



Effect of crown class and habitat type on climate–growth relationships of ponderosa pine and Douglas-fir

Gunnar C. Carnwath^{a,*}, David W. Peterson^b, Cara R. Nelson^a

^a Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, United States

^b USFS Forestry Sciences Laboratory, Wenatchee, WA 98801, United States

ARTICLE INFO

Article history:

Received 25 May 2012

Received in revised form 20 July 2012

Accepted 25 July 2012

Keywords:

Climate change

Climate–growth relationships

Dendrochronology

Douglas-fir

Ponderosa pine

ABSTRACT

There is increasing interest in actively managing forests to increase their resilience to climate-related changes. Although forest managers rely heavily on the use of silvicultural treatments that manipulate stand structure and stand dynamics to modify responses to climate change, few studies have directly assessed the effects of stand structure or canopy position on climate–growth relationships – or examined how this relationship may vary among species or across environmental gradients. In this study, we analyzed variability in tree-ring series from 15 low-elevation stands in northeastern Washington (USA) using time series analysis and linear mixed effects models. Our objective was to assess the relative influences of species (*Pinus ponderosa* vs. *Pseudotsuga menziesii*), crown class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic) on the climate responses of mature trees in unmanaged forests. We found that climate–growth relationships varied significantly between canopy classes and across habitat types but that these effects were highly species-specific. For *P. menziesii*, growth responses to temperature and precipitation did not vary between canopy classes. For *P. ponderosa*, however, regression coefficients for the relationship between temperature and radial growth were nearly twice as large for dominant trees compared to intermediate trees, and 84% of dominant trees were significantly influenced by precipitation, compared to only 62% of intermediate trees. In contrast, habitat-type did not significantly affect the climate responses of *P. ponderosa*, but did affect responses of *P. menziesii*. For example, for *P. menziesii* only 51% of trees in Dry-Mesic sites, were significantly affected by drought (PDSI), compared to 93% in Xeric sites. A better understanding of the relationship between climate sensitivity, species-specific hydraulic strategies, and stand dynamics is crucial for accurately predicting tree responses to climate change and designing forest treatments that will effectively reduce the climatic vulnerability of key forest species and habitats. Results may assist managers with understanding how altering stand dynamics will differentially affect climate-responses of individual species.

Published by Elsevier B.V.

1. Introduction

Forest responses to climate change are likely to be highly variable, reflecting both tree physiological responses and the outcomes of biotic interactions (Tylianakis et al., 2008). Understanding the sources and drivers of variability in responses to climate change will be crucial for developing appropriate and effective forest management practices for a changing climate. Although dendrochronologists have used tree rings to study the effect of climate on tree growth for nearly a century (Douglass, 1914), surprisingly little is known about the effects of competition and stand dynamics on the climate–growth relationships of mature trees. This is largely because tree-ring-based studies of climate–growth relationships

traditionally have assumed that endogenous factors – such as stand dynamics and competition – modify the direct effects of climate on tree processes, thereby reducing climate sensitivity (the degree of growth response to climate variability) and obscuring the true climate–growth relationship (Fritts, 1976; Cook and Briffa, 1990). For this reason, previous research has primarily been conducted on dominant canopy trees, and analyses are generally based on mean site chronologies – time series of detrended growth indices averaged across all trees at a single site (Cook et al., 1990). This approach assumes a common, shared growth response to climate among sampled trees on a site and uses averaging to reduce random variability among trees within years. Although this method effectively emphasizes the shared climate signal from a particular site, it also discards tree-to-tree variability in climate response.

There is reason, however, to suspect that climate–growth relationships could vary substantially among individuals within a site. At a local scale, stand density and structure are known to

* Corresponding author. Tel.: +1 406 396 5827; fax: +1 406 243 6656.

E-mail address: gcarnwath@montana.edu (G.C. Carnwath).

significantly influence microclimatic conditions and create sharp gradients in the environmental factors that regulate tree growth, including light, water and temperature (Aussenac, 2000; Zhu et al., 2000). Environmental conditions vary vertically within the forest canopy and at different soil depths; thus, trees growing in sub-dominant canopy positions are consistently exposed to different environmental conditions than dominant trees. This, in turn, may lead to significantly different morphological and physiological characteristics in suppressed trees relative to dominant trees, including a lower ratio of leaf-area to sapwood-area (McDowell et al., 2006; Renninger et al., 2007) and reduced rooting depths (McMinn, 1963). Differences in environmental conditions and morphological traits are likely to cause significant differences in resource requirements and growth-limiting factors and, therefore, significant differences in climate-growth relationships between dominant and sub-dominant trees within a site.

Previous research supports the idea that climate-growth relationships may vary significantly among trees of the same species within a stand, but results have been highly species-specific and even contradictory. For example, greater growth reductions during drought were found for dominant overstory trees relative to suppressed understory trees in studies of *Pinus nigra* (Martín-Benito et al., 2008) and *Picea sitchensis* Bong. (Wichmann, 2001). However, dominant trees were found to be less drought-sensitive than understory trees in studies of *Abies pinsapo* Boiss. (Linares et al., 2010), *Pinus sylvestris* (Pichler and Oberhuber, 2007), *Pinus strobus* L. (Vose and Swank, 1994), and *Picea Abies* L. (Van Den Brakel and Visser, 1996). In other studies of *P. Abies* L., Pichler and Oberhuber (2007) found that the effect of canopy class differed significantly between north- and south-facing sites (i.e. a significant site by canopy class interaction), but Meyer and Braker (2001) did not find significant differences in climate-growth relationships of dominant and suppressed trees at two sites with very different elevations. Although highly inconsistent and often based on small sample sizes, these studies demonstrate that stand structure can significantly alter tree growth responses to climatic variability, suggesting that targeted management actions that alter stand structure could also significantly modify tree growth responses to climatic variability and change.

The sensitivity of conifers to climate is also known to vary significantly among species (Hurteau et al., 2007) and within species over numerous environmental gradients such as latitude (Peterson and Peterson, 2001; Littell et al., 2008), elevation (Kienast et al., 1987; Peterson and Peterson, 2001; Kusnierczyk and Ettl, 2002), aspect (Villalba et al., 1994; Fekedulegn et al., 2003), and soil nutritional status (Ogle et al., 2000; Pinto et al., 2007). In general, environmental factors related to water supply, such as precipitation, are the most powerful controls on cambial activity in arid ecosystems, while energy (e.g., temperature and growing season duration) is most important in areas with adequate water supply, such as areas of high elevation and latitude (Gholz, 1982; Stephenson, 1990; Waring and Running, 1998). While some researchers have found that inter-specific differences in climate-growth relationships are more significant than site-to-site differences (Graumlich, 1993; Peterson and Peterson, 1994), others have reached the opposite conclusion (Villalba et al., 1994), underscoring the fact that tree growth responses to climate are highly context-dependent. This high degree of variability makes it difficult to apply results from one species to another or to draw general conclusions about variation in climate-growth relationships from site to site across heterogeneous landscapes. As such, it is becoming increasingly clear that well-replicated information at sub-regional or local scales is needed to successfully disentangle the numerous (and likely interacting) environmental factors that influence climate-growth relationships in heterogeneous landscapes (Rehfeldt et al., 1999).

