

Volume 43

An NRC Research
Press Journal

Une revue de
NRC Research
Press

2013

www.nrcresearchpress.com

Canadian Journal of
**Forest
Research**

Revue canadienne de
**recherche
forestière**

Growth–climate relationships for six subalpine tree species in a Mediterranean climate

Christopher R. Dolanc, Robert D. Westfall, Hugh D. Safford, James H. Thorne, and Mark W. Schwartz

Abstract: A better understanding of the growth–climate relationship for subalpine trees is key to improving predictions about their future distributions under climate change. In subalpine regions of Mediterranean mountains, drought is an annual event, yet many sites can have long-lasting snowpack. We analyzed the growth–climate relationship from 1896 to 2006 for the six most abundant subalpine tree species (red fir (*Abies magnifica* A. Murray bis), whitebark pine (*Pinus albicaulis* Engelm.), Sierra/Cascade lodgepole pine (*Pinus contorta* var. *murrayana* (Balf.) Engelm.), Jeffrey pine (*Pinus jeffreyi* Balf.), western white pine (*Pinus monticola* Douglas ex D. Don), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière)) of the central Sierra Nevada, California, USA, a region with deep spring snowpack followed by strong summer drought. Chronologies for the six species exhibited a high degree of synchrony in their response to annual fluctuations in temperature and precipitation. For all six species, cool, wet conditions in the year prior to growth are conducive to good radial growth, as well as warm springs with sufficient moisture during the year of growth. For species more common on protected slopes, such as mountain hemlock, deep spring snowpack can limit growth. Although predictions of future precipitation trends in the region are uncertain, drought stress appears to already be increasing. If this trend continues, radial growth is likely to be inhibited for most or all species in our study. Trees growing where snowpack is deep may be least likely to suffer reduced growth.

Résumé : Il est essentiel d’avoir une meilleure compréhension de la relation entre la croissance des arbres subalpins et le climat pour mieux prévoir l’impact des changements climatiques sur leur répartition future. La sécheresse est un événement annuel dans les régions subalpines des montagnes méditerranéennes mais dans plusieurs sites, le manteau neigeux peut persister longtemps. Nous avons analysé la relation entre la croissance et le climat de 1896 à 2006 chez les six espèces subalpines d’arbre (le sapin rouge (*Abies magnifica* A. Murray bis), le pin à écorce blanche (*Pinus albicaulis* Engelm.), le pin tordu de Murray (*Pinus contorta* var. *murrayana* (Balf.) Engelm.), le pin de Jeffrey (*Pinus jeffreyi* Balf.), le pin argenté (*Pinus monticola* Douglas ex D. Don) et la pruche subalpine (*Tsuga mertensiana* (Bong.) Carrière) les plus abondantes dans la Sierra Nevada centrale, en Californie, aux É.-U., une région où l’épais manteau neigeux au printemps est suivi d’une forte sécheresse estivale. Il y avait un haut degré de synchronisation dans les séries dendrochronologiques des six espèces quant à leur réaction aux fluctuations annuelles de température et de précipitation. Chez les six espèces, des conditions fraîches et humides durant l’année qui précède sont propices à une bonne croissance radiale, ainsi qu’un printemps chaud et suffisamment d’humidité durant l’année en cours. Dans le cas des espèces plus communes dans les sites où le manteau neigeux est épais au printemps, telles que la pruche subalpine, l’épais manteau neigeux peut limiter la croissance. Bien que les prédictions concernant la tendance future des précipitations dans la région soient incertaines, le stress causé par la sécheresse semble déjà être en train d’augmenter. Si cette tendance se maintient, la croissance radiale de la plupart sinon toutes les espèces visées par notre étude sera probablement inhibée. Les arbres qui poussent dans les endroits où le manteau neigeux est épais sont les moins susceptibles de subir une réduction de croissance. [Traduit par la Rédaction]

Introduction

Despite broad consensus among scientists that the earth’s climate will continue to warm over the next 100 years (IPCC 2007), our understanding of how individual species will respond to that change remains poor. Biologically linked climate models have predicted the extinction of hundreds of species from large regions (Thuiller et al. 2005; Loarie et al. 2008) and areal reduction of many habitat types (Guisan and Theurillat 2001; Rehfeldt et al. 2006; Iverson et al. 2008; Lenihan et al. 2008). Although these models may serve as a good preliminary estimate of the biological response to climatic change, they usually lack important information on

physiological tolerances of individual species and species interactions (Pearson and Dawson 2003).

In California, climatic changes projected to the end of the 21st century include an increase in temperature of 1.7–5.8 °C, a 30%–90% reduction in snowpack, and a greater likelihood of extended drought (Mastrandrea and Luers 2012). In response, major changes in the areal coverage of vegetation types in California are predicted, including a 54%–78% reduction of “alpine/subalpine forest” by 2099 (Lenihan et al. 2008). However, changes in tree species’ ranges are likely to lag well behind climatic change (Svenning and Skov 2004) and are likely to be species-specific, instead of as a vegetation type, as modeled in Lenihan et al. (2008).

Received 21 May 2013. Accepted 14 September 2013.

C.R. Dolanc. Department of Environmental Science and Policy, One Shields Avenue, University of California, Davis, CA 95616, USA; Department of Forest Management, 32 Campus Drive, University of Montana, Missoula, MT 59812, USA.

R.D. Westfall. USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan Street, Albany, CA 94710, USA.

H.D. Safford. Department of Environmental Science and Policy, One Shields Avenue, University of California, Davis, CA 95616, USA; USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA, 94592, USA.

J.H. Thorne and M.W. Schwartz. Department of Environmental Science and Policy, One Shields Avenue, University of California, Davis, CA 95616, USA.

Corresponding author: Christopher R. Dolanc (e-mail: crdolanc@ucdavis.edu).

To improve our understanding of the future distribution of subalpine forest in California and other montane Mediterranean regions, we need more information on individual species and their physiological response to climatic variability (Kearney and Porter 2009).

Dendrochronological studies that focus on the response of tree growth to environmental fluctuations (dendroecology) are valuable for elucidating limitations on growth by climate and can be used to predict future response to climate (Peterson and Peterson 2001; Tardif et al. 2006; Huang et al. 2010). Although growth does not necessarily directly translate to changes in species distribution, both growth and distribution are highly linked to climate in high-elevation ecosystems (Tranquillini 1979; Holtmeier 2003) and radial growth does clearly correlate with survival and mortality (Bigler and Bugmann 2004; Bigler et al. 2004).

In this paper, we present an analysis of the growth–climate relationship during the last century for the six most abundant tree species in subalpine forests of the central Sierra Nevada. Most sites are on the west slope of the range. We are not aware of any previous studies that have characterized the growth–climate relationship for subalpine trees in this region. Tree cores were collected from 83 sites in conjunction with forest inventory plots (see Dolanc et al. 2013) and include a wide range of site conditions. Traditional dendroclimatology studies collect from one or two stressful sites that accentuate the climate signal (Fritts 1976), limiting the applicability of results to the larger region. For each species in this study, cores were taken from both small and large trees and from a wide range of elevations and slope aspects, providing a more complete picture of the climate–growth relationship for each species across its distribution in the central Sierra Nevada.

We benefit from the considerable amount of previous dendrochronological work on subalpine trees in California (Lamarche 1974; Peterson et al. 1990; Graumlich 1991, 1993; Scuderi 1993; Millar et al. 2004, 2007, 2012; Bunn et al. 2005a; Potito and MacDonald 2008; Salzer et al. 2009). Many of these studies demonstrate a positive correlation between growth and precipitation and a negative correlation between growth and temperature. However, all of these studies were conducted in the eastern Sierra Nevada or adjacent White Mountains and comparatively little is known about subalpine trees on the west slope of the Sierra Nevada. Snowpack depths on the more mesic west slope can be quite high, but late summer drought is still an annual and pervasive event (Major 1990). Distribution of forests on the west slope have been tied to water balance (Stephenson 1998; Urban et al. 2000). The degree to which snowpack can moderate the negative impact of drought on growth, and how that varies from species to species in this region, may have interesting implications for tree growth and its response to future climate change for montane regions worldwide, especially Mediterranean mountains.

The main objective of this study was to characterize the relationship between radial growth and climatic variability for six subalpine conifers common on the west slope of the central Sierra Nevada. As a secondary objective, we hope that this information can be used to further our understanding and predictions of how subalpine trees will respond to continued climate change in this region and other Mediterranean mountain regions where the growing season is accompanied by annual drought.

Methods

Site description

Tree cores were collected from the subalpine zone of the central Sierra Nevada, California, USA (Fig. 1). Climate is heavily Mediterranean-influenced, with nearly all of the precipitation falling as snow between October and May and a short dry growing season lasting 6–9 weeks (Fites-Kaufman et al. 2007; Minnich 2007). The growing season where snowpack is deep runs from snow melt to the onset of late summer drought and, thus, varies

depending on available moisture in the snowpack (Peterson 1998). Interannual precipitation is highly variable because of the location of the region near the southern limit of the jet stream and fluctuations in the El Niño Southern Oscillation and the Pacific Decadal Oscillation (Minnich 2007). Despite this variability, the massive size of Pacific winter storms means the variability in snow depth from season to season is highly synchronized across the latitudinal distribution of the Sierra Nevada (Peterson et al. 2000). Annual precipitation in subalpine ranges from 750 to 1250 mm/year; temperatures are cool and frost can occur any month of the year. Soils are commonly thin and winds often severe, contributing to a generally stressful environment for tree growth (Fites-Kaufman et al. 2007).

