_a concentrations rapidly increased – six of the seven PIPO sites had > 50% of pentadal BAI values > 0, and FCR did not experience a single pentadal value of < 0 (Fig. 4a–g). For PSME, four of the seven sites had more than half of the pentads with positive BAI values since 1950 (Fig. 4a–g).

Temporal patterns of iWUE for PIPO and PSME are in-phase (Fig. 6a–h). All sites and the seven-site means have significant ($P < 0.001$) positive associations between PSME and PIPO, with r_s values ranging from 0.728 at WCR/WCD to 0.981 for the seven-site mean. At all sites and for the seven-site means, there are strong, positive, nonlinear temporal trends (1850–end of record) for iWUE for both species (Table 3, Fig. 6a–h). Except for WCR and WCD, iWUE values are consistently higher for PSME than for PIPO. However, there is a notable shift in iWUE between species for the multi-site mean conditions, with smaller differences in iWUE between PIPO and PSME occurring with time ($r_s = 0.521$, $P < 0.01$, $n = 32$; Fig. 6h), indicating greater iWUE increases for PIPO. Changes in iWUE ratios between PIPO and PSME are most marked post-1970 (Fig. 5).

The association between BAI and iWUE for individual sites is mixed, with two PIPO and three PSME sites having a significant positive association ($P < 0.05$) between BAI and iWUE, and one PIPO and two PSME sites with a significant

($P < 0.01$) negative association (Table 3). The association between BAI and iWUE for the seven-site mean is significant for PIPO ($r_s = 0.586$, $P < 0.001$, $n = 32$), but insignificant for PSME ($r_s = 0.197$, $P = 0.279$, $n = 32$). A positive and significant association also exists between the BAI and iWUE ratios for PIPO/PSME during 1850–2005 ($r_s = 0.515$, $P = 0.003$, $n = 32$) (Fig. 5).