In this study, we used time series analysis and mixed-effects models to analyze nearly 700 tree-ring growth index series and assess how canopy position and forest type affect the climate-growth relationships of *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir) in northeastern Washington, USA. In light of strong evidence that competitive interactions can profoundly influence vegetation responses to climate change (Brooker, 2006; Tylianakis et al., 2008), this information will be critical to accurately predict ecosystem responses to climate change (Araujo and Guisan, 2006). Moreover, silvicultural treatments such as thinning that change competition intensity and stand structure are a primary tool for forest restoration; therefore, a clear understanding of the relationship between competition, climate and growth is important for sustainable forest management.

2. Methods

2.1. Study area and site selection

This study was conducted on the Colville National Forest (CNF) in northeastern Washington between 48°N and 49°N latitude and 117°W and 119°W longitude (Fig. 1). With a range of 30–135 cm of precipitation per year, the west side of the CNF is strongly influenced by a rain shadow formed by the Northern Cascades, while the northeastern region has a near-maritime climate due to a westerly airflow forced over the Selkirk and Kettle River mountain ranges. These temperature and moisture gradients are reflected in vegetation patterns: Douglas-fir and ponderosa pine forests dominate to the west, while mixed-conifer forests dominate to the east.

Because we were interested in analyzing climate-growth relationships in contrasting environments, sampling was stratified by the Forested Plant Association Group (PAG) (Williams et al., 1995). Similar to the Habitat Type concept (Daubenmire and Daubenmire, 1968), PAGs aggregate geographical areas based on shared floristics, environment and productivity. We used PAGs for sample stratification because they effectively separate distinct biophysical environments and because they form the basic unit for vegetation modeling on the CNF. Stands were selected for sampling in the ponderosa pine-Douglas-fir/bluebunch wheatgrass plant association (*P. ponderosa*-*P. menziesii*/Agropyron spicatum [PIPO-PSME/AGSP]) and the Douglas-fir/ninebark plant association (*P. menziesii*/Physocarpus malcaeus [PSME/PHMA]). PIPO-PSME/AGSP is the hottest and driest plant association in the CNF and generally occurs at lower elevations on well-drained and coarse-textured soils. The vegetation is characterized by open stands of ponderosa pine and Douglas-fir with a bunch-grass-dominated understory and few shrubs. By contrast, PSME/PHMA is cooler and wetter than PIPO-PSME/AGSP and is the most common plant association group (hereafter, “habitat type”) in this region. It is found across a wider range of elevations and aspects, generally in gravelly to cobbly silts and loams. Douglas-fir is the most common tree species but stands are usually mixed with ponderosa pine. Ninebark and oceanspray (*Holodiscus discolor*) are the most prevalent shrubs; serviceberry (*Amelanchier arborea*) and Orgeon grape (*Mahonia aquifolium*) are also quite common.

To reduce stand-level variability and thereby minimize the influence of extraneous factors on the climate-growth relationship, we carefully selected sites within each habitat type that were as similar as possible. To do so, we used a geographic information system to identify stands with the following criteria: (1) southwest-southeast aspect; (2) mid-slope position on an approximately 40% slope; and (3) no significant disturbance (such as logging or fire) in the last 60 years. Prior to sampling, we visited all potential sites to see that these conditions were met and to verify that there was no evidence of pathogenic outbreaks, substantial mistletoe or windthrow.

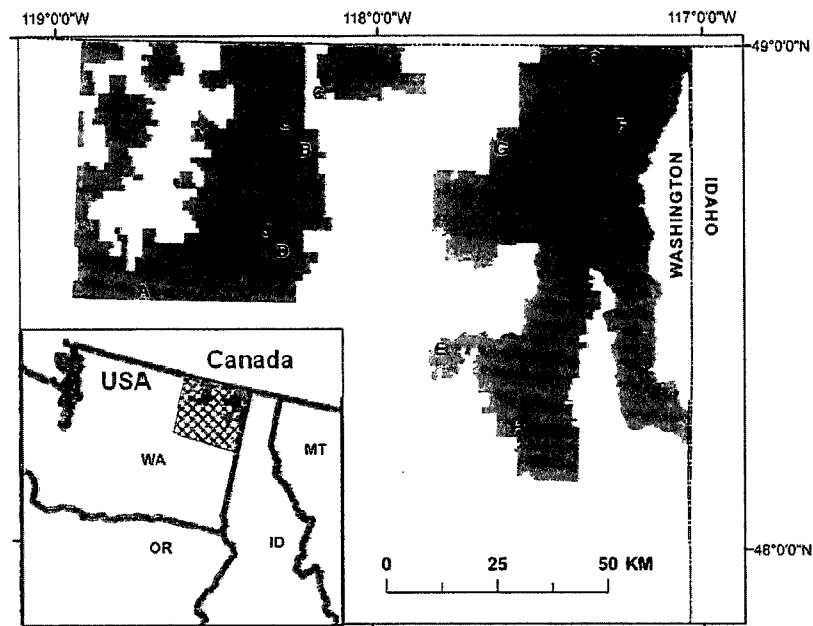


Fig. 1. Location of the study sites in the Xeric (letters A–E) and the Dry-Mesic (letters F–O) habitat types on the Colville National Forest (darker shaded area) in northeastern Washington State (inset). The lightly shaded area shows NCDC Climate Division 9.

Table 1

Attributes of the 15 study sites (see Fig. 1), including habitat type, elevation, mean growing season (May–July) climate (precipitation and temperature) from 1950–2007, and number of sampled *Pseudotsuga menziesii* and *Pinus ponderosa* trees (*n*) for dominant (DO) and intermediate (IN) canopy classes.