Vegetation of the subalpine zone of the Sierra Nevada is heterogeneous and diverse (Fites-Kaufman et al. 2007; Sawyer et al. 2009). Tree species in our study area include whitebark pine (*Pinus albicaulis* Engelm.), Sierra/Cascade lodgepole pine (*Pinus contorta* var. *murrayana* (Balf.) Engelm.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), western white pine (*Pinus monticola* Douglas ex D. Don), red fir (*Abies magnifica* A. Murray bis), Sierra juniper (*Juniperus grandis* R.P. Adams), Jeffrey pine (*Pinus jeffreyi* Balf.), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.), and quaking aspen (*Populus tremuloides* Michx.). Of these species, whitebark pine, lodgepole pine, and mountain hemlock can be found at tree line, whereas the others are generally distributed below tree line. Mountain hemlock and red fir are usually found on sites with greater soil moisture; whitebark pine, mountain juniper, and Jeffrey pine are usually found on drier sites and lodgepole pine can be found on either dry or moist sites (though is more common on dry sites at high elevations). Quaking aspen is typically associated with meadow complexes and riparian systems. Stands can be made up of single species or various combinations of multiple species and are typically sparse but can form closed-canopy stands on mesic sites; shrub cover is usually low-lying or absent (Sawyer et al. 2009). This structure, together with the short growing season, extensive exposed rock, and thin soils, make fire infrequent (van Wagtenonk and Fites-Kaufman 2006). For more information on Sierra Nevada subalpine vegetation see Parker (1988), Potter (1998), and Fites-Kaufman et al. (2007).

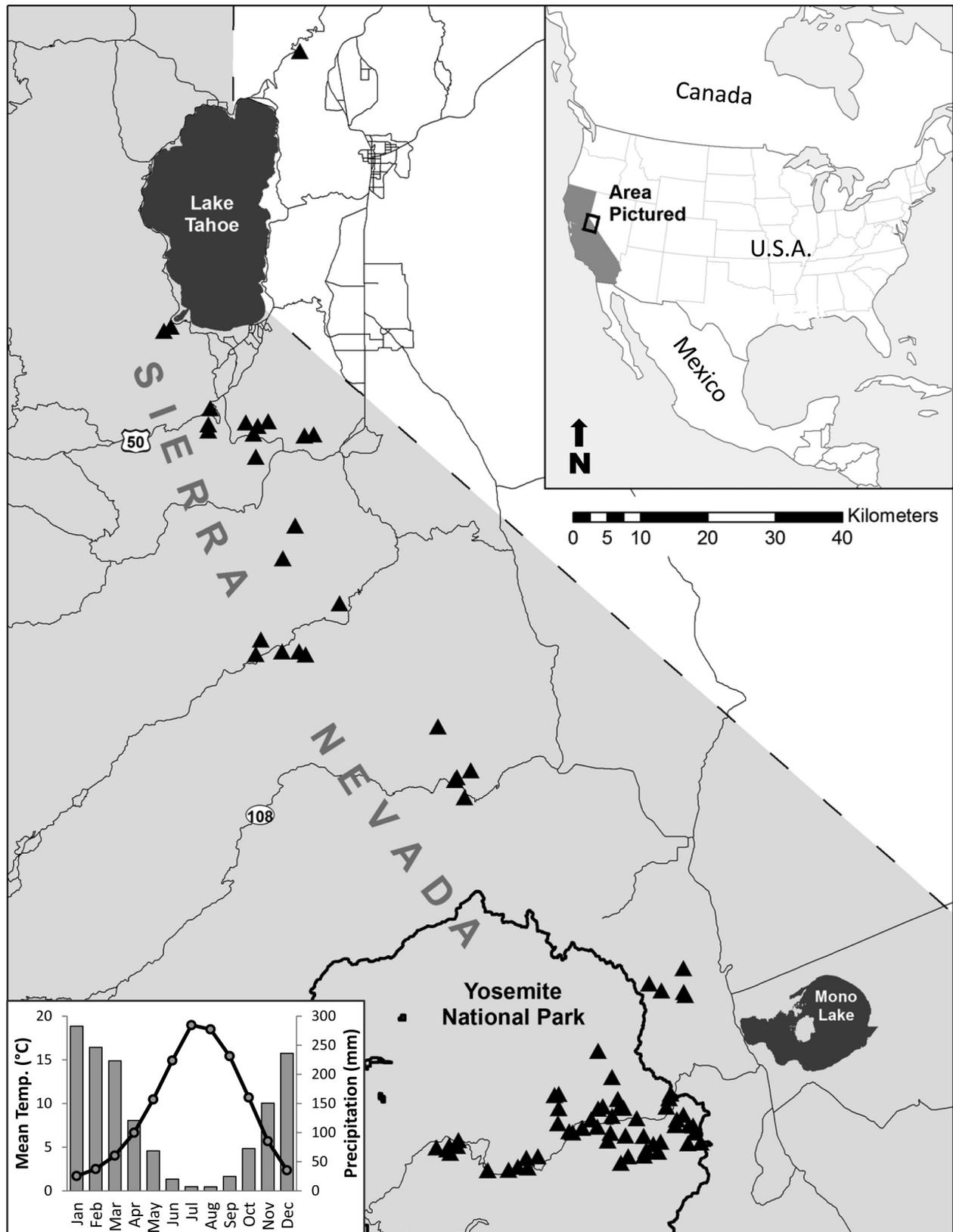
Field methods

Tree cores were collected between 2007 and 2009 from 83 sites ranging from Mono Pass in the south of our study area (37.812°N latitude) to the northeast edge of the Lake Tahoe basin in the north (39.312°N latitude), and ranging from 2300 m elevation up to tree line at about 3500 m (Fig. 1). Coring sites were collocated with vegetation plots that resampled historical US Forest Service plots that supported vegetation mapping in the early 1930s and, thus, each core has considerable stand structure and site physical data associated with it. See Dolanc et al. (2013) for details of historical and resampled plots. Most (>90%) sites occur west of the Sierra Nevada crest and all were in relatively undisturbed public land.

To more completely characterize the growth–climate relationship of each species, we collected cores from a wide gradient of elevation, slope, aspect, and latitude within the study area, as well as both small and large trees. Two to ten cores in total were collected per site, usually with two cores for each species present. Cores were taken from all the listed species with sample sizes more or less commensurate with the frequency of the species. Cores were collected from all nine species listed. Three species, white fir, mountain juniper, and quaking aspen were not included in analyses because of low sample sizes, leaving six species analyzed in this paper: red fir, whitebark pine, lodgepole pine, Jeffrey pine, western white pine, and mountain hemlock (Table 1).

Core extraction was done on the midslope side of the tree at breast height for large trees (≥ 25 cm DBH) and 30 cm above ground for small trees (<25 cm DBH). Only one core per tree was extracted and used in the analyses. Shading conditions of cored trees ranged from

Fig. 1. Map of the study area in the central Sierra Nevada, California, USA. Coring sites ($n = 83$) are indicated by dark triangles. All sites were in undisturbed locations between 2430 and 3397 m in elevation and 37.812° and 39.312° north latitude. Coring sites were collocated with forest inventory plots that resampled historical conditions across the subalpine region (Dolanc et al. 2013), and cover a range of site conditions, elevations, and slope aspects for each species. Inset climate diagram shows monthly mean temperature and precipitation for the Sierra Nevada region made available by the Western Regional Climate Center (Abatzoglou et al. 2009).



Can. J. For. Res. Downloaded from www.nrcresearchpress.com by CSP Staff on 12/03/13
For personal use only.

Table 1. Dating quality of tree cores prior to detrending and descriptive statistics of the six standard chronologies developed for this study.

	Tree species					
	ABMA	PIAL	PICO	PIJE	PIMO	TSME
Dating quality statistics^a						
No. of trees and (or) cores	50	64	136	24	55	58
Mean series length	103.1	171.4	111.8	163.1	143.5	108.4
Interseries correlation	0.49	0.35	0.31	0.29	0.40	0.59
Descriptive chronology statistics^b						
Standard deviation	0.11	0.10	0.13	0.11	0.12	0.14
First-order autocorrelation	-0.06	0.05	0.00	-0.10	-0.04	-0.11
Mean correlation (rbar) among all cores	0.35	0.14	0.14	0.18	0.20	0.39
EPS ^c	0.95	0.91	0.95	0.82	0.93	0.97

Note: Species codes are ABMA, *Abies magnifica*; PIAL, *Pinus albicaulis*; PICO, *Pinus contorta* var. *murrayana*; PIJE, *Pinus jeffreyi*; PIMO, *Pinus monticola*; and TSME, *Tsuga mertensiana*.

^aCalculated by COFECHA (Holmes 1983) on raw ring widths using a 32 year spline on 50 year segments lagged successively by 25 years.

^bCalculated with the dplR package (Bunn 2008) in R version 2.14.1 (R Core Team 2013) on detrended standard chronologies from 1895 to 2008 (2007 end year for ABMA and PIMO).

^cExpressed population signal (EPS) is a measure of the signal strength in a chronology (Cook and Kairiukstis 1990).

partial shade to full sun. Extracted cores were stored in plastic straws and transported to the laboratory for analysis.