DISCUSSION

The significant associations between BAI and climate identified during late spring to summer (e.g. July PDSI values, May–July precipitation) or the previous-year autumn (e.g. previous-September PDSI) indicate that radial growth for PSME and PIPO is affected by moisture supply and demand during the growing season of the current and previous year (Table 2). These results, based on an absolute measure of radial growth (BAI), are similar to those found by Soulé & Knapp (2013) at the same study sites when using a larger sample of trees to compare standardized values of radial growth with climate. PIPO and PSME are responding to climate, both on an annual basis (Table 2), and within extended periods either favourable or unfavourable for growth. For example, all sites experienced low radial growth concurrent with extended
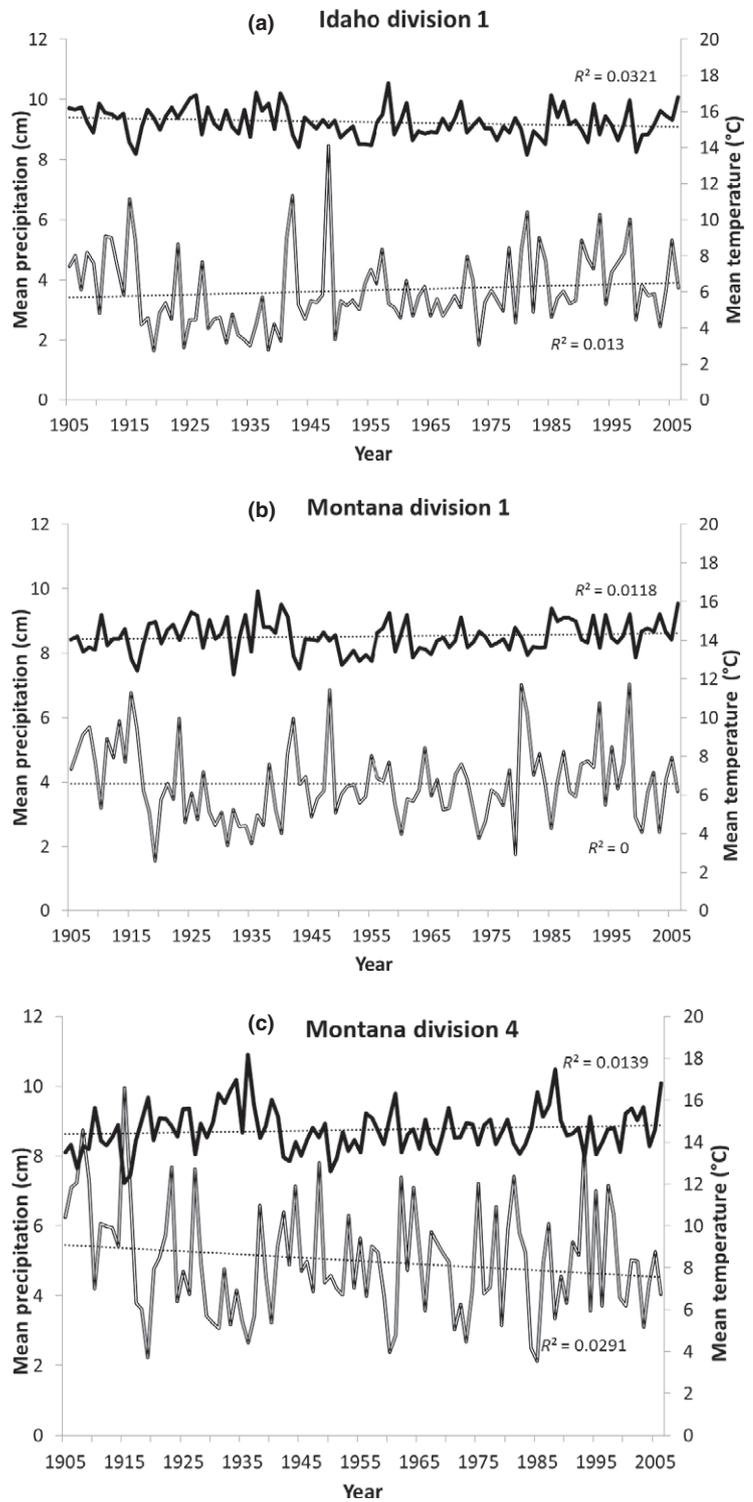
Figure 3 Yearly values of mean May to July temperature (°C) and May to July precipitation (cm) at: (a) Idaho Climate Division 1, (b) Montana Climate Division 1, and (c) Montana Climate Division 4, 1905–2006 within the northern Rocky Mountains, USA. The dotted line is a linear trend line with associated R^2 values. All linear trends were non-significant ($P > 0.05$). Thick black line: temperature; thick open line: precipitation; dotted lines: linear trends.

drought in the northern Rockies in the 1930s (Fig. 4). During the 1930s, mean July PDSI values for Montana Climate Division 4 (Fig. 2) were −3.6, with 9 of 10 years having PDSI values < 0. Similar mean July PDSI conditions occurred for Idaho Climate Division 1 (−2.2, 9/10 years) and Montana Climate Division 1 (−2.7, 9/10 years). While others have identified some level of differential growth/climate responses for PIPO and PSME (e.g. Watson & Luckman, 2002), our

results here using BAI and from a prior study (Soulé & Knapp, 2013) examining relationships between climate and standardized radial growth rates for the complete chronologies developed at the 14 study sites demonstrate there are no discernible differences between species. We find that the magnitude and direction of the strongest climatic responses for PIPO and PSME are consistent among seven different sites with a variety of topoedaphic conditions.

Table 3 Spearman correlations (*P*-values) from each study site (northern Rocky Mountains, USA) of basal area increment (BAI) from ponderosa pine (*Pinus ponderosa* var. *ponderosa*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees with time (via pentad 1850–2005[a]), intrinsic water use efficiency (iWUE) with time (via pentad 1850–2005), and Spearman correlations between BAI and iWUE with significant relationships ($P < 0.05$) in bold (see Table 1 for complete study site names and chronology details).