Site ID	Habitat type	Elev. (m)	Total precip. (mm)	Max temp. (°C)	Sample size (<i>n</i>)			
					<i>Pseudotsuga menziesii</i>		<i>Pinus ponderosa</i>	
					DO	IN	DO	IN
A	Xeric	945	110	26.2	12	17	10	17
B	Xeric	640	140	27.4	12	18	12	17
C	Xeric	975	153	27.2	14	10	16	11
D	Xeric	930	130	26.3	15	10	14	14
E	Xeric	1066	158	28.3	15	13	14	11
F	Dry-Mesic	1097	199	23.3	13	15	–	–
G	Dry-Mesic	1158	180	27.9	14	15	13	8
H	Dry-Mesic	1128	157	26	18	10	17	9
I	Dry-Mesic	914	153	27.2	15	12	19	5
J	Dry-Mesic	1250	188	24.8	17	11	16	5
K	Dry-Mesic	1250	176	25.7	15	12	–	–
L	Dry-Mesic	1311	166	23.3	16	10	–	–
M	Dry-Mesic	1128	131	25.2	15	8	–	–
N	Dry-Mesic	975	162	26.1	13	12	16	15
O	Dry-Mesic	884	162	26.7	15	14	13	15

We identified a total of 15 suitable sites broadly distributed across the study area: five in the PIPO-PSME/AGSP habitat type (hereafter “Xeric”) and 10 in the PSME-PHMA type (hereafter “Dry-Mesic”; Fig. 1). Xeric sites received, on average, 20% less total precipitation in the months of May, June, and July than Dry-Mesic sites during the period 1950–2007. Average maximum temperatures during this period were 1.5 °C hotter on Xeric sites than on Dry-Mesic sites, in part because the Xeric sites were at lower elevations (Table 1).

2.2. Dendrochronological methods

From each stand, we sampled 10–20 dominant/co-dominant trees (trees receiving full light from above and partly from the

sides; hereafter “dominant”) and 10–20 intermediate trees (trees in definitively subordinate positions, receiving little direct light from above and no light from the sides; hereafter, “intermediate”) of each species. Trees selected for sampling met the following criteria: (1) no obvious defects such as cankers, scars, rot, substantial lean or mistletoe infestation; (2) >50 years old at breast height (1.3 m); (3) >50 m from the edge of the stand and other sampled trees of the same canopy class; (4) >10 cm diameter at breast height (DBH); and (5) >10 m from any dead or dying trees. For each sampled tree, we extracted two cores with an increment borer at breast height from opposite sides of the stem and perpendicular to the fall line of the slope.

We transported tree cores to the lab in protective straws and mounted and sanded them using standard techniques (Stokes, 1968; Fritts, 1976). We visually crossdated all cores and recorded their age at breast height. When the pith was absent from increment cores, we used a pith locator to estimate age (Applequist, 1958). We scanned increment cores using an optical scanner at 1200 dpi resolution and measured ring-widths using the CooRecorder software (Larsson, 2003b). We then checked for missing rings and other crossdating errors with the software programs COFECHA (Holmes et al., 1986) and CDendro 7.1 (Larsson, 2003a). To minimize potential dating errors, cores that could not be accurately crossdated were excluded from further analysis. Finally, we averaged tree-ring measurements from the same tree by year to produce one mean ring-width time series for each sampled tree. This resulted in a total for 693 tree-ring series for analysis (Table 2).

To remove age-related growth trends from each ring-width time series, we fit a 30-year cubic spline function with a 50% frequency response cut off (Cook and Peters, 1981). We then calculated ring-width indices (RWIs) by computing the ratio between observed ring-widths and the corresponding expected values produced by the spline function (Fig. 2). We chose this method because it is a simple technique that could be applied to all trees and resulted in high correlations between the standardized ring-width indices and climate variables. Detrending was accomplished in R (R Development Core Team, 2010) using the package dplR (Bunn, 2008).

Table 2

Tree characteristics, including number of sampled trees (n), mean tree age (Age), diameter at breast height (DBH), and height for dominant (DO) and intermediate (IN) *Pinus ponderosa* and *Pseudotsuga menziesii*.

Species	Canopy class	Tree characteristics			
		n	Age	DBH (cm)	Height (m)
<i>Pseudotsuga menziesii</i>	DO	220	110 (37)	48 (12)	27 (5)
	IN	187	90 (28)	23 (6)	17 (4)
<i>Pinus ponderosa</i>	DO	161	143 (61)	53 (14)	28 (5)
	IN	125	96 (36)	26 (7)	18 (4)

2.3. Climate data

To identify the most important climate variables for analysis, we first developed mean growth chronologies for the study area that represented the shared, high frequency variation of each population (species–habitat combination). We first calculated mean ring-width index series (stand-level chronologies) for each canopy class–species combination at each site by averaging the standardized ring-width index series using a bi-weighted robust mean (Cook et al., 1990). We averaged those stand-level chronologies

across sites and canopy classes (with equal weights) to obtain one mean growth chronology for each species–habitat combination (Cook et al., 1990). We then calculated product moment correlations between these mean growth chronologies and monthly climate variables for the study area using a 15-month climate window in which tree growth in year t was compared to monthly climate variables for a period extending from June of year $t - 1$ to September of year t . We estimated the mean climate response using correlation functions from the R package bootRes (Zang, 2009), based on DENDROCLIM2002 (Biondi and Waikul, 2004).

We used temperature, precipitation and estimated soil water availability as our climate predictors. To select the best source of available temperature and precipitation data, we compared correlations between the mean growth chronologies for each species and monthly climate data from two sources: (1) the regional total precipitation and average daily temperature data from NCDC Climate Division 9 of Washington State (available from the National Climate Data Center; <http://www.ncdc.noaa.gov>); and (2) gridded total precipitation and average daily maximum temperature data obtained from PRISM (Parameter-elevation Regressions on Independent Slopes Model), a 4-km gridded model that accounts for topographic and elevation differences (Daly et al., 2008). Precipitation and temperature data in the months of May,