Chronology development

Tree cores were prepared in the laboratory using standard techniques (Stokes and Smiley 1968). Cores were cross-dated visually using the list method (Yamaguchi 1991). Rings were measured to the nearest 0.001 mm width using a Velmex stage measuring system and associated MeasureJ2X software (Velmex Inc., Bloomfield, New York). After measurement, cross-dating accuracy was verified with COFECHA (Holmes 1983; Grissino-Mayer 2001), using a 32 year spline on 50 year segments lagged successively by 25 years. Problematic cores flagged by COFECHA were checked and, if changed, remeasured and reanalyzed with COFECHA.

We developed one chronology for each of the six species across our entire study area. Since our sites cover a range of conditions, the resulting chronologies should be a more robust average of how growth of each species responds to climate in the region. Chronology development and standardization were carried out using the dendrochronology program library (dplR; Bunn 2008) in R version 2.14.1 (R Core Team 2013). The fit of every core was examined using the interactive plot feature of dplR and graphical examination of curve fits. Our emphasis in this paper on the short-term growth-climate dendroecological relationship warranted an aggressive detrending method (i.e., a flexible smoothing spline) to remove low-frequency variance owing to stand-level disturbance. This approach is especially important, since our study area is large and our cores were collected from a range of site types. As a check on this, we also applied a range of smoothing splines: 100, 60, 30, and 15 year, and monitored how spline length affected mean correlation (rbar) and expressed population signal (EPS; Cook and Kairiukstis 1990). To reduce the effect of outliers and further enhance the climate signal, we averaged the resulting chronologies using a biweight robust mean (Cook and Kairiukstis 1990).

Climate data and analyses

Climate data used in this study were accessed from multiple online resources: (1) Monthly and annual data for maximum temperature (Tmax), mean temperature (Tmean), minimum temperature (Tmin), and precipitation (Prec) for the Sierra Nevada region from 1895 to 2009 from the California Climate Tracker Web site (<http://www.wrcc.dri.edu/monitor/cal-mon/>; accessed 15 March 2013). These data are a composite of station data and PRISM (Parameter-elevation regressions on independent slopes model; Daly et al. 2008) gridded data (Abatzoglou et al. 2009). A summary of monthly Tmean and Prec are shown inset in Fig. 1; a summary of annual Tmax, Tmin, and Prec from 1895 to 2009 are shown in Fig. 2A. (2) Monthly mean snowpack depth (SnDp) from 1938 to 2009 for

Tahoe City, California (39.168°N, 120.143°W, and 1899 m elevation) from the US Historical Climatology Network (Menne et al. 2013) (<http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html>; accessed 19 March 2013). (3) April 1 snowpack depth from the California Department of Water Resources, California Data Exchange Center (<http://cdec.water.ca.gov/>; accessed 19 March 2013). Multiple stations throughout our study area across a range of elevations were accessed: Dana Meadows, California (37.897°N, 119.257°W, and 2987 m); Sonora Pass, California (38.313°N, 119.607°W, and 2667 m); Caples Lake, California (38.710°N, 120.042°W, and 2438 m); and Echo Summit, California (38.828°N, 120.037°W, and 2271 m). Data from 1925 to 2009 from these stations, plus April 1 snowpack depth from the Tahoe City station from source 2, is summarized in Fig. 2B. (4) Monthly data for the Palmer Drought Severity Index (PDSI; Palmer 1965) for the period 1895–2009 from the National Oceanic and Atmospheric Administration, National Climatic Data Center for US Climatological Divisional data for the region CA-5, San Joaquin Drainage (<http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp>; accessed 29 March 2013).

The PDSI integrates temperature and precipitation and is calculated in a way that is cumulative over time. Use of PDSI for western North American systems has been criticized, as it was developed from data in the central US (Alley 1984). However, PDSI values are significantly correlated with soil moisture content in many regions of the world (Dai et al. 2004) and correlate well with tree growth, including sites in the Sierra Nevada (Potito and MacDonald 2008).

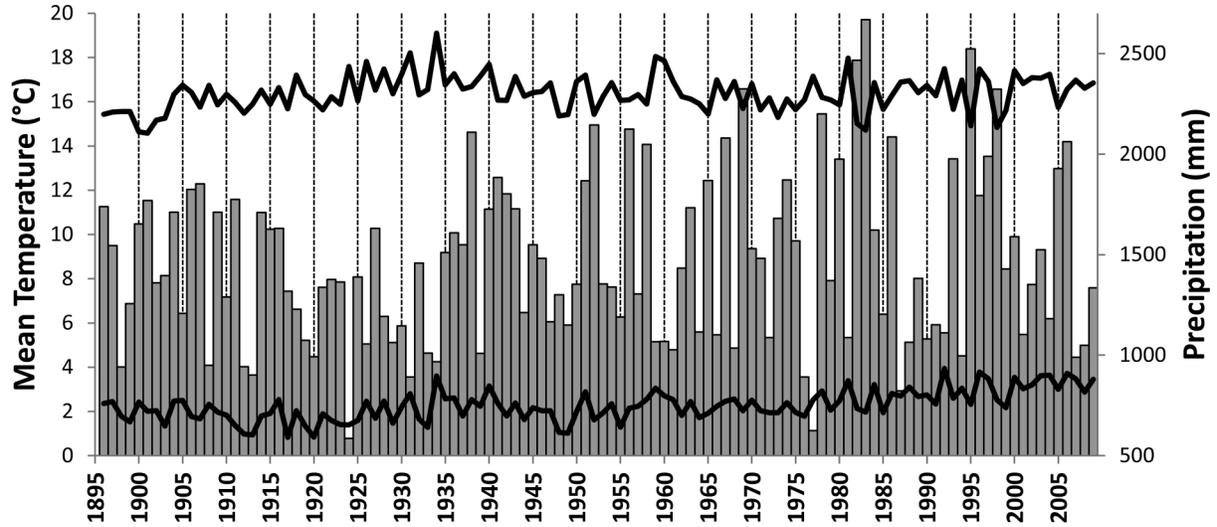
The relationship between radial growth and climate from 1896 to 2006 was quantified using DENDROCLIM2002 (Biondi and Waikul 2004). DENDROCLIM conducts correlation and response function analysis using bootstrapped estimates to test for significance (Biondi 1997; Biondi and Waikul 2004). We carried out correlation and response function analysis between the standard chronologies and the following monthly climate variables: Tmax, Tmin, Prec (from source 1), mean snowpack depth (from source 2), and PDSI (from source 4). A 22 month window, from January of the year prior to the growth ring of interest through October of the current year, was analyzed for every pair of variables for the entire 1896–2006 window of time. To check the evolution of the climate-growth relationship, we also carried out moving interval analyses in DENDROCLIM on PDSI and radial growth during the previous and current growing season (June–September) for all species.

Results

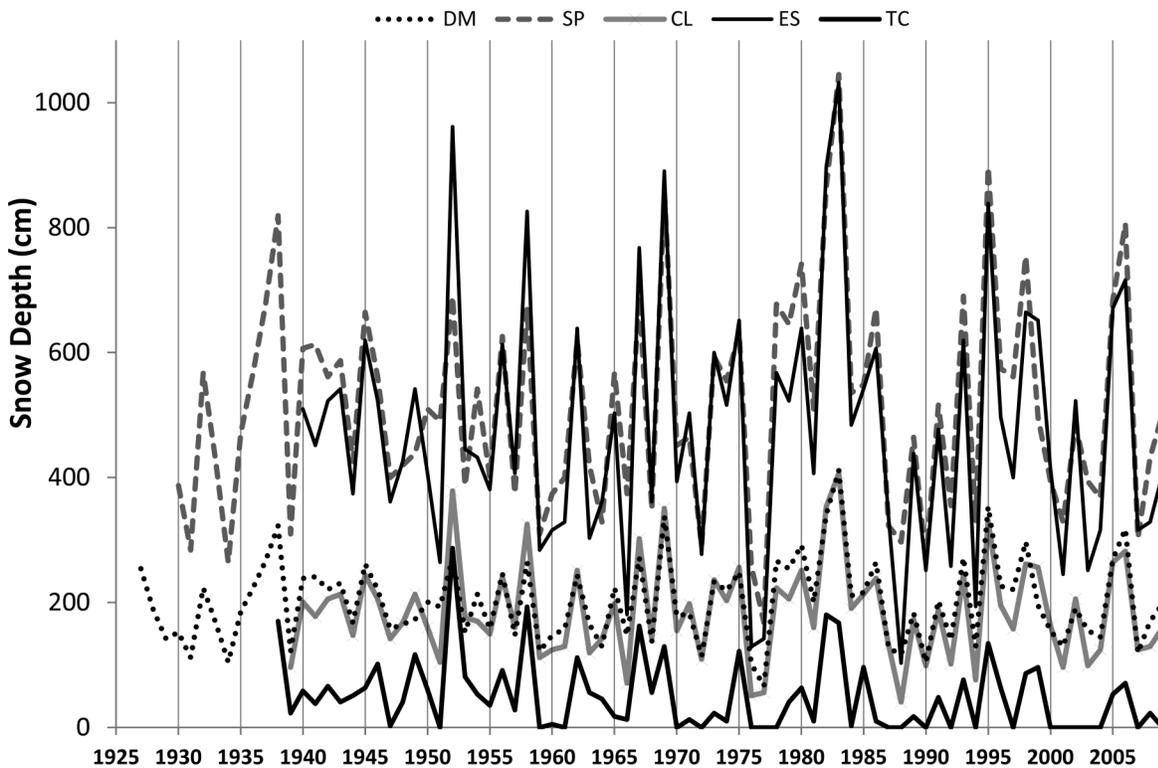
Signal strength and chronologies

Interseries correlation for our raw ring widths (from COFECHA) ranged from 0.29 to 0.59 for our six species (Table 1). Of the four

Fig. 2. Climate summary for the Sierra Nevada. (A) Mean annual maximum and minimum temperature and annual precipitation for 1896–2009 for the Sierra Nevada region. Data were compiled and made available by the Western Regional Climate Center (Abatzoglou et al. 2009) and represent a composite of PRISM (Daly et al. 2008) gridded data and station data for the region. Data are based on the water year (1 October – 30 September). (B) Snowpack depth on 1 April for five weather stations maintained by the California Department of Water Resources. These five stations cover a range of elevations and are all located within the study area. Stations are Dana Meadows, California (DM; 37.897°N, 119.257°W, and 2987 m); Sonora Pass, California (SP; 38.313°N, 119.607°W and 2667 m); Caples Lake, California (CL; 38.710°N, 120.042°W, and 2438 m); Echo Summit, California (ES; 38.828°N, 120.037°W, and 2271 m); and Tahoe City, California (TC; 39.168°N, 120.143°W, and 1899 m).



