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, even if there are sites that 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 un 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 le 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 (Thullier 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).
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 dendroclimatological 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; Scuderí 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 demonstrated 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 demonstrated 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 demonstrated 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 demonstrated 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).

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 it 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 Wagendonk 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 of 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 mid-slope 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).
Table 1. Dating quality of tree cores prior to detrending and descriptive statistics of the six standard chronologies developed for this study.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>ABMA</th>
<th>PIAL</th>
<th>PICO</th>
<th>PIJE</th>
<th>PIMO</th>
<th>TSME</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of trees and (or) cores</td>
<td>50</td>
<td>64</td>
<td>136</td>
<td>24</td>
<td>55</td>
<td>58</td>
</tr>
<tr>
<td>Mean series length</td>
<td>103.1</td>
<td>171.4</td>
<td>111.8</td>
<td>163.1</td>
<td>143.5</td>
<td>108.4</td>
</tr>
<tr>
<td>Interseries correlation</td>
<td>0.49</td>
<td>0.35</td>
<td>0.31</td>
<td>0.29</td>
<td>0.40</td>
<td>0.59</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.11</td>
<td>0.10</td>
<td>0.13</td>
<td>0.11</td>
<td>0.12</td>
<td>0.14</td>
</tr>
<tr>
<td>First-order autocorrelation</td>
<td>−0.06</td>
<td>0.05</td>
<td>0.00</td>
<td>−0.10</td>
<td>−0.04</td>
<td>−0.02</td>
</tr>
<tr>
<td>Mean correlation (rbar) among all cores</td>
<td>0.35</td>
<td>0.14</td>
<td>0.14</td>
<td>0.18</td>
<td>0.20</td>
<td>0.39</td>
</tr>
<tr>
<td>EPS</td>
<td>0.95</td>
<td>0.91</td>
<td>0.95</td>
<td>0.82</td>
<td>0.93</td>
<td>0.97</td>
</tr>
</tbody>
</table>

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.