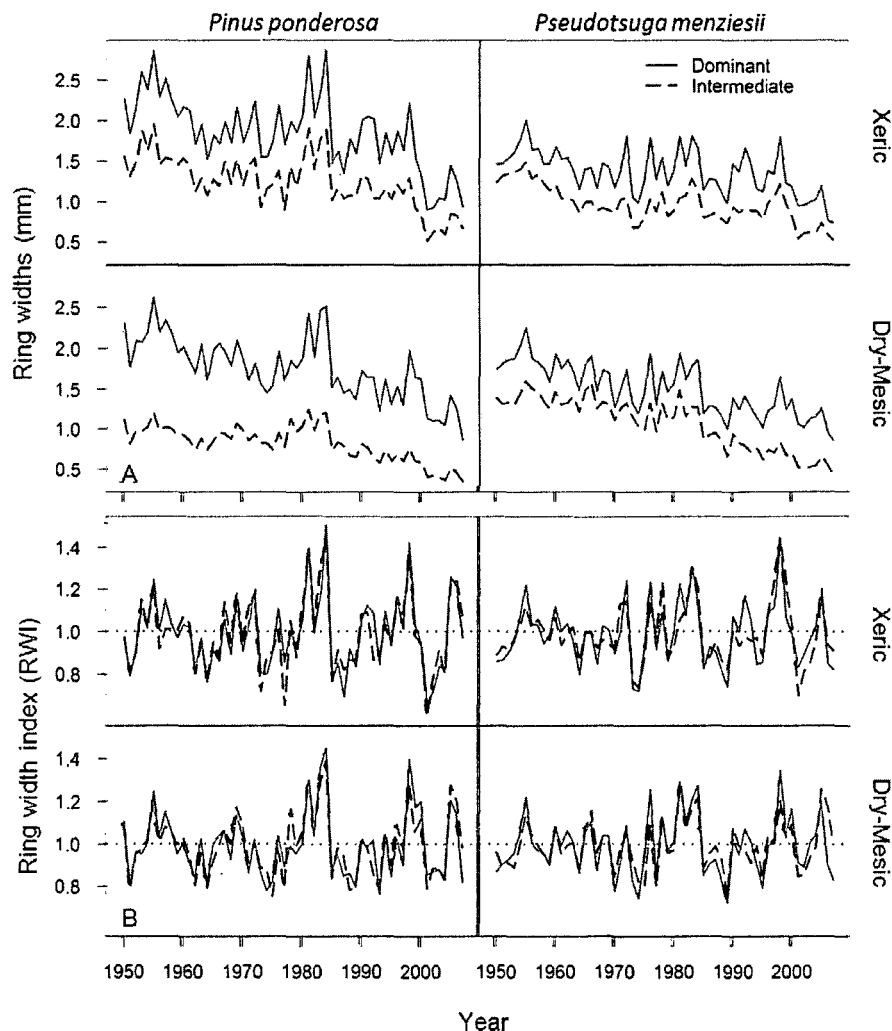


Fig. 2. Time series from primary period of analysis (1950–2007) showing variation for dominant (solid traces) and intermediate (dashed traces) canopy classes of *Pinus ponderosa* (left column) and *Pseudotsuga menziesii* (right column) in (A) mean raw ring widths and (B) mean ring width indices (RWIs) in Xeric and Dry-Mesic habitat types. Dotted line indicates average ring-width (RWI = 1).

June and July (hereafter “the growing season”) from PRISM were the most consistent and significant predictors of growth as represented by the mean growth chronologies; we therefore used these data in our analyses. Specifically, we used PRISM estimates of the total precipitation during the growing season (hereafter “precipitation”) and the mean maximum daily temperature from the warmest month in each year (hereafter “temperature”) as predictor variables.

To analyze the combined effects of precipitation and temperature on radial growth, we again compared climate–growth correlations from two sources: (1) the Palmer drought severity index (PDSI) – an estimate of overall, regional departures from average soil moisture conditions (Alley, 1985) – obtained from NCDC Climate Division 9; and (2) gridded estimates of actual evapotranspiration, soil moisture storage and water deficit calculated using PRISM data along with the USGS Thornthwaite monthly water balance model (McCabe and Markstrom, 2007). For water balance calculations, we assumed a field capacity of 100 mm (Stephenson 1998) and a latitude of 49° north for all stands. We found that, overall, divisional PDSI was the best linear predictor of the standardized chronologies. Here again, climate–growth correlation values for the months of the growing season in the year of ring formation were similar and all highly significant. As such, we used the average of the divisional PDSI throughout the growing season (May–July) as a metric of water availability during the entire growing season. PDSI data was obtained from the National Climate Data Center for Climate Division 9 of Washington State (northeastern Washington, available at <http://www.ncdc.noaa.gov>). To insure that climate data was highly accurate and consistent across the study area, we limited our analysis of climate–growth relationships to the time period of 1950–2007.

2.4. Statistical analysis

We assessed tree growth responses to climate in three steps. First, we equalized the variance among trees by subtracting the mean RWI and dividing by the standard deviation for each series. Next, we estimated each tree's growth response to single climate variables by developing linear regression models with an autoregressive error structure for each tree and each climate variable (693 trees $\times$ 3 climate variables [PDSI, precipitation, and temperature] = 2079 models). For all models, temporal autocorrelation of the error term was modeled using a first-order (AR1) autocorrelation structure, but the coefficients were allowed to vary in the optimization of each model correlation. Finally, we analyzed the variability in the estimated regression coefficients using linear mixed-effects (LMEs) models to assess the statistical significance and relative influence of the three fixed effects of interest: species (ponderosa pine vs. Douglas-fir), canopy class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic). We designated tree age as a covariate and site as a random effect (to account for the statistical effects [non-independence] of analyzing trees from the same stand).

To evaluate which fixed effects were the most important for explaining tree growth responses to each climate variable, we followed the mixed-model selection protocol outlined by Zuur et al. (2009). To do this, we began with a “beyond optimal” model containing all fixed effects and their possible interactions and then compared a series of reduced models that differed only by the term being tested (the least significant term in the model). We used maximum likelihood parameter estimations and compared nested models using likelihood-ratio tests and then refit the final model using restricted maximum likelihood estimation. We plotted residuals against fitted values to verify normality and homogeneity of variance.

Climate variables were standardized by subtracting the mean and dividing by the standard deviation to allow for direct comparison of climate coefficients among different predictor variables. Model fitting was done in R using the nlme package (Pinheiro et al., 2010). To test for statistically significant differences among groups in the number of trees exhibiting significant ($p < 0.05$) climate–growth relationships, we used a function for analyzing LME models with binomial data distribution within the R-package MASS (Venables and Ripley, 2002). Post hoc comparisons between groups were carried out using Tukey contrasts with the package multcomp (Hothorn et al., 2008).

3. Results

We found that climate–growth relationships varied significantly between canopy classes and habitat types, and that effects were highly species-specific. However, for both species, canopy class effects were consistent across habitat types (i.e. we found no significant interactions between habitat type and canopy class). Tree age did not emerge as an important variable in any of the LME models.

3.1. Species-specific effects of canopy class on climate sensitivity

Results of LME models showed a significant interaction between canopy position and species for all three climate variables ($t = 4.15$ and $p = < 0.001$ for PDSI; $t = 3.08$ and $p = 0.002$ for precipitation; and $t = -5.07$ and $p = < 0.001$ for temperature; Table 3). For ponderosa pine, dominant trees were significantly more sensitive to PDSI than were intermediate trees (i.e. estimated PDSI–growth coefficients were statistically higher in the dominant class vs. the intermediate class; $p < 0.001$; Fig. 3) and a substantially greater percentage of the dominant trees exhibited a significant relationship to PDSI compared to intermediates (70% vs. 53%, respectively; $p = 0.003$; Fig. 4). For Douglas-fir, however, dominant trees were

Table 3

Results of the linear mixed-effects model including effect of species (*Pinus ponderosa* vs. *Pseudotsuga menziesii*), canopy class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic) on tree responses to monthly measures of average PDSI, total precipitation and average maximum temperature during the growing season (May–July). Results for insignificant covariates are not shown.