(A) Mean Annual Temperature and Precipitation



(B) April 1 Snowpack Depth

Can. J. For. Res. Downloaded from www.nrcresearchpress.com by CSP Staff on 12/03/13
For personal use only.

Table 2. Correlations (r) among the six standard chronologies developed in this study for the 1896–2006 year period used in growth–climate analyses for (A) the correlation matrix showing correlations between species pairs for the entire 111 year length of each chronology (all values listed are statistically significant at $p < 0.001$) and (B) synchrony of species chronologies over time, showing correlations between each species and a master chronology of all six chronologies for 30 year intervals with a 5 year lag.

Tree species	Tree species						Average
	ABMA	PIAL	PICO	PIJE	PIMO	TSME	
(A) Correlation matrix^a							
ABMA		0.54	0.69	0.69	0.73	0.82	
PIAL			0.71	0.33	0.65	0.43	
PICO				0.56	0.69	0.55	
PIJE					0.60	0.58	
PIMO						0.74	
Time period	Tree species						Average
	ABMA	PIAL	PICO	PIJE	PIMO	TSME	
(B) Synchrony over time^b							
1896–1924	0.80	0.52	0.75	0.65	0.76	0.67	0.69
1900–1929	0.75	0.39	0.79	0.60	0.80	0.66	0.67
1905–1934	0.75	0.33	0.80	0.59	0.77	0.70	0.66
1910–1939	0.74	0.39	0.79	0.56	0.76	0.76	0.67
1915–1944	0.74	0.56	0.81	0.65	0.82	0.71	0.71
1920–1949	0.76	0.55	0.75	0.68	0.88	0.72	0.72
1925–1954	0.74	0.51	0.75	0.73	0.89	0.69	0.72
1930–1959	0.74	0.64	0.71	0.74	0.87	0.71	0.73
1935–1964	0.76	0.67	0.75	0.72	0.85	0.71	0.74
1940–1969	0.78	0.61	0.76	0.74	0.87	0.70	0.74
1945–1974	0.80	0.58	0.81	0.75	0.86	0.75	0.76
1950–1979	0.79	0.55	0.83	0.66	0.85	0.74	0.74
1955–1984	0.84	0.66	0.81	0.65	0.81	0.81	0.76
1960–1989	0.87	0.59	0.79	0.62	0.81	0.74	0.74
1965–1994	0.86	0.58	0.77	0.62	0.84	0.71	0.73
1970–1999	0.90	0.75	0.79	0.61	0.86	0.80	0.78
1975–2004	0.92	0.70	0.79	0.63	0.84	0.79	0.78
1980–2006	0.91	0.74	0.79	0.69	0.82	0.81	0.79

Note: See Table 1 for species code definitions.

^aCorrelations and test of significance using the Student's t test with 109 degrees of freedom for each species were carried out using R version 2.14.1 (R Core Team 2013).

^bCalculated using COFECHA (Holmes 1983) with a 15 year spline on 30 year intervals lagged by 5 years.

different spline lengths used, the 15 year spline produced the highest mean correlation for standardized chronologies (r_{bar}) and EPS, with a mean r_{bar} of 0.23 and mean EPS of 0.92 (Table 1). The r_{bar} of our six chronologies is low for several species, but this is expected based on our large study area and high site variability. Despite this, EPS for the period corresponding to the climate–growth analyses (1896–2006) was higher than 0.9 for five of six species, suggesting our signal strength is good (Table 1). Correlation (r) of the six chronologies ranged from 0.33 for to 0.82; all correlations were positive and significant at $p < 0.05$ (Table 2).

The standard chronologies for all six species from 1895 to 2006 are shown in Fig. 3. The 15 year spline we applied resulted in chronologies with very minimal long-term trends and very low autocorrelation (Table 1). Several common growth patterns and peaks are synchronous across all or most species. All six species show quite poor growth in 1995, with three of six showing the poorest growth (narrowest ring) during that year over the entire 111 year period. All six species recovered in 1996 with two of six having their greatest growth of the record during that year. All six species show a peak in growth in 1984 and all but mountain hemlock show a decline in 1985, followed by another peak in 1986. Further back in the record, all six species show a strong decline in growth in 1929, and most exhibit quite variable growth in the years following. Other years of notably good or poor growth common in all or most

species include 1926, 1954, 1969, and 2000 (good growth); 1906, 1925, 1944, 1956, 1971, 1989, and 2003 (poor growth) (Fig. 3).

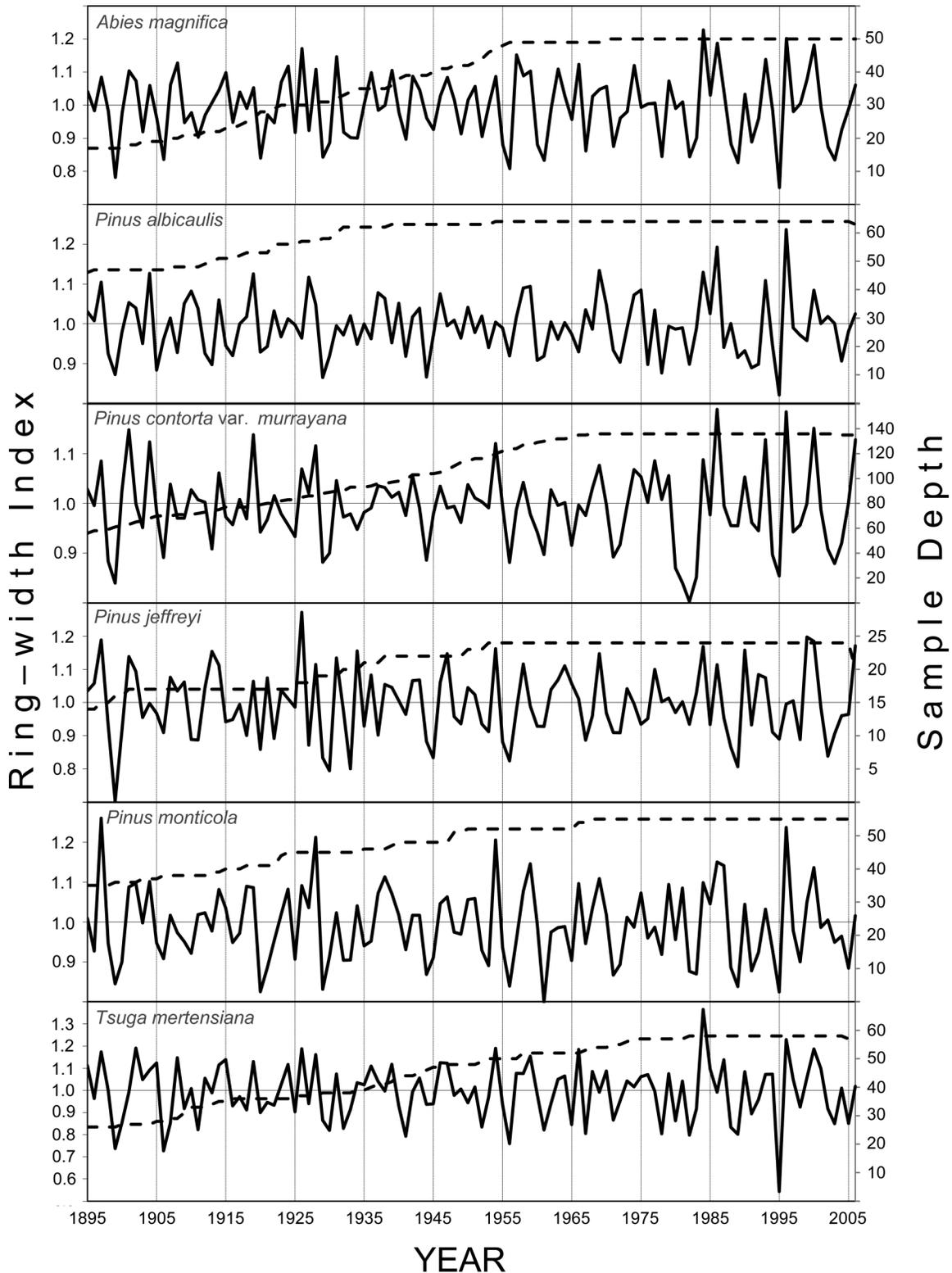
Climate–growth analyses

Response and correlation functions showed similar trends in our analyses, but trends in correlation functions were slightly stronger; thus, we present only those trends in this paper. Correlation between growth and temperature was generally negative in the year preceding growth and positive during the current growing season (Figs. 4A and 4B and Table S1).¹ The negative correlation between growth and temperature in the previous growing season was much stronger for T_{max} than for T_{min} , especially for red fir, Jeffrey pine, and mountain hemlock, and persisted late into the summer (July–September). Growth of all species except whitebark pine was significantly correlated with T_{max} in August of the previous year. The positive correlation between growth and temperature in the current growing season was similar for both T_{max} and T_{min} . Both variables were significantly positively correlated with growth during the current May for all six species (Figs. 4A and 4B and Table S1).¹

The correlation function for precipitation was generally positive during the previous year, especially for red fir, Jeffrey pine, and mountain hemlock (Fig. 4C and Table S1).¹ All six species exhibited positive, significant correlations with Prec during at least 1 month of

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0196>.

