The Effects of Aridity on Conifer Radial Growth, Recruitment, and Mortality Patterns in The Eastern Sierra Nevada, California

Authors: Potito, Aaron P., and MacDonald, Glen M.

Source: Arctic, Antarctic, and Alpine Research, 40(1) : 129-139

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(05-080)[POTITO]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 40, No. 1, 2008, pp. 129–139

The Effects of Aridity on Conifer Radial Growth, Recruitment, and Mortality Patterns in the Eastern Sierra Nevada, California

Aaron P. Potito and*
Glen M. MacDonald†

*Corresponding author: Department of Geography, National University of Ireland, Galway, University Road, Galway, Ireland.
aaron.potito@nuigalway.ie
†Department of Geography, University of California, Los Angeles, 1255 Bunche Hall, Los Angeles, California 90095-1524, U.S.A.

Abstract

Understanding natural variability in precipitation and drought, and the resulting effects on Sierra Nevada forests, is crucial for successful resource management in this environmentally sensitive area of California. This study assessed the species-specific influence of precipitation variations on radial growth, recruitment, and mortality patterns for three conifer species (*Pinus jeffreyi*, *Juniperus occidentalis*, and *Pinus contorta*) in two mid-elevation lake catchments over the past 550 years. The *P. jeffreyi* chronology was the most highly correlated with winter precipitation patterns, although the other two species also exhibited significant correlations. Ring-width patterns suggest the influence of the Pacific Decadal Oscillation (PDO) and El Niño–Southern Oscillation (ENSO) on winter precipitation over the length of the records. Recruitment patterns displayed significant, though directionally distinct, correlations with winter drought: *P. contorta* exhibited increased recruitment during extended drought periods, while *P. jeffreyi* and *J. occidentalis* showed increased recruitment during wetter intervals. Finally, a ring of dead trees around both lakes is evidence of a late 20th century water level rise, likely caused by earlier snowmelt and/or wetter conditions. Moisture availability has exerted a strong influence on Sierra Nevada forests through time, but the strength of tree-growth response, and even the sign of tree population response, has been species-specific.

DOI: 10.1657/1523-0430(05-080)[POTITO]2.0.CO;2

Introduction

Instrumental climate records and observations over the past 100 years have highlighted the importance of water stress and the occurrence of significant annual to multi-annual droughts on the functioning of forest ecosystems in many parts of California, including the Sierra Nevada Mountains. Understanding the magnitude, frequency, and causal mechanisms of prolonged arid periods is essential not only for long-term water resources planning in California, but for management and conservation of Sierra Nevada forests. In addition to aiding in understanding the long-term development and functioning of present Sierra Nevada forests, this study will also offer a baseline for assessing and potentially managing the changes that might occur due to global warming over the next century.

Dendroclimatological and dendroecological studies provide a means of reconstructing variations in precipitation, as well as individual tree and population response to such changes, over several centuries. The goals of the study presented here were threefold. First, long-term ring-width records from three dominant conifer species typical of moisture stressed low to mid-elevation sites (Royce and Barbour, 2001) in the Sierra Nevada were used to determine species-specific growth trend responses to changes in effective moisture through time. Second, recruitment (establishment and survival) patterns for the three conifer species were compared to the above climate reconstruction to ascertain the impact of differences in moisture on recruitment patterns (North et al., 2005; Kitzberger et al., 2000; Swetnam and Betancourt, 1998; Szeicz and MacDonald, 1995). Finally, an apparently climate-induced mortality event, evidenced by drowned tree snags around at least four lakes in the study region, was dated and its causal mechanisms investigated.

Study Sites

This study is concentrated within two small, mid-elevation lake catchments along the eastern slope of the Sierra Nevada (Fig. 1). The catchments are situated within mixed forest ecosystems just west of the Great Basin/lower montane boundary, and receive approximately 75 cm of precipitation annually (Leavitt Meadows SnoTel station; http://www.wcc.nrcs.usda.gov/snotel). The Roosevelt Lake catchment (2213 m above sea level [a.s.l.] at the lakeside) is dominated by *Pinus jeffreyi* Graf. and Balf. (Jeffrey pine) forest, although open *Juniperus occidentalis* Hook. (western juniper) woodland and some *Pinus contorta* Louden (lodgepole pine) are also present. The Hidden Lake catchment (2379 m a.s.l. at the lakeside) is dominated by *P. contorta* forest on the north-facing slopes and open *J. occidentalis* woodland and mixed *J. occidentalis* and *P. jeffreyi* forest on the south-facing slopes and ridge tops. Hidden Lake also has a dense, young *P. contorta* stand surrounding the immediate lakeside, likely due to enhanced recruitment of shade-intolerant *P. contorta* following a recent mortality event of lakeside trees. Soils in this area are gravelly loamy coarse sand to fine sandy loam, and soil conditions are patchy (Blake, 2006). Deeper soils (30–40 cm) with higher nutrient and water-holding capacity are found in flatter areas within the lake basins, while shallower (10–20 cm) and sandier soils are found along the ridgetops and on steeper slopes.