SITE	r_s BAI with time	r_s iWUE with time	r_s BAI/iWUE
WCR	0.287 (0.111)	**0.719 (0.000)**	0.055 (0.763)
WCD	**0.522 (0.000)**	**0.773 (0.000)**	**0.548 (0.001)**
FLR	**0.601 (0.000)**	**0.801 (0.000)**	**0.466 (0.008)**
FLD	**0.720 (0.000)**	**0.815 (0.000)**	**0.600 (0.000)**
RCR	0.072 (0.696)	**0.667 (0.000)**	−0.115 (0.529)
RCD	**0.446 (0.011)**	**0.916 (0.000)**	**0.351 (0.049)**
FCR	**0.870 (0.000)**	**0.910 (0.000)**	**0.785 (0.000)**
FCD	0.131 (0.474)	**0.900 (0.000)**	0.268 (0.138)
RKR	**−0.463 (0.008)**	**0.916 (0.000)**	**−0.523 (0.002)**
RKD	**−0.533 (0.002)**	**0.741 (0.002)**	**−0.573 (0.001)**
BCR	**0.703 (0.000)**	**0.665 (0.000)**	0.280 (0.127)
BCD	−0.086 (0.641)	**0.612 (0.000)**	−0.116 (0.528)
CGR	−0.139 (0.447)	**0.840 (0.000)**	−0.081 (0.658)
CGD	**−0.608 (0.000)**	**0.930 (0.000)**	**−0.666 (0.000)**
PIPO[b]	**0.406 (0.021)**	**0.930 (0.000)**	0.266 (0.142)
PSME	0.135 (0.462)	**0.895 (0.000)**	0.008 (0.965)

[a]The final pentad for BCR and FLR is 2000, thus $n = 31$. For all other sites $n = 32$.
[b]PIPO and PSME are the multi-site means.

Despite the physiological linkages that suggest trees should perform better in a C_a-rich environment, increasing rates of iWUE may not translate into enhanced radial growth (e.g. Gedalof & Berg, 2010; Silva *et al.*, 2010; Andreu-Hayles *et al.*, 2011; Peñuelas *et al.*, 2011; Silva & Anand, 2013). Silva & Anand (2013) propose a latitudinal control of the relationship, with higher latitude trees showing a positive radial growth response associated with the synergistic effects of C_a enrichment and warming. Conversely, low-latitude trees are dominated by negative trends in radial growth with the suggestion that moisture stress induced by warming is more important than photosynthetic gains associated with increasing iWUE. Our results show that mixed growth responses can occur within a given geographical region (latitudinal zone). We found that both positive and negative radial growth trends occurred among our seven sites in the northern Rockies, and in the absence of any substantive increases in temperature in the region (Fig. 3, Table 3). However, BAI values for the seven-site means are remarkable for the consistency of positive values during the post-1950 period, particularly for PIPO (Fig. 4h). Positive values have occurred despite several pentads with droughts, including the severe drought of 2000–2004, which recorded 60 consecutive months of drought conditions in both Montana Climate Divisions 1 and 4. Thus, above-average radial growth occurred for both species, but particularly for PIPO, during the period with the highest C_a values yet without significant changes to the climatic drivers of radial growth (Soulé & Knapp, 2013).

Some (Silva & Anand, 2013; Silva & Horwath, 2013) have argued that observed increases in iWUE in trees are not a physiological response, but occurred independently of $\delta^{13}C$ changes because of continual increases in C_a. In contrast, Brooks (2013) argues that what is being observed is a physiological response, thus heterogeneity in iWUE rates should be expected in natural settings. Several studies have reported a levelling of iWUE at the end of the record (e.g. Waterhouse *et al.*, 2004; Gagen *et al.*, 2011; Wang *et al.*, 2012) or no change in iWUE during the 20th century (Marshall & Monserud, 1996), while others have found significant positive trends in iWUE (Bert *et al.*, 1997; Feng, 1999; Tang *et al.*, 1999; Arneth *et al.*, 2002; Saurer *et al.*, 2004; Liu *et al.*, 2007; Knapp & Soulé, 2011). Results from our 14 study sites are consistent with the studies reporting increases, and at all sites the highest iWUE was recorded in one of the last two pentads.