Fig. 3. Standard chronologies and sample depth for the six subalpine tree species in this study: red fir (*Abies magnifica*), whitebark pine (*Pinus albicaulis*), Sierra/Cascade lodgepole pine (*Pinus contorta* var. *murrayana*), Jeffrey pine (*Pinus jeffreyi*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*) for the 1895–2006 period.



the previous year. All six species were significantly positively correlated with Prec during the current February. Red fir, western white pine, and mountain hemlock were also significantly negatively correlated with Prec during the current growing season (Fig. 4C and Table S1).¹

The correlation function for snow depth showed a significant positive trend during the previous winter and spring (January–May), with the strongest correlations occurring in March and April (Fig. 5A and Table S1);¹ red fir, lodgepole pine, western white pine, and mountain hemlock all exhibited significant correlations

Can. J. For. Res. Downloaded from www.nrcresearchpress.com by CSP Staff on 12/03/13
For personal use only.

Fig. 4. Statistically significant ($p < 0.05$) correlation functions from DENDROCLIM2002 between standardized growth increment and climatic variables (monthly (A) mean maximum temperature, (B) mean minimum temperature, and (C) precipitation) for the 1896–2006 period, across a 22 month climatic window (Fritts 1976) from January of the previous year to October of the current year. Climate data were compiled and made available by the Western Regional Climate Center (Abatzoglou et al. 2009) and represent a hybrid of PRISM (Daly et al. 2008) gridded data and station data for the Sierra Nevada region. Species codes are ABMA, red fir (*Abies concolor*); PIAL, whitebark pine (*Pinus albicaulis*); PICO, Sierra/Cascade lodgepole pine (*Pinus contorta* var. *murrayana*); PIJE, Jeffrey pine (*Pinus jeffreyi*); PIMO, western white pine (*Pinus monticola*); and TSME, mountain hemlock (*Tsuga mertensiana*).

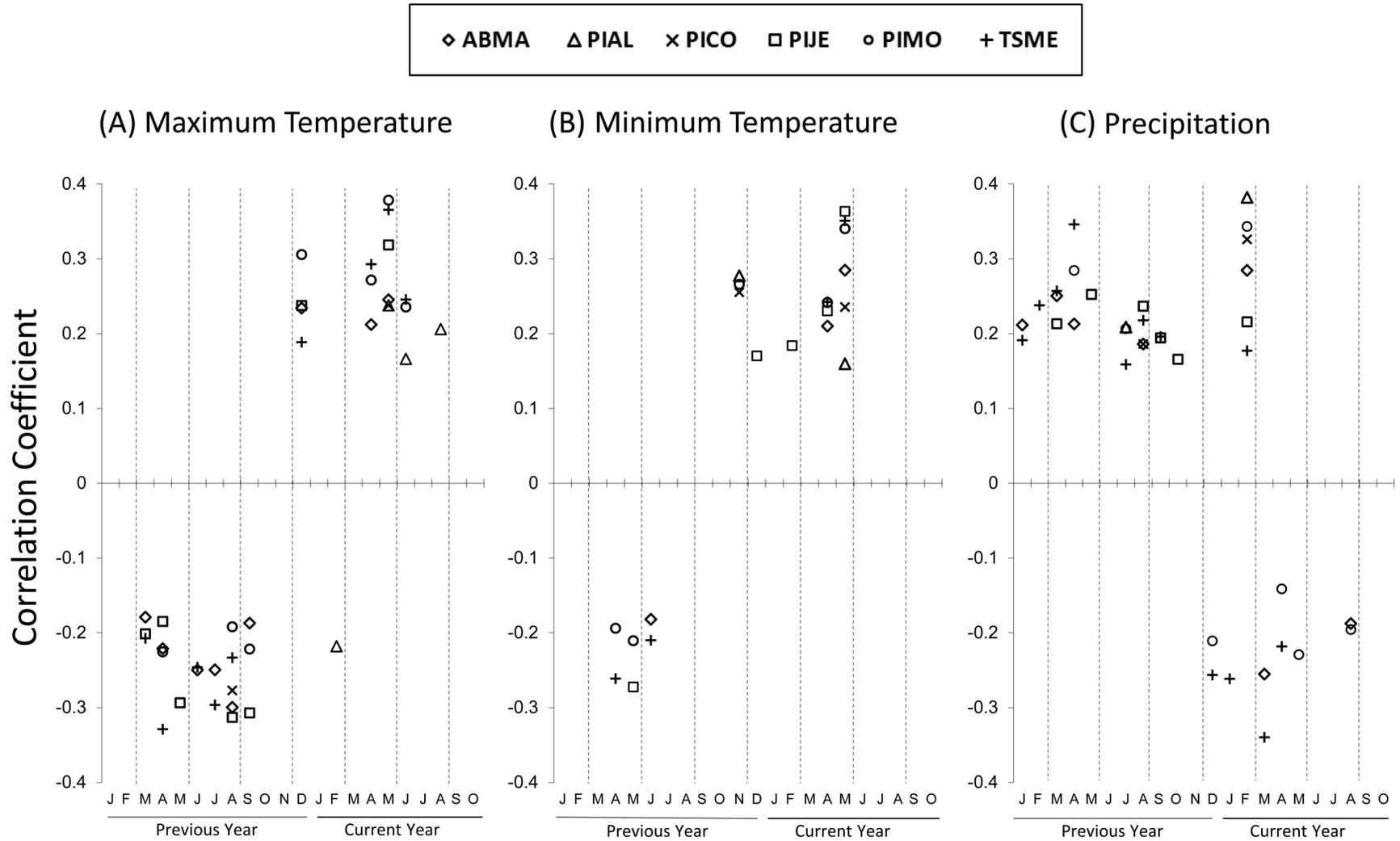
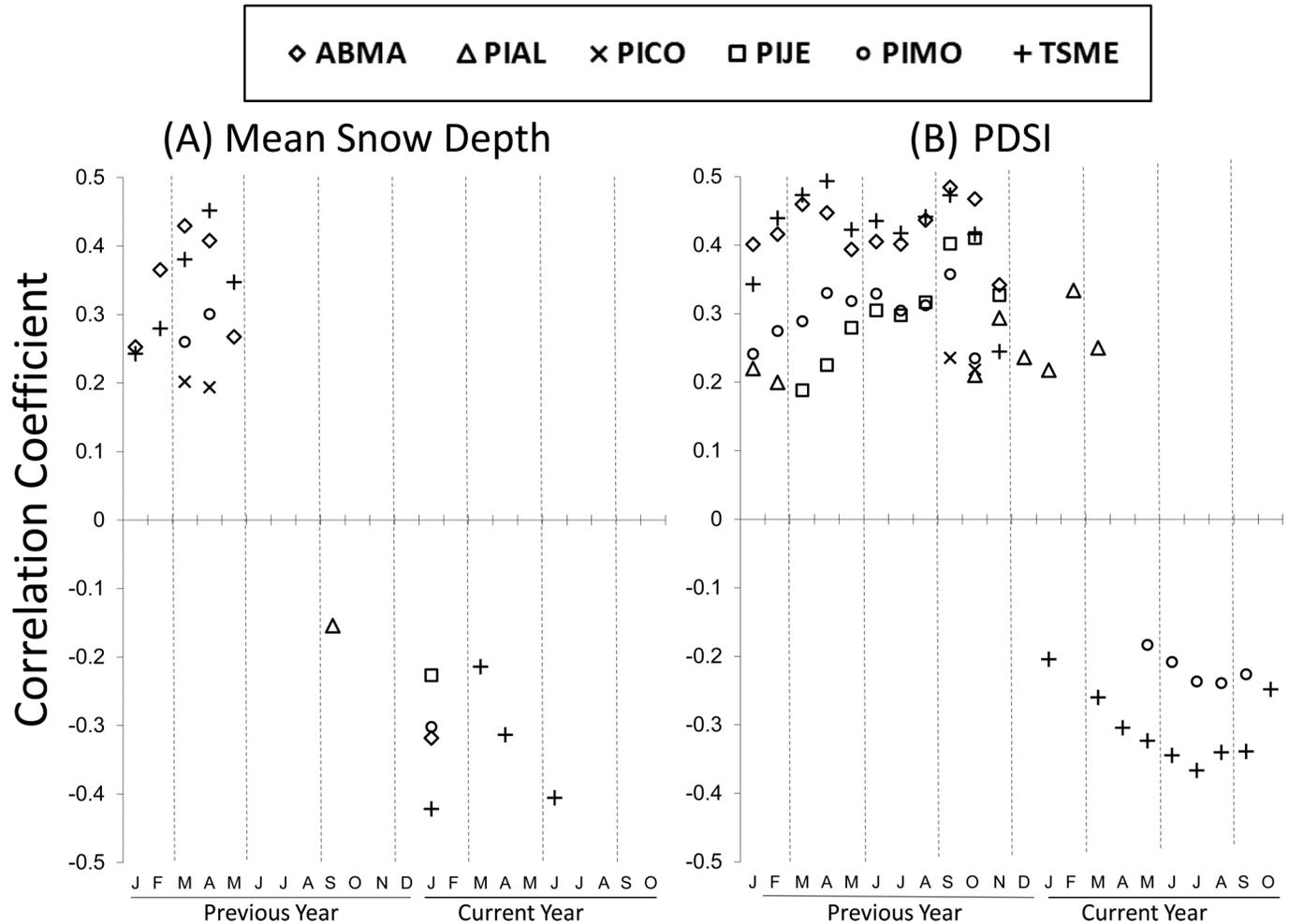