*Calculated by COFECHA (Holmes 1983) on raw ring widths using a 32 year spline on 50 year segments lagged successively by 25 years.
*Calculated 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).
Expressed population signal (EPS) is a measure of the signal strength in a chronology (Cook and Kairiukstis 1990).
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).
**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.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>ABMA</th>
<th>PIAL</th>
<th>PICO</th>
<th>PIJE</th>
<th>PIMO</th>
<th>TSME</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Correlation matrixa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ABMA</td>
<td>0.54</td>
<td>0.69</td>
<td>0.69</td>
<td>0.73</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>PIAL</td>
<td>0.71</td>
<td>0.33</td>
<td>0.65</td>
<td>0.65</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>PICO</td>
<td>0.56</td>
<td>0.69</td>
<td>0.56</td>
<td>0.58</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>PIJE</td>
<td>0.60</td>
<td>0.58</td>
<td>0.58</td>
<td>0.60</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>PIMO</td>
<td>0.74</td>
<td>0.60</td>
<td>0.58</td>
<td>0.60</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>TSME</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.74</td>
<td>0.60</td>
<td>0.58</td>
<td>0.60</td>
<td>0.58</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tree species</th>
<th>ABMA</th>
<th>PIAL</th>
<th>PICO</th>
<th>PIJE</th>
<th>PIMO</th>
<th>TSME</th>
</tr>
</thead>
<tbody>
<tr>
<td>(B) Synchrony over timeb</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1896–1924</td>
<td>0.80</td>
<td>0.52</td>
<td>0.75</td>
<td>0.65</td>
<td>0.76</td>
<td>0.67</td>
</tr>
<tr>
<td>1900–1929</td>
<td>0.73</td>
<td>0.39</td>
<td>0.79</td>
<td>0.60</td>
<td>0.80</td>
<td>0.66</td>
</tr>
<tr>
<td>1905–1934</td>
<td>0.75</td>
<td>0.33</td>
<td>0.80</td>
<td>0.59</td>
<td>0.77</td>
<td>0.70</td>
</tr>
<tr>
<td>1910–1939</td>
<td>0.74</td>
<td>0.39</td>
<td>0.79</td>
<td>0.56</td>
<td>0.76</td>
<td>0.76</td>
</tr>
<tr>
<td>1915–1944</td>
<td>0.74</td>
<td>0.56</td>
<td>0.81</td>
<td>0.65</td>
<td>0.82</td>
<td>0.71</td>
</tr>
<tr>
<td>1920–1949</td>
<td>0.76</td>
<td>0.55</td>
<td>0.75</td>
<td>0.68</td>
<td>0.88</td>
<td>0.72</td>
</tr>
<tr>
<td>1925–1954</td>
<td>0.74</td>
<td>0.51</td>
<td>0.75</td>
<td>0.73</td>
<td>0.89</td>
<td>0.72</td>
</tr>
<tr>
<td>1930–1959</td>
<td>0.74</td>
<td>0.64</td>
<td>0.71</td>
<td>0.74</td>
<td>0.87</td>
<td>0.71</td>
</tr>
<tr>
<td>1935–1964</td>
<td>0.76</td>
<td>0.67</td>
<td>0.75</td>
<td>0.72</td>
<td>0.85</td>
<td>0.71</td>
</tr>
<tr>
<td>1940–1969</td>
<td>0.78</td>
<td>0.61</td>
<td>0.76</td>
<td>0.74</td>
<td>0.87</td>
<td>0.70</td>
</tr>
<tr>
<td>1945–1974</td>
<td>0.80</td>
<td>0.38</td>
<td>0.81</td>
<td>0.65</td>
<td>0.81</td>
<td>0.76</td>
</tr>
<tr>
<td>1950–1979</td>
<td>0.79</td>
<td>0.35</td>
<td>0.82</td>
<td>0.66</td>
<td>0.85</td>
<td>0.74</td>
</tr>
<tr>
<td>1955–1984</td>
<td>0.84</td>
<td>0.66</td>
<td>0.81</td>
<td>0.65</td>
<td>0.81</td>
<td>0.76</td>
</tr>
<tr>
<td>1960–1989</td>
<td>0.87</td>
<td>0.59</td>
<td>0.79</td>
<td>0.62</td>
<td>0.81</td>
<td>0.74</td>
</tr>
<tr>
<td>1965–1994</td>
<td>0.86</td>
<td>0.58</td>
<td>0.77</td>
<td>0.62</td>
<td>0.81</td>
<td>0.74</td>
</tr>
<tr>
<td>1970–1999</td>
<td>0.90</td>
<td>0.75</td>
<td>0.79</td>
<td>0.61</td>
<td>0.86</td>
<td>0.78</td>
</tr>
<tr>
<td>1975–2004</td>
<td>0.92</td>
<td>0.70</td>
<td>0.79</td>
<td>0.63</td>
<td>0.84</td>
<td>0.79</td>
</tr>
<tr>
<td>1980–2006</td>
<td>0.91</td>
<td>0.74</td>
<td>0.79</td>
<td>0.69</td>
<td>0.82</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Note: See Table 1 for species code definitions.

a Correlations and test of significance using the Students t test with 109 degrees of freedom for each species were carried out using R version 2.14.1 (R Core Team 2013).
b Calculated 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 (rbar) and EPS, with a mean rbar of 0.23 and mean EPS of 0.92 (Table 1). The rbar 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 all six 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 Tmax than for Tmin, 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 Tmax in August of the previous year. The positive correlation between growth and temperature in the current growing season was similar for both Tmax and Tmin. 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
the previous year. All six species were significantly positively corre-
lated with Prec during the current February. Red fir, western white
pine, and mountain hemlock were also significantly negatively cor-
related with Prec during the current growing season (Fig. 4C and
Table S1). The correlation function for snow depth showed a signifi-
cant positive trend during the previous winter and spring (January-
May), with the strongest correlations occurring in March and
April (Fig. 5A and Table S1); red fir, lodgepole pine, western white
pine, and mountain hemlock all exhibited significant correlations

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.
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 ($Tsuga mertensiana$).

The correlations between radial growth and PDSI were generally stronger and more prevalent than all other variables (Fig. 5A and Table S1). 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 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). (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).
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). 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).