	Coefficient value	Standard error	t-Value	p-Value
PDSI				
Intercept	0.324	0.037	8.676	<0.001
Habitat type	−0.083	0.046	−1.818	0.092
Species	0.093	0.020	4.590	<0.001
Canopy class	−0.047	0.017	−2.741	0.006
Species $\times$ canopy class	0.091	0.022	4.154	<0.001
Species $\times$ habitat type	−0.102	0.023	−4.387	<0.001
Precipitation				
Intercept	0.434	0.031	14.169	<0.001
Habitat type	−0.073	0.037	−1.956	0.072
Species	0.054	0.022	2.472	0.014
Canopy class	−0.089	0.018	−4.878	<0.001
Species $\times$ canopy class	0.073	0.024	3.076	0.002
Species $\times$ habitat type	−0.064	0.025	−2.577	0.010
Temperature				
Intercept	−0.214	0.014	−15.826	<0.001
Species	0.108	0.013	8.121	<0.001
Canopy class	0.099	0.015	6.605	<0.001
Species $\times$ canopy class	−0.098	0.019	−5.066	<0.001

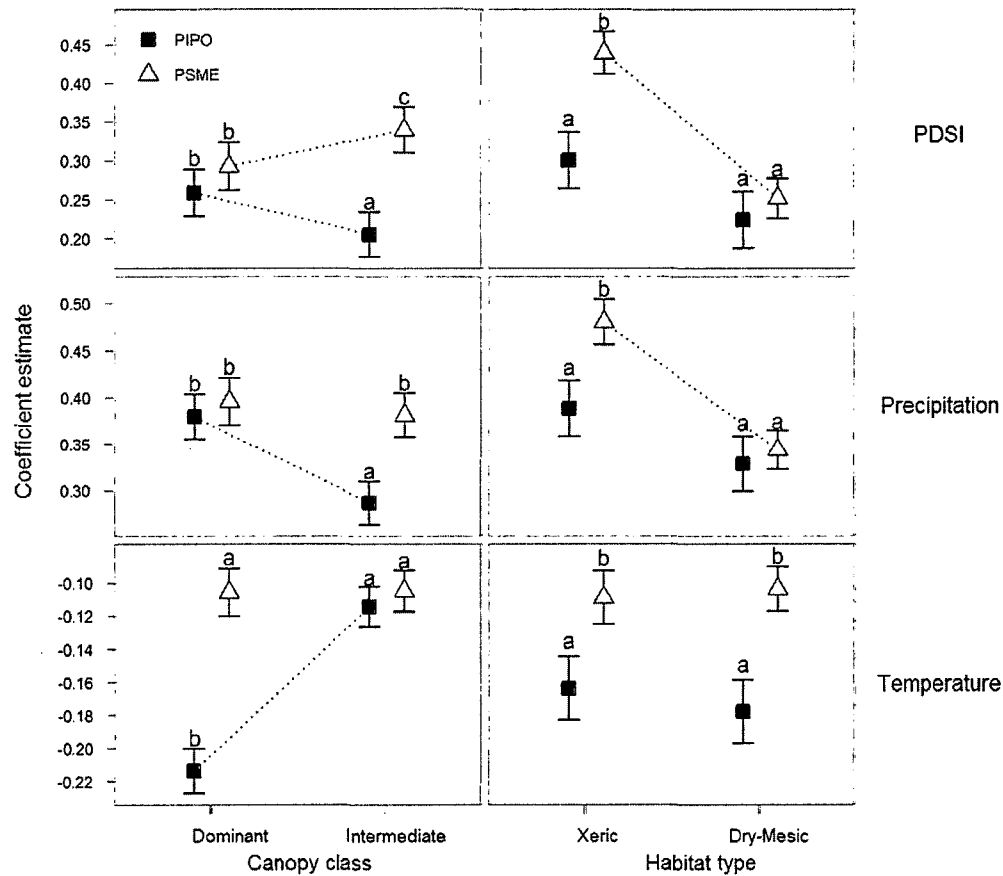


Fig. 3. Mean climate response (±SE) of *Pinus ponderosa* (PIPO; squares) and *Pseudotsuga menziesii* (PSME; triangles) between canopy classes (left column) and habitat types (right column). Letters indicate significant mean contrasts between groups; symbols with the same letter are not significantly different from each other. Dotted lines indicate significant within-species differences. Greater deviation from 0 (either positive or negative) indicates greater sensitivity.

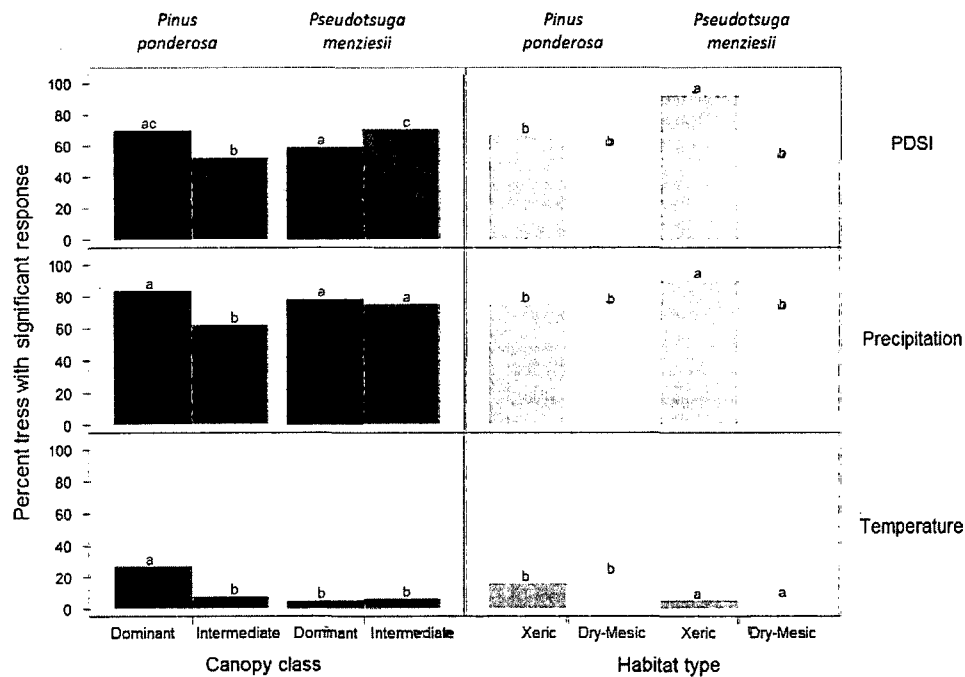


Fig. 4. Percent of *Pinus ponderosa* and *Pseudotsuga menziesii* trees exhibiting significant relationships with PDSI (top panel), precipitation (middle panel), and temperature (bottom panel). Data are grouped by canopy classes (left column) and habitat types (right column). Letters indicate significant mean contrasts among groups; bars with the same letter are not significantly different from each other.

significantly less sensitive to PDSI than were intermediate trees ($p < 0.001$), and fewer dominant Douglas-fir trees than intermediate trees exhibited significant growth responses to PDSI (60% vs. 71%, respectively; $p = 0.018$; Fig. 4). Dominant ponderosa pine trees were also significantly more sensitive to precipitation ($p = 0.016$) and temperature ($p < 0.001$) than were intermediate ponderosa pine (Fig. 3), but there were no between-canopy-class differences in sensitivity to precipitation or temperature for Douglas-fir (Fig. 3).