Fig. 5. Statistically significant ($p < 0.05$) correlation functions from DENDROCLIM2002 between standardized growth increment and climatic variables (monthly (A) mean snow depth for Tahoe City, California (39.168°N, 120.143°W, and 1899 m) and (B) Palmer drought severity index (PDSI) for the Sierra Nevada region) for the 1896–2006 period, across a 22 month climatic window (Fritts 1976) from January of the previous year to October of the current year. Climate data for (A) are from the US Historical Climatology Network (Menne et al. 2013). PDSI values are from the National Oceanic and Atmospheric Administration, National Climatic Data Center for US Climatological Divisional data for the region CA-5, San Joaquin Drainage. Species codes are ABMA, red fir (*Abies concolor*); PIAL, whitebark pine (*Pinus albicaulis*); PICO, Sierra/Cascade lodgepole pine (*Pinus contorta* var. *murrayana*); PIJE, Jeffrey pine (*Pinus jeffreyi*); PIMO, western white pine (*Pinus monticola*); and TSME, mountain hemlock (*Tsuga mertensiana*).



during this period. Growth was significantly negatively correlated with SnDp for red fir, Jeffrey pine, western white pine, and mountain hemlock in January of the current year. Significant negative correlations were also found between SnDp and mountain hemlock growth in March, May, and June of the current year (Fig. 5A and Table S1).¹

The correlations between radial growth and PDSI were generally stronger and more prevalent than all other variables (Fig. 5B and Table S1).¹ All six species showed significant positive correlations with PDSI at some point during the previous year. Red fir, western white pine, and mountain hemlock were significantly positively correlated with PDSI in every month from January to through September of the previous year; Jeffrey pine was also significantly positively correlated with PDSI during most of this period. Whitebark pine was significantly positively correlated with PDSI during the winter of both the previous year and current year. In addition, radial growth was significantly negatively correlated with PDSI during most of the current year for mountain hemlock and during summer (May–September) for western white pine (Fig. 5B and Table S1).¹ (Note that because PDSI is a cumulative

measure, significant correlations can occur late in the summer, after the cessation of growth).

The positive correlation between radial growth and PDSI during the previous growing season was stronger during the second half of the 20th century for red fir, western white pine, and mountain hemlock, but weaker for Jeffrey pine. The negative correlation between these variables during the current growing season was weaker for Jeffrey pine and western white pine, but similar for mountain hemlock (Table 3).

Many of the trends elucidated by correlation analyses can also be seen by comparing the chronologies visually with the climate record. All six species exhibited below mean growth in 1925 (Fig. 3). This year followed the driest year on record (1924; Fig. 2A). Five of six species (all but whitebark pine) recovered with a spike in growth in 1926, following a cooler, wetter year. All six species show a spike in growth in 1984, following the wettest year on record and cool temperatures in 1983. Growth in all six species was poor for 2 years, in 1982 and 1983, when spring snowpack was deep, and dropped initially in response to warm, dry conditions in 1981 (Figs. 2 and 3).

Table 3. Relationship between radial growth and the Palmer drought severity index (PDSI) during the growing season for the first and second halves of the 20th century.

Month	Tree species											
	ABMA		PIAL		PICO		PIJE		PIMO		TSME	
	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2
Previous year												
June	0.30 ^a	0.42	-0.23				0.25			0.34		0.49
July	0.30	0.43	-0.23				0.25			0.35		0.49
August	0.37	0.44					0.24			0.38		0.51
September	0.42	0.49		0.31			0.32	0.39	0.24	0.44	0.33	0.54
Current year												
June							-0.25		-0.23		-0.35	-0.36
July							-0.27		-0.28		-0.37	-0.38
August									-0.27		-0.35	-0.35
September										-0.28	-0.31	-0.38

Note: T1, 1901–1950; T2, 1951–2000.

^aCorrelation coefficients for radial growth and PDSI were calculated by DendroClim 2002. Only significant values at $p < 0.05$ are shown.

The three species more common on mesic sites — red fir, western white pine, and mountain hemlock — were generally better correlated (more often and greater strength) with climate variables, especially Prec, SnDp, and PDSI (Fig. 5 and Table S1).¹ Whitebark pine and lodgepole pine were least often correlated with climate variables. Whitebark pine was the only species not negatively correlated with either Tmax or Tmin during any month of the previous year. Neither species exhibited more than 2 months of significant correlations with Prec or SnDp over the entire 22 month window. Whitebark pine did have several positive significant correlations with PDSI, but correlations for both species were still less frequent than the other four species (Table S1).¹

Discussion

The six subalpine species analyzed in this study demonstrate a high degree of synchrony in their response to climate, despite having come from 83 different sites, over a large range of stand conditions, and over an area ranging 1.5° of latitude and 1200 m of elevation. Synchrony is evident in both the chronologies (Fig. 3 and Table 2) and their responses to climatic variables (Figs. 4 and 5 and Table S1),¹ and suggests these species respond strongly to regional macroclimate variation.

Our correlations with temperature demonstrate that the radial growth of subalpine trees in the central Sierra Nevada responds positively to cool temperatures leading up to the current growing season and warm temperatures in spring (April–June) of the current growing season. At the same time, radial growth of most species was greater when conditions were wetter during the previous year (as shown in the correlations with Prec, SnDp, and PDSI), and drier during the current growing season, especially for species that grow on more mesic sites (red fir, western white pine, and mountain hemlock). Previous studies on subalpine conifers from the southern and eastern Sierra Nevada demonstrated the dependence of radial growth on precipitation leading up to the growing season and warmth during the growing season (Peterson et al. 1990; Graumlich 1991). Our results extend this understanding to multiple subalpine species growing on the more mesic west slope of the central Sierra Nevada, and increase our understanding of the climate–growth relationship over the course of the several month period that impacts radial growth.

Our results highlight the influence of the dry Sierra Nevada summer on growth and the role of snowpack in moderating soil moisture. Negative correlations with temperature during the previous growing season probably reflect improved soil moisture retention under cool temperatures. These correlations roughly mirror the positive correlations in Prec, SnDp, and PDSI during the same period. Radial growth of subalpine trees from the east-

ern Sierra Nevada also was positively correlated with precipitation and PDSI and negatively correlated with climatic water deficit (Potito and MacDonald 2008; Millar et al. 2012). Increased tree mortality of Sierran subalpine trees has been linked to periods of drought (Lloyd and Graumlich 1997; Millar et al. 2007, 2012) and, conversely, increases in recruitment have occurred during periods of greater moisture retention (Lloyd 1997) and cooler temperatures (Millar et al. 2004).

Snowpack can also limit radial growth. As shown in Fig. 2B, snow depth on 1 April can be several metres in the Sierra Nevada. This limitation manifests in multiple correlations: (i) the negative relationship between snow depth and growth in the winter and spring of the current year; (ii) the positive relationship between both maximum and minimum temperature and growth in the spring of the current year; and (iii) the negative relationship between both precipitation and PDSI and growth for much of the current growing season, for species more abundant on mesic sites. Limitation of radial growth by snowpack or winter precipitation has been observed for multiple species, including mountain hemlock, in the Pacific Northwest (Graumlich and Brubaker 1986; Peterson and Peterson 1994, 2001; Gedalof and Smith 2001). Snowpack also limits tree recruitment on windward slopes in this region (Rochefort and Peterson 1996).

In conifers of high-elevation sites, conditions in a given year have a major bearing on radial growth the following year. Most of the photosynthate (food product of photosynthesis, usually glucose) produced during the first year is used for crown and leaf growth, instead of stem radial growth. Also, photosynthate continues to be produced long after the cessation of radial growth in the stem (Fritts 1976). However, the initiation of radial growth of the stem requires soil temperatures to warm to at least 4 °C (Tranquillini 1979) and can thus be affected by temperature and snowpack conditions in the spring of the current year as well (Fritts 1976; Peterson 1998).

An examination of our data from 1994 to 1996 provides an interesting example of how these physiological mechanisms interact with climate. The year 1995 was a marker year for all species and is represented as the poorest growth year on record in three of six chronologies, with all six showing very poor growth (Fig. 3). Drought conditions in 1994 limited the production of photosynthate to be used the following year, leading to a very narrow ring in 1995. Deep snowpack in the spring of 1995 delayed growth initiation and may have ultimately reduced the growing season, further reducing growth in 1995. Interestingly, since 1995 was so wet, food production was likely good long after radial growth ceased, contributing to a very wide ring in 1996, which was warmer, with above-average precipitation (Figs. 2 and 3). Extremely short growing

seasons can actually improve growth the following year by shunting photosynthate reserves into the next year (Fritts 1976).