While PSME currently exhibits greater iWUE than PIPO, PIPO is increasing iWUE more rapidly and the differences between the two species are becoming smaller (Fig. 5). Our sampling strategy minimizes the possibility that some within-site factor such as increasing soil moisture or greater nutrient availability has preferentially influenced iWUE in one species more greatly than the other. Further, both species have similar climate responses, so the differential temporal response in iWUE is unlikely to be climatically driven, but may reflect inherent physiological differences between species. Physiological differences between these species that could impact iWUE were identified by Stout & Sala (2003, p. 48) who determined that PIPO had 'greater stomatal sensitivity to water stress, shifts in biomass allocation and enhanced capacity to store water' relative to PSME, and concluded that PIPO is more drought resistant. Similarly, Marshall & Monserud (2006) found differences in stable oxygen-isotope ratios ($\delta^{18}O$) between co-occurring PIPO and PSME. PIPO became more $\delta^{18}O$-enriched through time and expressed no autocorrelation with lagged $\delta^{18}O$ values, inferring a strong dependence on near-surface water availability. These results contrast with the responses of PSME and illustrate the differential behaviour between the two species through time under near-identical settings.

For the region as a whole, a significant differential response between PIPO BAI and PSME BAI occurred temporally (Figs 4h & 5). As the difference in iWUE between PIPO and PSME has also been decreasing in recent decades (Fig. 6h), it raises questions of whether the two are causally related: that is, have improvements in iWUE for PIPO relative to PSME been responsible for the shift in BAI ratio, and if so, could there be longer-term ecosystem implications related to the increasing performance of PIPO relative to PSME? While the comparative changes in BAI between species began during the 1930s drought, a response expected via the findings of Stout & Sala (2003), these changes continued through to the end of the record and represent a reversal of the relative growth rates during 1850–1930 (Fig. 4h).