The Sierra Nevada receives the bulk of its precipitation as winter snowfall, when the polar front shifts southward resulting in the

1523-0430/08 $7.00

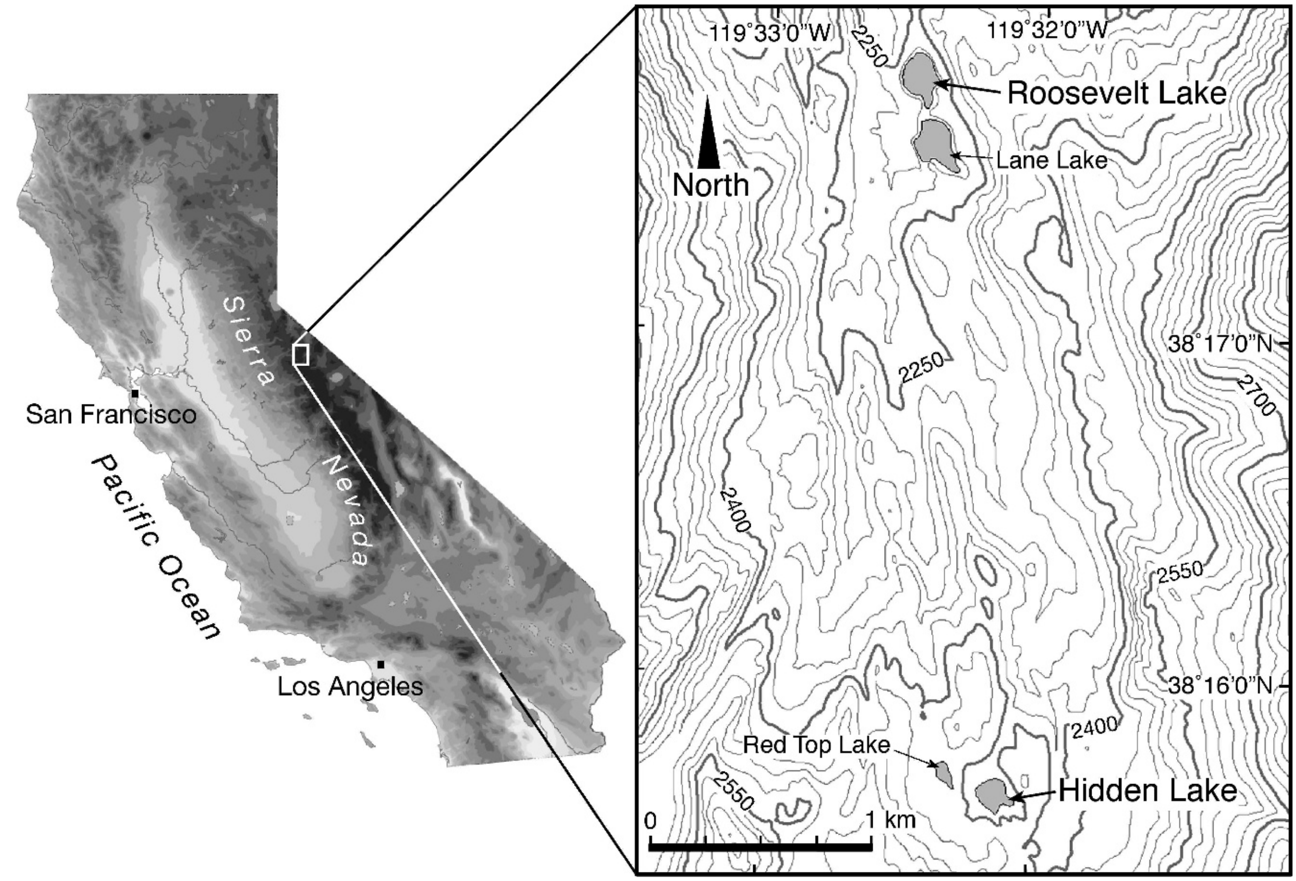

FIGURE 1. Map of study sites. Contour interval = 30 m.