It is unclear whether deep spring snowpack actually shortens the growing season in the Sierra Nevada. In a study from the southern Sierra Nevada from the same 1994–1995 dry-wet period, growth initiation for Jeffrey pine, western white pine, and red fir began roughly 3 weeks later in 1995, the year of the big spring snowpack, yet the period of radial growth in 1995 was about the same length (started later and ended later) as it was in 1994, a year that was warm and dry (Royce and Barbour 2001). In bristlecone pine (*Pinus longaeva* D.K. Bailey), radial growth terminates after 45 days even if conditions remain good for growth (Fritts 1976). These studies suggest the duration of radial growth during the growing season is not dependent on climatic conditions. Still, as with numerous studies in the Pacific Northwest (e.g., Gedalof and Smith 2001), our data suggest that deep spring snowpack can limit current-year radial growth.

The strong dependence on water balance for good growth apparent in our results suggests that growth response to future climate will depend greatly on water balance. Lloyd and Graumlich (1997) came to the same conclusion for tree line position in the southern Sierra Nevada. Temperatures in California are likely to rise over the next 100 years, but there is much less certainty regarding annual precipitation (Cayan et al. 2008; Mastrandrea and Luers 2012). Still, earlier snowmelt (Maurer 2007; Kapnick and Hall 2010) and increasing proportions of rain to snow (Knowles et al. 2006) mean that, regardless, trees will probably become more drought-stressed during the growing season.

Extended drought stress seems likely to inhibit growth, eventually leading to death for certain species or certain sites, as already shown for whitebark pine and limber pine (*Pinus flexilis* E. James) (Millar et al. 2007, 2012). Battles et al. (2008) predicted decreased stem growth by 2100 using a model based on conifers growing at middle elevations in the Sierra Nevada; increased summer temperatures drove this decrease for their four different climate scenarios. Our data suggest that the effect of growing-season drought stress on radial growth was greater in the last half of the 20th century, at least for species typically found on mesic sites (Table 3). Also, the response of our six species to climate became more cohesive during the last few decades, suggesting strengthening dominance (limitation) by regional climate (Table 2B). The abundance of subalpine trees in the Sierra Nevada has increased since the first half of the 20th century (Dolanc et al. 2013), but growth suppression owing to increased drought stress could eventually reverse this trend.

Microsite variability is likely to play a big role in how the growth–climate relationship evolves with changing climate (Bunn et al. 2005b). Our results highlight a difference between species typical of mesic sites (red fir, western white pine, and mountain hemlock) and those typical of drier sites (whitebark pine, Jeffrey pine, and lodgepole pine). Whether those differences are more related to site or species warrants further investigation. Lodgepole pine might make a good study species for an analysis of the growth–climate relationship on different site types — it can be found in a variety of site types, from meadow edges to dry ridge tops. We attempted an analysis by site type by subdividing into topographic groups (e.g., north versus south slopes, high versus low elevations), but signal strength was low for these groups. However, our preliminary data, and the interspecies synchrony exhibited in this study, suggest that response to regional macroclimate is stronger than site-to-site variability.

Finally, we note the relationship between mountain hemlock and other species in our study. Its positive response to dry conditions during the current year is consistent with findings from the Pacific Northwest. Still, because the species is relegated to cooler, wetter slopes and is near the southern end of its latitudinal range in North America (Little 1971), a climate-envelope model (see Pearson and Dawson 2003) should predict mountain hemlock to

lose nearly all of its current habitat (or climate envelope) in the central Sierra Nevada. Our data suggest that mountain hemlock growth would not respond any more negatively to warmer temperatures than other species in the region, and might actually see improved growth on sites with deep snowpack. Although growth response does not equal distribution response, this exemplifies how climate-envelope models should be informed or complemented by physiological data.

Conclusion

Radial growth of subalpine conifers of the central Sierra Nevada is closely tied to the balance of winter precipitation and summer drought, as has been shown in other Mediterranean-type mountains (Biondi 1993; Martin-Benito et al. 2013). Warm, dry conditions lead to reduced radial growth, except in years when snowpack is deep and long-lasting. Deep Sierra Nevada snowpack helps to mitigate the effects of drought but can also limit growth for species generally restricted to snowy slopes, such as mountain hemlock. The six species we examined demonstrate a cohesive response to climate, suggesting that regional macroclimate limits growth, but more work is needed on the contribution of site-to-site variability.

Acknowledgements

We thank D. Peterson, M. Barbour, and two anonymous reviewers for helpful comments on earlier drafts of this paper. F. Ye helped with core preparation and ring measurement. C. Calloway helped with core preparation and field work. A. Holguin provided help with figure preparation and field work. C. Delong, E. Peck, K. Farrell, N. Le, D. Showers, C. Peters, and D. Ingrasia helped with field work. Funding came from National Science Foundation award No. 0819493, the California Energy Commission PIER Program CEC PIR-08-006, the USDA Forest Service Pacific Southwest Region Ecology Program, The Tahoe Conservancy, The Ernest Hill Foundation of UC-Davis, The Davis Botanical Society, Northern California Botanists, and the California Native Plant Society.

References

- Abatzoglou, J.T., Redmond, K.T., and Edwards, L.M. 2009. Classification of regional climate variability in the state of California. *J. Appl. Meteorol. Climatol.* **48**(8): 1527–1541. doi:10.1175/2009JAMC2062.1.
- Alley, W.M. 1984. The Palmer drought severity index — Limitations and assumptions. *J. Clim. Appl. Meteorol.* **23**(7): 1100–1109. doi:10.1175/1520-0450(1984)023<1100:TPDSIL>2.0.CO;2.
- Battles, J.J., Robards, T., Das, A., Waring, K., Gilles, J.K., Biging, G., and Schurr, F. 2008. Climate change impacts on forest growth and tree mortality: a data-driven modeling study in the mixed-conifer forest of the Sierra Nevada, California. *Clim. Change*, **87**: S193–S213. doi:10.1007/s10584-007-9358-9.
- Bigler, C., and Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. *Ecol. Appl.* **14**(3): 902–914. doi:10.1890/03-5011.
- Bigler, C., Grisar, J., Bugmann, H., and Cufar, K. 2004. Growth patterns as indicators of impending tree death in silver fir. *For. Ecol. Manag.* **199**(2–3): 183–190. doi:10.1016/j.foreco.2004.04.019.
- Biondi, F. 1993. Climatic signals in tree-rings of *Fagus sylvatica* L. from the central Apennines, Italy. *Acta Oecol.* **14**(1): 57–71.
- Biondi, F. 1997. Evolutionary and moving response functions in dendrochronology. *Dendrochronologia*, **15**: 139–150.
- Biondi, F., and Waikul, K. 2004. Dendroclim 2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* **30**: 303–311. doi:10.1016/j.cageo.2003.11.004.
- Bunn, A.G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**(2): 115–124. doi:10.1016/j.dendro.2008.01.002.
- Bunn, A.G., Graumlich, L.J., and Urban, D.L. 2005a. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *Holocene*, **15**(4): 481–488. doi:10.1191/0959683605hl827rp.
- Bunn, A.G., Waggoner, L.A., and Graumlich, L.J. 2005b. Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA. *Global Ecol. Biogeogr.* **14**(2): 103–114. doi:10.1111/j.1466-822X.2005.00141.x.
- Cayan, D.R., Luers, A.L., Franco, G., Hanemann, M., Croes, B., and Vine, E. 2008. Overview of the California climate change scenarios project. *Clim. Change*, **87**: S1–S6. doi:10.1007/s10584-007-9352-2.
- Cook, E.R., and Kairiukstis, L.R. 1990. *Methods of dendrochronology: applications in the environmental sciences.* Kluwer, Dordrecht.