In summary, both PSME and PIPO have recorded exponentially increasing iWUE since the mid-19th century and this response occurred at all sites, suggesting a pan-regional effect.
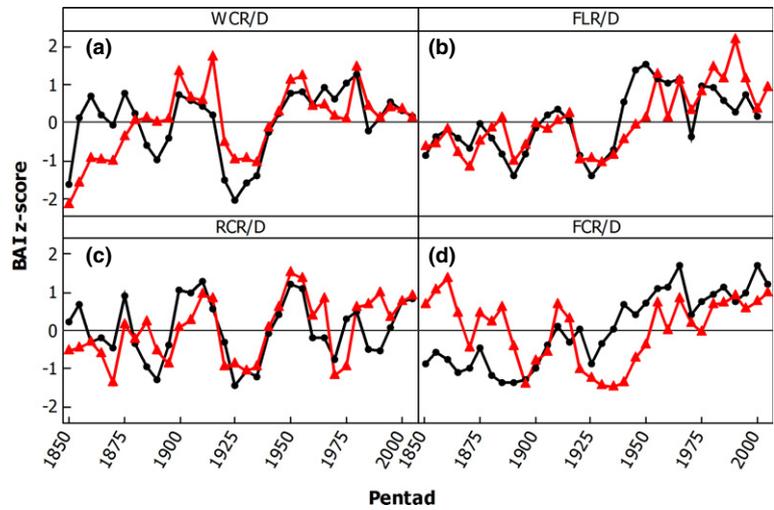
Figure 4 Pentadal basal-area index values (BAI) during AD 1850–2005 (except for BCR and FLR, which end in 2000) for: (a) WCR/WCD, (b) FLR/FLD, (c) RCR/RCD, (d) FCR/FCD, (e) RKR/RKD, (f), BCR/BCD, (g) CGR/CGD, and (h) the seven-site means (five-sites for the 2005 pentad) for ponderosa pine (*Pseudotsuga menziesii* var. *glauca*; PSME) and Douglas-fir (*Pinus ponderosa* var. *ponderosa*; PIPO) trees growing in the northern Rocky Mountains, USA. Red lines with triangle markers represent PSME and black lines with circle markers represent PIPO.
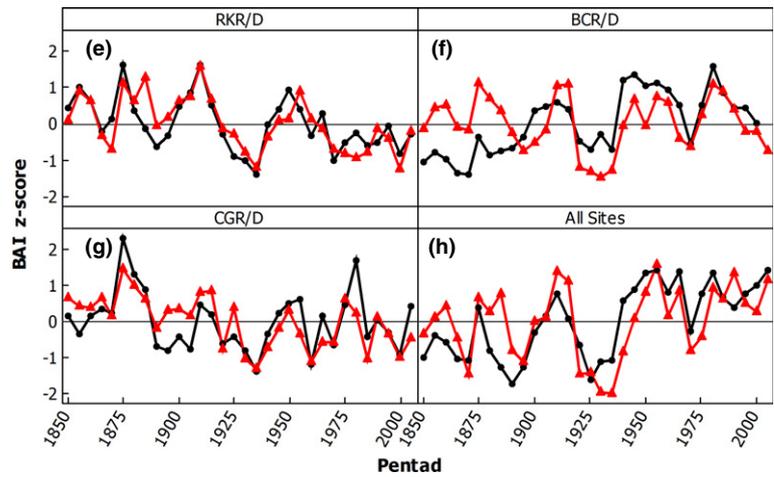
Figure 5 The black line with square markers shows the ratio of ponderosa pine (*Pinus ponderosa* var. *ponderosa*; PIPO) basal area index (BAI) to Douglas-fir (*Pseudotsuga menziesii* var. *glauca*; PSME) radial tree growth, by pentad, within the northern Rocky Mountains, USA. The ratio was created by adding a constant of 10 to the pentadal standardized values for the seven-site (five-site for the 2005 pentad) mean, then dividing PIPO growth by PSME growth. The red line with diamond markers shows the same ratio for intrinsic water-use efficiency (iWUE).
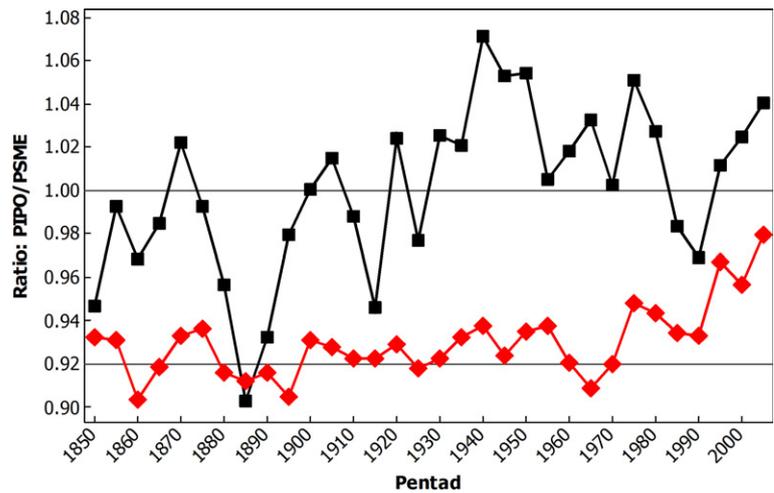