movement of cyclonic storms into California (Raphael and Mills, 1996). A major organizing force on winter snowpack variability in the Sierra Nevada and the western United States during the last 200+ years has been the Pacific Decadal Oscillation (PDO) (Biondi et al., 2001; Gedalof and Smith, 2001; Millar et al., 2004; MacDonald and Case, 2005), with El Niño–Southern Oscillation (ENSO) also exhibiting an influence on precipitation at the annual to multi-annual time scales (Latif and Barnett, 1994). It is the influence of these annual to multi-decadal variations in the winter precipitation regime, driven by PDO and ENSO among other factors, and their effects on forest dynamics that were investigated in this study.

Methodology

Field data were collected in three phases. First, two cores were extracted from 30 of the oldest trees of each conifer species: *P. jeffreyi*, *P. contorta*, and *J. occidentalis*. Second, to assess the local forest structure presently surrounding the lakes, a sampling of all-aged trees within each catchment were systematically cored along transects radiating away from each lake at every 45° angle from north (total of 8 transects per catchment) using the point-centered quarter method (Bonham, 1989; Mitchell, 2001). Finally, there was a ring of drowned snags lining the shores of at least four lakes in the region: Hidden Lake, Roosevelt Lake, Red Top Lake, and Lane Lake (Fig. 1). The least rotted of the dead trees were cored or cross-sectioned, and 30 cross-datable series were obtained to accurately date the occurrence of this recent lake level rise. Several fire scars were obtained from dead trees around the four lakes to aid in reconstructing fire events.

Tree cores were collected using a standard increment borer, and cross sections were obtained using handsaws. Standard procedures were used in preparing tree ring cores and disks for analysis (Stokes and Smiley, 1968; Fritts, 1976). Ring widths were measured to a 0.001-mm accuracy using a Velmex Unislide traversing table and an AcuRite III digital counter and computer. Cross-dating of dead and living trees was performed using the skeleton plot method (Stokes and Smiley, 1968). A computer-assisted program, COFECHA (Holmes, 1986), was used in support of cross-dating.

TREE RING–WIDTH CLIMATE RECONSTRUCTION

Tree cores for climate reconstruction were taken at breast height, with replicate cores extracted from opposite sides of trees. These trees were mainly located along ridges surrounding the catchments and rock outcrops within the catchments. Identification of old trees relied on branch width, needle loss in the upper portion of the trees, and tree size. Cross-dating for long chronologies was completed using a 32-year cubic smoothing spline with a 50% wavelength cutoff for filtering. To maximize the common signal within each chronology, only the most highly inter-correlated radii were retained, and complacent tree ring records (showing benign growth sites or an invariable limiting growth factor) were discarded (Biondi, 2001). Detrending of growth variations associated with age was accomplished using ARSTAN software (Holmes, 1992). Each series was detrended using a negative exponential curve, a linear regression line of negative slope, or a horizontal line through the mean. This detrending method is relatively conservative and was used to preserve low frequency, climate-related trends in the chronology (Cook et al., 1995).

The standard chronologies were correlated with monthly values of mean temperature, total precipitation, and the mean

Palmer Drought Severity Index (PDSI; Palmer, 1965) for California Climate Division 3 (Great Basin; http://www.ncdc.noaa.gov). Pearson correlation coefficients were calculated for the interval of overlap (1895–2002) between the standardized chronologies and the monthly instrumental data for the 16-month interval beginning June of the previous year and ending September of each growth year (Blasing et al., 1981).

After it was determined that California Climate Division 3 winter PDSI was the best predictor of annual changes in the ring-width series (see **Results** section), the monthly PDSI indices were used to run a principal components analysis (PCA) and stepwise regression to form a transfer function to predict ring-width measurements. For a thorough review of the PCA and stepwise regression techniques used for this study see Hidalgo et al. (2000). The resulting best-fit model was applied to tree ring–width variations that predate station records, establishing a long-term winter PDSI reconstruction.