- Dai, A., Trenberth, K.E., and Qian, T.T. 2004. A global data set of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *J. Hydrometeorol.* 5(6): 1117–1130. doi:10.1175/JHM-386.1.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., and Pasteris, P.P. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28(15): 2031–2064. doi:10.1002/joc.1688.
- Dolanc, C.R., Thorne, J.H., and Safford, H.D. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Global Ecol. Biogeogr.* 22(3): 264–276. doi:10.1111/j.1466-8238.2011.00748.x.
- Fites-Kaufman, J.A., Rundel, P., Stephenson, N.L., and Weixelman, D.A. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In *Terrestrial vegetation of California*. Edited by M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr. University of California Press, Berkeley, Los Angeles, London. pp. 456–501.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London.
- Gedalof, Z., and Smith, D.J. 2001. Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America. *Can. J. For. Res.* 31(2): 322–332. doi:10.1139/x00-169.
- Graumlich, L.J. 1991. Subalpine tree growth, climate, and increasing CO₂ — An assessment of recent growth trends. *Ecology*, 72(1): 1–11. doi:10.2307/1938895.
- Graumlich, L.J. 1993. A 1000-year record of temperature and precipitation in the Sierra-Nevada. *Quat. Res.* 39(2): 249–255. doi:10.1006/qres.1993.1029.
- Graumlich, L.J., and Brubaker, L.B. 1986. Reconstruction of annual temperature (1590–1979) for longmire, Washington, derived from tree rings. *Quat. Res.* 25(2): 223–234. doi:10.1016/0033-5894(86)90059-1.
- Grissino-Mayer, H.D. 2001. Evaluating cross-dating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57(2): 205–221.
- Guisan, A., and Theurillat, J. 2001. Assessing alpine plant vulnerability to climate change: a modeling perspective. *Integrated Assessment*, 1: 14.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43: 69–75.
- Holtmeier, F.-K. 2003. *Mountain timberlines, ecology, patchiness, and dynamics*. Kluwer Academic Publishers, Dordrecht.
- Huang, J.G., Tardif, J.C., Bergeron, Y., Denneler, B., Berninger, F., and Girardin, M.P. 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biol.* 16(2): 711–731. doi:10.1111/j.1365-2486.2009.01990.x.
- IPCC. 2007. Summary for Policymakers. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Edited by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge University Press, Cambridge, UK. p. 21.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., and Peters, M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For. Ecol. Manag.* 254(3): 390–406. doi:10.1016/j.foreco.2007.07.023.
- Kapnick, S., and Hall, A. 2010. Observed climate–snowpack relationships in California and their implications for the future. *J. Clim.* 23(13): 3446–3456. doi:10.1175/2010JCLI2903.1.
- Kearney, M., and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12(4): 334–350. doi:10.1111/j.1461-0248.2008.01277.x. PMID:19292794.
- Knowles, N., Dettinger, M.D., and Cayan, D.R. 2006. Trends in snowfall versus rainfall in the western United States. *J. Clim.* 19(18): 4545–4559. doi:10.1175/JCLI3850.1.
- Lamarche, V.C. 1974. Paleoclimatic inferences from long tree-ring records. *Science*, 183(4129): 1043–1048. doi:10.1126/science.183.4129.1043. PMID:17738961.
- Lenihan, J.M., Bachelet, D., Neilson, R.P., and Drapek, R. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Clim. Change*, 87: S215–S230. doi:10.1007/s10584-007-9362-0.
- Little, E.L. 1971. *Atlas of United States trees. Vol. 1. Conifers and important hardwoods*. USDA Miscellaneous Publication 1146.
- Lloyd, A.H. 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. *Can. J. For. Res.* 27(6): 936–942. doi:10.1139/x97-028.
- Lloyd, A.H., and Graumlich, L.J. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, 78(4): 1199–1210. doi:10.1890/0012-9658(1997)078[1199:HDOTF]2.0.CO;2.
- Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A., and Ackerly, D.D. 2008. Climate change and the future of California's endemic flora. *Plos One*, 3(6): e2502. doi:10.1371/journal.pone.0002502. PMID:18648541.
- Major, J. 1990. California climate in relation to vegetation. In *Terrestrial vegetation of California*. Edited by M. Barbour and J. Major. California Native Plant Society, Sacramento, California, USA. pp. 11–74.
- Martin-Benito, D., Beeckman, H., and Canellas, I. 2013. Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest. *Eur. J. For. Res.* 132(1): 33–45. doi:10.1007/s10342-012-0652-3.
- Mastrandrea, M.D., and Luers, A.L. 2012. Climate change in California: scenarios and approaches for adaptation. *Clim. Change*, 111: 5–16. doi:10.1007/s10584-011-0240-4.
- Maurer, E.P. 2007. Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. *Clim. Change*, 82(3–4): 309–325. doi:10.1007/s10584-006-9180-9.
- Menne, M., Williams, C., and Vose, R.S. 2013. United States historical climatology network daily temperature, precipitation, and snow data. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Millar, C.I., Westfall, R.D., Delany, D.L., King, J.C., and Graumlich, L.J. 2004. Response of subalpine conifers in the Sierra Nevada, California, U.S.A., to 20th-century warming and decadal climate variability. *Arct. Antarct. Alp. Res.* 36(2): 181–200. doi:10.1657/1523-0430(2004)036[0181:ROSCIT]2.0.CO;2.
- Millar, C.I., Westfall, R.D., and Delany, D.L. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. *Can. J. For. Res.* 37(12): 2508–2520. doi:10.1139/X07-097.
- Millar, C.I., Westfall, R.D., Delany, D.L., Bokach, M.J., Flint, A.L., and Flint, L.E. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA: influence of environmental context, bark beetles, climatic water deficit, and warming. *Can. J. For. Res.* 42(4): 749–765. doi:10.1139/x2012-031.
- Minnich, R.A. 2007. Climate, paleoclimate, and paleovegetation. In *Terrestrial vegetation of California*. Edited by M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr. University of California Press, Berkeley, Los Angeles, London. pp. 43–70.
- Palmer, W.C. 1965. Meteorological drought. In *Research Paper 45*. US Department of Commerce, Weather Bureau, Washington, D.C.
- Parker, A.J. 1988. Stand structure in subalpine forests of Yosemite National Park, California. *For. Sci.* 34(4): 1047–1058.
- Pearson, R.G., and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 12(5): 361–371. doi:10.1046/j.1466-822X.2003.00042.x.
- Peterson, D.L. 1998. Climate, limiting factors and environmental change in high-altitude forests of western North America. In *The impacts of climate variability on forests*. Springer, Berlin/Heidelberg. pp. 191–208.
- Peterson, D.W., and Peterson, D.L. 1994. Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. *Can. J. For. Res.* 24(9): 1921–1932. doi:10.1139/x94-247.
- Peterson, D.W., and Peterson, D.L. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, 82(12): 3330–3345. doi:10.1890/0012-9658(2001)082[3330:MHGRT]2.0.CO;2.
- Peterson, D.L., Arbaugh, M.J., Robinson, L.J., and Derderian, B.R. 1990. Growth trends of whitebark pine and lodgepole pine in a subalpine Sierra Nevada forest, California, U.S.A. *Arct. Alp. Res.* 22(3): 233–243. doi:10.2307/1551586.
- Peterson, D.H., Smith, R.E., Dettinger, M.D., Cayan, D.R., and Riddle, L. 2000. An organized signal in snowmelt runoff over the western United States. *J. Am. Water Resour. Assoc.* 36(2): 421–432. doi:10.1111/j.1752-1688.2000.tb04278.x.
- Potito, A.P., and MacDonald, G.M. 2008. The effects of aridity on conifer radial growth, recruitment, and mortality patterns in the eastern Sierra Nevada, California. *Arct. Antarct. Alp. Res.* 40(1): 129–139. doi:10.1657/1523-0430(05-080)[POTITO]2.0.CO;2.
- Potter, D.A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. USDA For. Serv., Pacific Southwest Forest and Range Experiment Station, Albany, California. Gen. Tech. Rep. PSW-GTR-169.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., and Evans, J.S. 2006. Empirical analyses of plant–climate relationships for the western United States. *Int. J. Plant Sci.* 167(6): 1123–1150. doi:10.1086/507711.
- Rochefort, R.M., and Peterson, D.L. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, U.S.A. *Arct. Alp. Res.* 28(1): 52–59. doi:10.2307/1552085.
- Royce, E.B., and Barbour, M.G. 2001. Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone. *Am. J. Bot.* 88(5): 919–932. doi:10.2307/2657045. PMID:11353717.
- Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmüller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proc. Natl. Acad. Sci. U.S.A.* 106(48): 20348–20353. doi:10.1073/pnas.0903029106. PMID:19918054.
- Sawyer, J.O., Keeler-Wolf, T., and Evens, J. 2009. *A manual of California vegetation*. 2nd ed. California Native Plant Society, Sacramento, California.
- Scuderi, L.A. 1993. A 2000-year tree-ring record of annual temperatures in the Sierra Nevada Mountains. *Science*, 259(5100): 1433–1436. doi:10.1126/science.259.5100.1433. PMID:17801276.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* 25(5): 855–870. doi:10.1046/j.1365-2699.1998.00233.x.
- Stokes, M.A., and Smiley, T.L. 1968. *An introduction to tree ring dating*. The University of Chicago Press, Chicago, Illinois.
- Svenning, J.C., and Skov, F. 2004. Limited filling of the potential range in European tree species. *Ecol. Lett.* 7(7): 565–573. doi:10.1111/j.1461-0248.2004.00614.x.
- Tardif, J.C., Conciatori, F., Nantel, P., and Gagnon, D. 2006. Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus*

- rubra*) at the northern distribution limit of white oak in Quebec, Canada. *J. Biogeogr.* **33**(9): 1657–1669. doi:10.1111/j.1365-2699.2006.01541.x.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., and Prentice, I.C. 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U.S.A.* **102**(23): 8245–8250. doi:10.1073/pnas.0409902102. PMID:15919825.
- Tranquillini, W. 1979. *Physiological ecology of the Alpine timberline; tree existence at high altitudes with special reference to the European Alps.* Springer, Berlin Heidelberg, New York.
- Urban, D.L., Miller, C., Halpin, P.N., and Stephenson, N.L. 2000. Forest gradient response in Sierran landscapes: the physical template. *Landsc. Ecol.* **15**(7): 603–620. doi:10.1023/A:1008183331604.
- van Wageningen, J.W., and Fites-Kaufman, J.A. 2006. Sierra Nevada bioregion. *In Fire in California's ecosystems.* Edited by N.G. Sugihara, J.W. Van Wageningen, K.E. Shaffer, J.A. Fites-Kaufman, and A.E. Thode. University of California Press, Berkeley, Los Angeles, London. pp. 264–294.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**(3): 414–416. doi:10.1139/x91-053.