With respect to *between-species* differences in canopy-class effects, intermediate Douglas-fir were more sensitive to PDSI and precipitation relative to intermediate ponderosa pine ($p < 0.001$ for both variables) and, accordingly, a greater proportion of intermediate Douglas-fir were significantly sensitive to PDSI and precipitation compared to intermediate ponderosa pine (for PDSI, 71% vs. 53% respectively, and $p < 0.001$; and for precipitation 75% vs. 62%, respectively, and $p < 0.001$; Fig. 4). There were no significant between-species differences in the response of intermediate trees to temperature (Fig. 3). Conversely, dominant trees did not have significant species-related differences in sensitivity to PDSI or precipitation, but dominant ponderosa pine were approximately twice as temperature-sensitive as dominant Douglas-fir ($p < 0.001$, coefficient estimates = -0.21 [SE = 0.01] and -0.11 [SE = 0.01], respectively; Fig. 3). Approximately 27% of dominant ponderosa pine exhibited a significant relationship to temperature compared to only 5% of dominant Douglas-fir (Fig. 4).

3.2. Species-specific effects of habitat type on sensitivity to climate

We found a significant interaction between species and habitat type for both PDSI and precipitation ($t = -4.39$ and $p < 0.001$ for PDSI; and $t = -2.56$ and $p = 0.01$ for precipitation; Table 3), but the effect of temperature did not vary for either species between habitat types. While both species trended toward greater sensitivity to PDSI and precipitation in Xeric relative to Dry-Mesic sites, this difference was only significant for Douglas-fir ($p < 0.001$ for both variables; Fig. 3). Approximately 93% of Douglas-fir trees in Xeric sites were significantly influenced by PDSI compared to 51% in Dry-Mesic sites ($p < 0.001$; Fig. 4). The relative proportion of trees with a significant sensitivity to precipitation followed a similar pattern as PDSI (Fig. 4).

With respect to between-species differences in the effect of habitat type on climate sensitivity, we found that for Xeric sites, Douglas-fir was significantly more sensitive to PDSI and precipitation relative to ponderosa pine ($p < 0.001$ for both variables; Fig. 3), but for Dry-Mesic sites, there were no significant between-species differences in response to these variables. In both Xeric and Dry-Mesic habitat types, ponderosa pine was significantly more sensitive to temperature than was Douglas-fir ($p < 0.001$ for both variables; Fig. 3). Only approximately 5% of Douglas-fir exhibited a significant relationship to temperature in each habitat type, compared to approximately 16% of ponderosa pine in the Xeric habitat type and 21% in the Dry-Mesic habitat (Fig. 4).

4. Discussion

4.1. Species-specific effects of canopy class on climate sensitivity

We found strong evidence that canopy position affects climate-growth relationships of ponderosa pine but not Douglas-fir: dominant ponderosa pines are significantly more responsive to precipitation and substantially more sensitive to high temperatures than are intermediate ponderosa pines. Perhaps the most striking example of this key finding can be seen in the dramatically different responses to temperature. Whereas the temperature

sensitivity of Douglas-fir did not vary across canopy classes, temperature had a substantially impact greater (approximately double) on dominant ponderosa pine relative to intermediate ponderosa pine. The contrasting effects of canopy position on temperature responses of these two species likely reflect fundamental differences in their physiology, morphology and hydraulic strategies. For example, relative to Douglas-fir, ponderosa pine is able to substantially modify stomatal conductance in response to changing environmental conditions (Stout and Sala, 2003; Domec et al., 2004) – better stomatal control greatly reduces the chance of hydraulic failure (McDowell et al., 2008). Because the leaves of dominant trees are exposed to full sunlight and significantly higher temperatures than those of intermediate trees, growth of dominant ponderosa pine is much more tightly coupled to temperature compared to intermediate ponderosa pines that are buffered from the direct effects of temperature by shading. This idea is consistent with numerous studies showing that shading is a primary mechanism by which neighboring plants modify external environmental conditions, in this case ameliorating the negative impact of high temperatures and low water-availability on growth (Callaway, 2007; Brooker et al., 2008). Relative to ponderosa pine, however, there are important differences in basic life history traits of Douglas-fir, including significantly greater shade tolerance (Niemets and Valladares, 2006). As such, it is not surprising that canopy positioning is not an important factor influencing climate sensitivity for this species.

Based on previous observations showing greater climate sensitivity – i.e. a tighter coupling of stemwood production to climate – in trees that die from abiotic stress compared to those that survive (Pedersen, 1998; Ogle et al., 2000; Suarez et al., 2004; McDowell et al., 2010), our results suggest that dominant ponderosa pine may be more vulnerable to climate change than intermediate ponderosa pine. This conclusion seems consistent with several recent investigations showing a positive relationship between tree size and drought sensitivity among *Pinus* species. For example, Ganey and Vojta (2011) found that mortality in *P. ponderosa* forests was significantly lower than expected in smaller-diameter size classes but larger than expected in the largest size classes. Also, in a tree-ring study of *P. sylvestris*, Martínez-Vilalta et al. (2012) analyzed 1433 trees from 393 plots and concluded that large trees were significantly more drought sensitive than smaller ones. If these observed differences in tree sizes and mortality rates are related to stand dynamics, such as competition and social status, thinning treatments in dry ponderosa pine forests may not effectively create stands that are more resilient to climate change (USFS, 2008). Although reducing stand density and leaf area could reduce water stress for residual trees (Stone et al., 1999; Wallin et al., 2004), thinning small-diameter trees growing beneath the dominant canopy actually may remove the individuals that are the least vulnerable to the negative effects of increasing temperatures and extreme drought events associated with climate change.