Overall, PIPO experienced greater iWUE and BAI increases than PSME, demonstrating that differential responses to environmental drivers occurred for these species with geographically extensive and overlapping ranges. Further, the difference in iWUE between species has markedly decreased during the past 30 years concurrent with the highest levels of C_a, with PIPO rates increasing faster than those of PSME. Tree growth and iWUE are important components of forest dynamics that respond to changing climate and atmospheric conditions (Aber *et al.*, 2001; Ollinger *et al.*, 2008), but the full extent of ecosystem modification potentially extends to changing composition, density, spatial extent, biomass accumulation and carbon sequestration
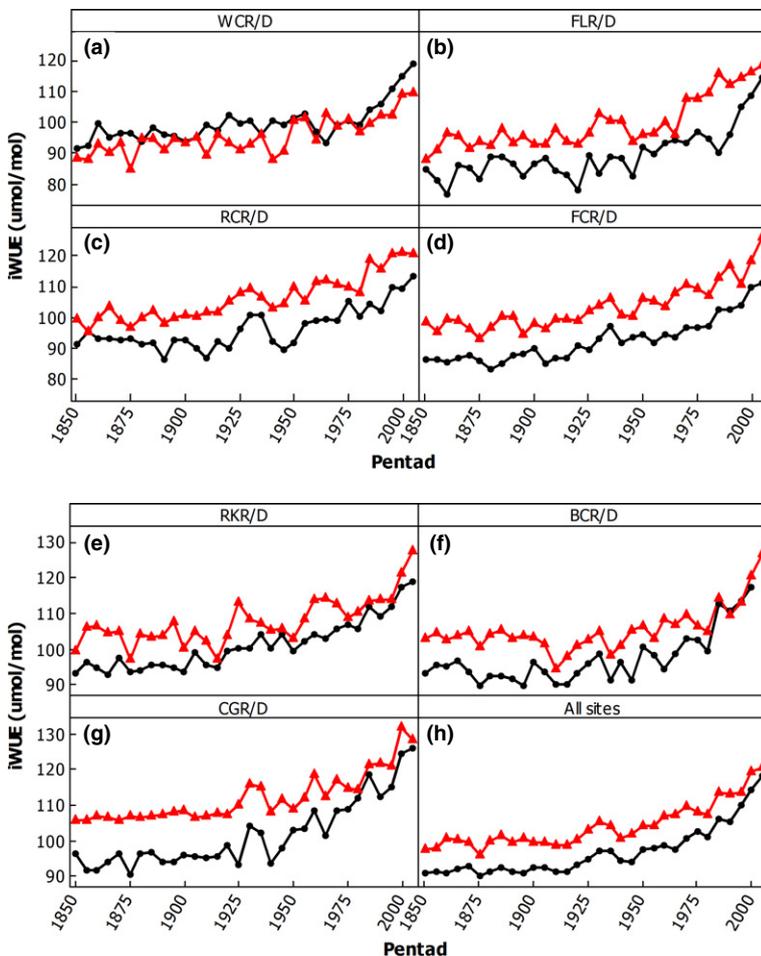
Figure 6 Pentadal values (μmol/mol) of intrinsic water-use efficiency (iWUE) from 1850 to 2005 (except BCR and FLR which end in 2000) for: (a) WCR/WCD, (b) FLR/FLD, (c) RCR/RCD, (d) FCR/FCD, (e) RKR/RKD, (f), BCR/BCD, (g) CGR/CGD, and (h) the seven-site means (five-site for the 2005 pentad) for ponderosa pine (*Pseudotsuga menziesii* var. *glauca*; PSME) and Douglas-fir (*Pinus ponderosa* var. *ponderosa*; PIPO) trees growing in the northern Rocky Mountains, USA. Red lines with triangle markers represent PSME, while black lines with circle markers represent PIPO.

(Bonan, 2008). Given the extensive geographical range and economic value of PSME and PIPO forests to North American forestry, any substantive change in forest dynamics should have both ecological and economic implications. Our findings may extend to other ecosystems with co-occurring and co-dominant trees experiencing differential responses to changing environmental conditions.

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