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), 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-

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.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>ABMA</th>
<th>PIAL</th>
<th>PICO</th>
<th>PIJE</th>
<th>PIMO</th>
<th>TSME</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Month</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Previous year</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>0.30*</td>
<td>0.42</td>
<td>-0.23</td>
<td></td>
<td>0.25</td>
<td>0.34</td>
</tr>
<tr>
<td>July</td>
<td>0.30</td>
<td>0.43</td>
<td>-0.23</td>
<td></td>
<td>0.25</td>
<td>0.35</td>
</tr>
<tr>
<td>August</td>
<td>0.37</td>
<td>0.44</td>
<td></td>
<td></td>
<td>0.24</td>
<td>0.38</td>
</tr>
<tr>
<td>September</td>
<td>0.42</td>
<td>0.49</td>
<td>0.31</td>
<td></td>
<td>0.32</td>
<td>0.39</td>
</tr>
<tr>
<td><strong>Current year</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>-0.25</td>
<td></td>
<td></td>
<td>-0.28</td>
<td>-0.35</td>
<td>-0.36</td>
</tr>
<tr>
<td>July</td>
<td>-0.27</td>
<td></td>
<td></td>
<td>-0.28</td>
<td>-0.37</td>
<td>-0.38</td>
</tr>
<tr>
<td>August</td>
<td>-0.27</td>
<td></td>
<td></td>
<td>-0.27</td>
<td>-0.35</td>
<td>-0.35</td>
</tr>
<tr>
<td>September</td>
<td>-0.28</td>
<td></td>
<td></td>
<td>-0.31</td>
<td>-0.38</td>
<td></td>
</tr>
</tbody>
</table>

Note: T1, 1901–1950; T2, 1951–2000.

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

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 photosynthetic 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 shunt-
photospahs 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 ap-
parent in our results suggests that growth response to future cli-
mate 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 re-
garding annual precipitation (Cayan et al. 2006; 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, even-
tually leading to death for certain species or certain sites, as
already shown for whitebark pine and limber pine (Pinus flexilis E.
decreased stem growth by 2100 using a model based on conifers
growing at middle elevations in the Sierra Nevada; increased sum-
mer temperatures drove this decrease for their four different cli-
mate 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 strength-
ening 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 eventu-
ally 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. 2005a). 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 macro-
climate 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 condi-
tions 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 tem-
peratures 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 comple-
mented by physiological data.

Conclusion

Radial growth of subalpine conifers of the central Sierra Nevada
2013 is closely tied to the balance of winter precipitation and summer
drought, as has been shown in other Mediterranean-type moun-
tains (Biondi 1993; Martin-Benito et al. 2013). Warm, dry condi-
tions 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. O819493, 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 Foun-
dation of UC-Davis, The Davis Botanical Society, Northern Califor-
nia Botanists, and the California Native Plant Society.

References

Abatzoglou J.T., Redmond, K.T., and Edwards, L.M. 2009. Classification of re-
gional climate variability in the state of California. J. Appl. Meteorol. Clima-

Alley, W.M. 1984. The Palmer drought severity index — limitations and assump-
023<1100:TPDSIL>2.0.CO.2.

2008. Climate change impacts on forest growth and tree mortality: a data-
driven modeling study in the mixed-conifer forest of the Sierra Nevada, Cali-

Bigler, C., and Bugmann, H. 2004. Predicting the time of tree death using den-

Bigger, C., Gricar, J., Bugmann, H., and Cufar, K. 2004. Growth patterns as indi-

Biondi, F. 1993. Climatic signals in tree-rings of Fagus sylvatica L. from the central

Biondi, F. 1997. Evolutionary and moving response functions in dendrochronol-
ygy. Dendrochronologia, 15: 139–150.

calibration of climate signals in tree-ring chronologies. Comput. Geosci. 30:

Bunn, A.G. 2008. A dendrochronology program library in R (dplR). Dendro-

tree growth at high elevations in the Sierra Nevada and White Mountains,

of growth in high elevation foxtail pine (Pinus halepensis Grev. et Balf.) forests


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.