4.2. Species-specific effects of habitat type on sensitivity to climate

We found that Douglas-fir, but not ponderosa pine, was significantly more sensitive to water availability in Xeric sites relative to Dry-Mesic ones. This observation is consistent with previous work showing that relatively small differences in elevation can significantly influence climate-growth relationships of Douglas-fir but are generally less important to ponderosa pine (Kienast et al., 1987; Kusnierczyk and Ettl, 2002; Case and Peterson, 2005). Here again, species-specific differences in climate responses most likely reflect the contrasting hydraulic strategies and life history traits of ponderosa pine and Douglas-fir. Despite the fact that ponderosa pine is a more drought-tolerant species (Niemets and Valladares, 2006), Douglas-fir is actually more resistant to cavitation under

high pressure gradients (Pinol and Sala, 2000; Domec and Gartner, 2002; Stout and Sala, 2003). This ability to withstand (but not avoid) significant water stress allows Douglas-fir to persist in dry habitats, but it also means that fluctuations in soil water and physiological processes become more tightly coupled in increasingly xeric sites. Ponderosa pine, on the other hand, has developed structural adaptations that allow it to avoid dangerously low water potentials. For example, Barnard et al. (2011) found that ponderosa pine had almost twice the sapwood area supplying water to a given leaf area as Douglas-fir, leading to a 50% decrease in the pressure gradient required to conduct a given amount of water. Moreover, ponderosa pine, but not Douglas-fir, is able to significantly modify the ratio of biomass in leaf area relative to sapwood area ($A_L:A_S$) across environmental gradients in response to increasing aridity (Delucia et al., 2000). Thus, through a combination of better stomatal control, lower $A_L:A_S$, and better regulation of $A_L:A_S$ across contrasting sites, ponderosa pine is less affected by an overall decrease in mean water availability in increasingly xeric sites. Consequently, greater sensitivity to water availability of Douglas-fir, but not ponderosa pine, in xeric sites most likely reflects known differences in hydraulic architecture and life history strategies of these two species and is consistent with the idea of an adaptive tradeoff between xylem efficiency and hydraulic safety (e.g. Pinol and Sala, 2000; Barnard et al., 2011).

We also found that ponderosa pine was significantly more sensitive to temperature than Douglas-fir, regardless of habitat type. Unlike soil water deficits, the effects of air temperature on tree growth processes are significantly more direct and immediate. As such, sensitivity to maximum temperatures reflects a tree's capacity to respond quickly to discrete events (e.g. heat waves during the growing season), and a short-term tradeoff between carbon assimilation and loss of water to transpiration. The consistent high temperature-sensitivity of ponderosa pine (i.e. greater reductions in radial growth in response to high temperatures) is again consistent with this species' "stress-avoidance" strategy and higher stomatal sensitivity. These results suggest that differences in climate sensitivity among species reflect fundamental differences in physiology and life history traits and, as such, are not necessarily correlated to vulnerability to drought-induced mortality.

5. Conclusions

We found that climate sensitivity of tree growth is significantly modulated by tree social status (canopy class) and habitat conditions, but these effects are highly species-specific. Most notably, we found that canopy position substantially modified tree growth responses to high temperatures and precipitation for ponderosa pine, but not Douglas-fir. These findings may have important implications for understanding the effects of stand structure on climate sensitivity and the differential effects of altering stand structure on climate-growth relationships of common forest trees, both of which may help managers promote forests that are resilient to future climatic conditions. We also found that differences in climate sensitivity were closely related to species-specific strategies for coping with water stress. This means that for certain species, high climate sensitivity may indicate a close coupling between environmental conditions and physiological stress, while for others a high degree of climate sensitivity may reflect an adaptive trait for avoiding dangerously low water potentials. Therefore, in contrast to numerous tree-ring studies demonstrating a positive correlation between climate sensitivity and drought-induced mortality within-species (e.g. Pedersen, 1998; Ogle et al., 2000; Suarez et al., 2004; McDowell et al., 2010), differences in climate sensitivity among-species does not necessarily reflect differences in vulnerability to climate change. Future research should investigate the is-

sue of climate sensitivity within a framework of species-specific life history traits and adaptive hydraulic strategies to more clearly establish the relationship between climate sensitivity and vulnerability to climate change.

Acknowledgements

We thank the USDA Forest Service Region 6 Area Ecology Program and Colville National Forest, especially M. Borysewicz, for logistical support; M. Yager, J. Bohlert, K. Bednarczyk, P. Stothart, T. Anfinson, and B. Maddox for data collection and core processing; and E. Sutherland, S. Running, J. Goodburn, and A. Sala for help with study design and manuscript review. This material is based on work supported by McIntire-Stennis appropriations to the University of Montana, USDA Forest Service (PNW Research Station, Region 6 Area Ecology Program and Student Career Experience Program), and the Montana Institute on Ecosystems by the National Science Foundation EPSCoR program grant EPS-1101342. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the Montana Institute on Ecosystems or the National Science Foundation.

References

- Alley, W.M., 1985. Palmer drought severity index as a measure of hydrologic drought. *Journal of the American Water Resources Association* 21, 105–114.
- Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. *Journal of Forestry* 56, 141.
- Araujo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33, 1677–1688.
- Aussenac, G., 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* 57, 287–301.
- Barnard, D.M., Meizner, F.C., Lachenbruch, B., McCulloh, K.A., Johnson, D.M., Woodruff, D.R., 2011. Climate related trends in sapwood biophysical properties in two conifers: avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance. *Plant, Cell and Environment* 34, 643–654.
- Biondi, F., Waikul, K., 2004. DENDROCLIM 2004: a C++ program for statistical calibration of climate signals in tree ring chronologies. *Computers and Geosciences* 30, 303–311.
- Brooker, R.W., 2006. Plant-plant interactions and environmental change. *New Phytologist* 171, 271–284.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.J., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielborger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffrers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96, 18–34.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124.
- Callaway, R., 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer Verlag.
- Case, M.J., Peterson, D.L., 2005. Fine-scale variability in growth climate relationships of Douglas-fir, North Cascade Range, Washington. *Canadian Journal of Forest Research* 35, 2743–2755.
- Cook, E., Briffa, K., 1990. A conceptual linear aggregate model for tree-rings. In: Cook, E.R., A., K.L. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht.
- Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* 41, 45–53.
- Cook, E.R., Shiyatov, S., Mazepa, V., 1990. Estimation of the mean chronology. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, p. 394.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28, 2031–2064.
- Daubenmire, R., Daubenmire, J.B., 1968. Forest vegetation of eastern Washington and northern Idaho. *Washington Agricultural Experiment Station Technical Bulletin* 60, 103.
- Delucia, E.H., Maherali, H., Carey, E.V., 2000. Climate-driven changes in biomass allocation in pines. *Global Change Biology* 6, 587–593.
- Domec, J.C., Gartner, B.L., 2002. How do water transport and water storage differ in coniferous earlywood and latewood? *Journal of Experimental Botany* 53, 2369–2379.