The reconstruction was run through a Morlet wavelet analysis to determine the dominant modes of variability within the time series and how those modes vary through time (Torrence and Compo, 1998). This analysis offered information on the dominant periodicities within the record, and can indicate the underlying causal mechanisms by highlighting patterns of variation (Gray et al., 2003). Finally, tree ring chronologies were correlated to a 400-year record of reconstructed North Pacific PDO (Biondi et al., 2001) to assess if the reconstructions are capturing regional PDO patterns.

TRANSECT DATA

Each transect was begun 5 m from the lakeside, so as not to leave empty quadrants at the first sampling point. Along each 100-m transect, there were six sampling points spaced 20 m apart (from Bonham, 1989). At each point, the area around the point was divided into four 90° quadrants, the tree closest to the point in each quadrant was identified and cored, and distance from node was measured. In addition, the nearest stand-dominant tree, as determined by species, tree height in relation to canopy, and surrounding trees, was identified and cored to ensure that a representative sample of dominant trees was studied. Trees were cored or cross-sectioned as close to the ground as possible, usually within 20 to 30 cm of ground level for larger trees and at ground level for seedlings and small saplings. If coring missed the pith, the number of rings to the pith was estimated geometrically (Baker, 1992). Ring-width series were cross-dated with the master chronologies where possible. A correction was made for time to coring height by determining the age of a representative 20- to 30-cm seedling at each site. There were 5 years added to *P. contorta* and *P. jeffreyi* ages, and 9 years added to *J. occidentalis* ages.

Age structure data were aggregated into 5-year age classes, and histograms were constructed for each of the three dominant species. Age structure histograms were further separated by lake catchment and proximity to lakeside (mostly to account for recent lakeside recruitment). The resulting histograms were compared to two models that have commonly been used to depict the age structure of tree populations: the exponential function (constant natality and mortality) and the power function (constant natality) (Hett and Loucks, 1976; Légère and Payette, 1981). As the exponential function consistently displayed a higher significance level when compared with the histograms, this model was used for the remainder of the study.

Deviations of the actual age structures from the modeled exponential curves were used to reflect deviations from the expected constant rates in recruitment over time (Ågren and Zackrisson, 1990; Szeicz and MacDonald, 1995). When constructing the age structure models, the oldest 2% of the individuals in each histogram were eliminated to avoid the disproportional influence of outliers on the age model. Furthermore, a value of 1 was added to each age class to permit inclusion of empty age classes in the model (Szeicz and MacDonald, 1995).

Statistical relationships between recruitment and winter PDSI were tested by calculating Pearson correlation coefficients between the above residuals and the aforementioned reconstruction of winter PDSI (averaged over 5-year intervals to correspond with age classes). The local reconstruction was used over regional climate indicators as it represents a local manifestation of regional climate signals. Since age class patterns are partially determined by post-establishment mortality, particularly when young (Kozlowski et al., 1991), recruitment residuals may show a significant relationship with PDSI for a period following establishment. To test this, aggregated PDSI data were averaged forward in time (10-, 15-, 20-, and 25-year aggregates). Pearson correlation coefficients were then calculated between recruitment residuals and each of these forward mean classes.

LAKESIDE MORTALITY EVENT

Cross-dating of lakeside snags, mostly *P. contorta*, with a tree ring chronology from living trees proved problematic, as dry years might not result in narrow rings along the lakeside. Four steps were taken to overcome these cross-dating difficulties. First, the general timing of the mortality event was determined by comparing the decay state of the lakeside snags with an existing snag decay model for *P. contorta* in the eastern Sierra Nevada (Raphael and Morrison, 1987; Morrison and Raphael, 1993). Second, living lakeside species were grouped into 5-year age classes and a histogram was constructed to determine when the bulk of young, shade-intolerant *P. contorta* (Bartolome, 1983) seedlings and saplings established themselves along the lakeside. Third, lakeside ring-width series were cross-dated with each other using the skeleton plot method and COFECHA (non-splined) to obtain a fully cross-dated floating dead tree chronology (Holmes, 1986). Finally, this chronology was matched with several old living trees using fire scars and marker rings to determine exact dates of the mortality event.