- Domec, J.C., Warren, J., Meinzer, F., Brooks, J., Coulombe, R., 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141, 7–16.
- Douglass, A.E., 1914. Method of estimating rainfall by the growth of trees. *Bulletin of the American Geographic Society* 46, 321–335.
- Fekedulegn, D., Hicks, R.R., Colbert, J.J., 2003. Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *Forest Ecology and Management* 177, 409–425.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Blackburn Press, Caldwell, New Jersey.
- Ganey, J.L., Vojta, S.C., 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. *Forest Ecology and Management* 261, 162–168.
- Gholz, H.L., 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63, 469–481.
- Graumlich, L.J., 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research* 23, 133–143.
- Holmes, R.L., Adams, R., Fritts, H., 1986. Quality control of crossdating and measuring: a users manual for program COFECHA. Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Tucson, Laboratory of Tree-Ring Research, University of Arizona. *Chronology Series* 6, 41–49.
- Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., 2008. Multcomp: Simultaneous Inference in General Parametric Models. R package version, 1.0-0.
- Hurteau, M., Zald, H., North, M., 2007. Species-specific response to climate reconstruction in upper-elevation mixed-conifer forests of the western Sierra Nevada, California. *Canadian Journal of Forest Research* 37, 1681–1691.
- Kienast, F., Schweingruber, F.H., Braeker, O.U., Schaer, E., 1987. Tree-ring studies on conifers along ecological gradients and the potential of single-year analyses. *Canadian Journal of Forest Research* 17, 683–696.
- Kusnierczyk, E.R., Ettl, G.J., 2002. Growth response of ponderosa pine (*Pinus ponderosa*) to climate in the eastern Cascade Mountains, Washington, USA: implications for climatic change. *Ecoscience* 9, 544–551.
- Larsson, L.A., 2003a. CDendro: Cybis Dendro Dating Program. Cybis Elektronik & Data AB, Saltsjöbaden, Sweden.
- Larsson, L.A., 2003b. Coorecorder: Image Coordinate Recording Program. Cybis Elektronik & Data AB, Saltsjöbaden, Sweden.
- Linares, J., Camarero, J., Carreira, J., 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *Journal of Ecology* 98, 592–603.
- Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecological Monographs* 78, 349–368.
- Martin-Benito, D., Cherubini, P., del Río, M., Cañellas, I., 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees-Structure and Function* 22, 363–373.
- Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168, 877–888.
- McCabe, G.J., Markstrom, S.L., 2007. A monthly water-balance model driven by a graphical user interface. U.S. Geological Survey Open-File Report 2007-1088, 6 p.
- McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications* 16, 1164–1182.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178, 719–739.
- McDowell, N., Allen, C.D., Marshall, L., 2010. Growth, carbon isotope discrimination, and drought associated mortality across a *Pinus ponderosa* elevational transect. *Global Change Biology* 16, 399–415.
- McMinn, R., 1963. Characteristics of Douglas-fir root systems. *Canadian Journal of Botany* 41, 105–122.
- Meyer, F.D., Braker, O.U., 2001. Climate response in dominant and suppressed spruce trees, *Picea abies* (L.) Karst., on a subalpine and lower montane site in Switzerland. *Ecoscience*, 105–114.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76, 521–547.
- Ogle, K., Whitham, T.G., Cobb, N.S., 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81, 3237–3243.
- Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology* 79, 79–93.
- Peterson, D.W., Peterson, D.L., 1994. Effects of climate on radial growth of subalpine conifers in the North Cascade mountains. *Canadian Journal of Forest Research* 24, 1921–1932.
- Peterson, D.W., Peterson, D.L., 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology* 82, 3330–3345.
- Pichler, P., Oberhuber, W., 2007. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *Forest Ecology and Management*, 688–699.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.D.C., 2010. nlme: Linear and Nonlinear Mixed Effects Models.
- Pinol, J., Sala, A., 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. *Functional Ecology* 14, 538–545.
- Pinto, P.E., Gegout, J.C., Herve, J.C., Dhote, J.F., 2007. Changes in environmental controls on the growth of *Abies alba* Mill. in the Vosges Mountains, north-eastern France, during the 20th century. *Global Ecology and Biogeography* 16, 472–484.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton Jr., D.A., 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs* 69, 375–407.
- Renninger, H.J., Meinzer, F.C., Gartner, B.L., 2007. Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas-fir and western hemlock. *Tree Physiology* 27, 33.
- Stephenson, N.L., 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135, 649.
- Stephenson, N., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25, 855–870.
- Stokes, M.A.S.T.L., 1968. *An Introduction to Tree Ring Dating*. University of Chicago Press, Chicago, IL.
- Stone, J.E., Kolb, T.E., Covington, W.W., 1999. Effects of restoration thinning on presettlement *Pinus ponderosa* in northern Arizona. *Restoration Ecology* 7, 172–182.
- Stout, D.L., Sala, A., 2003. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. *Tree Physiology* 23, 43–50.
- Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus*-site, climatic sensitivity and growth trends. *Journal of Ecology* 92, 954–966.
- Team, R.D.C., 2010. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351–1363.
- USFS, 2008. Forest Service Strategic Framework for Responding to Climate Change. Version 1.0. Unpublished paper on file at the U.S. Forest Service, Washington, DC. <http://www.fs.fed.us/climatechange/documents/strategic-framework-climate-change-1-0.pdf> > (accessed January 2009).
- Van Den Brakel, J.A., Visser, H., 1996. The influence of environmental conditions on tree-ring series of Norway spruce for different canopy and vitality classes. *Forest Science* 42, 206–219.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth Ed. Springer, New York.
- Villalba, R., Veblen, T.T., Ogden, J., 1994. Climatic influences on the growth of subalpine trees in the Colorado front range. *Ecology* 75, 1450–1462.
- Vose, J., Swank, W., 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. *Forest Ecology and Management* 64, 25–39.
- Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M.R., 2004. Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. *Restoration Ecology* 12, 239–247.
- Waring, R.H., Running, S.W., 1998. *Forest Ecosystems: Analysis at Multiple Scales*. Academic Press.
- Wichmann, L., 2001. Annual variations in competition symmetry in even-aged Sitka spruce. *Annals of Botany* 88, 145–151.
- Williams, C.K., Smith, B.G., Lillybridge, T.R., 1995. *Forested Plant Associations of the Colville National Forest*. PNW-GTR-360.
- Zang, C., 2009. bootRes: Bootstrapped Response and Correlation Functions.
- Zhu, J., Matsuzaki, T., Sakioka, K., 2000. Wind speeds within a single crown of Japanese black pine (*Pinus thunbergii* Parl.). *Forest Ecology and Management* 135, 19–31.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Verlag.