Results

TREE RING–WIDTH CHRONOLOGIES

After eliminating complacent records, rotted cores, and those cores that were not cross-datable, there were 25 trees and 49 ring-width series from *P. contorta*, 26 trees and 44 ring-width series from *P. jeffreyi*, and 20 trees and 33 ring-width series from *J. occidentalis* (Table 1). Although the oldest trees date back further, only the statistically viable portions of the tree ring chronologies (those with a subsample signal strength [SSS] of ≥0.75; Wigley et al. 1984) were used for analysis in this study. Series intercorrelation is at similar levels for all three species, although intercorrelation was highest for *J. occidentalis*.

Although all three standardized chronologies tend to follow each other closely over the past 200 years, the *J. occidentalis* and *P. jeffreyi* chronologies follow less closely prior to 1750 (Fig. 2a). During this time, the *J. occidentalis* chronology becomes unstable, as seen by the increasing sample-size-adjusted (Osborn et al., 1997) 30-year standard deviation (Fig. 2b). The *P. jeffreyi* chronology regularly exhibited higher correlations with monthly indicators

TABLE 1

(A) ARSTAN chronology statistics. SSS = subsample signal strength. (B) Statistics for best fit regression for the winter Palmer Drought Severity Index (PDSI) reconstruction using the standardized *P. jeffreyi* ring-width chronology. CVSE = cross-validation standard error.

A.

Chronology statistic	*P. contorta*	*P. jeffreyi*	*J. occidentalis*
Total # of trees	25	26	20
Total # of series	49	44	33
Oldest sampled tree (yrs)	328	579	712
Full chronology interval	1674–2002	1423–2002	1290–2002
Chronology interval (SSS ≥ 0.75)	1800–2002	1482–2002	1450–2002
# of trees/radii to reach SSS threshold	4/5	5/6	3/4
Series intercorrelation	0.246	0.227	0.288
Mean sensitivity	0.108	0.141	0.204
Standard deviation	0.131	0.164	0.252
First order autocorrelation	0.452	0.422	0.511

B.

Best Fit Regression:

$(\text{Oct–Feb PDSI}) = 0.0037031(\text{PJ-std}) + 0.0028885(\text{PJ-std})_{t-1} - 9.9588$

Where **Oct–Feb PDSI** = averaged monthly PDSI from winter prior to growing season and **PJ-std** = standardized *P. jeffreyi* chronology

$R^2_{adj} = 0.3360^{**}$
CVSE = 0.1733

** $p \leq 0.01$.

than the *J. occidentalis* chronology (monthly correlations not shown here). The *P. jeffreyi* chronology also showed higher monthly correlations with PDSI than with temperature or precipitation. Furthermore, PDSI records from the winter prior to the growth season exhibited the highest correlation with *P. jeffreyi* ring width. Therefore, the standardized *P. jeffreyi* chronology was used to reconstruct winter (October to February) PDSI for California Climate Division 3 from 1482 to 2002.

The observed and estimated PDSI data follow each other closely, as the model captured year-to-year changes and general trends in the instrumental data (Fig. 3). Through Morlet wavelet analysis, the reconstructed winter PDSI chronology shows variability similar to ENSO frequencies, exhibited both by the significant contour lines between 4 and 8 years periodicity in the wavelet power spectrum (Fig. 4a) and the small but significant spike in the global wavelet centered at ~7 years periodicity (Fig. 4c) (Diaz and Markgraf, 2000). There is also a 60–80 year periodicity from the mid-1700s to the end of the record that is marked by darker colors in the wavelet power spectrum (Fig. 4b) and a peak in the global wavelet centered at ~70 years (Fig. 4c). The 10% significance contour line (as used by Gray et al., 2003) shows that this signal was strongest from the mid-1800s to the mid-1900s.

The standardized *P. jeffreyi* chronology is significantly correlated with a 400-year reconstructed North Pacific PDO record (Fig. 5; Biondi et al., 2001; Pearson correlation coefficient = 0.208, $p \leq 0.001$), and even more highly correlated with the PDO record after 1750 (0.223, $p \leq 0.001$). Radial growth trends in *J. occidentalis* are also significantly correlated to the PDO through the entire record (0.142, $p \leq 0.01$) and after 1750 (0.139, $p \leq 0.01$). Growth trends for *P. contorta* are not significantly correlated to the PDO. None of the chronologies exhibited a direct correlation with ENSO through time.

RECRUITMENT PATTERNS

Recruitment of the living *P. contorta* trees showed an increase in successful establishment from 1840, and a peak in establishment from 1970 to 2000 (Fig. 6a). The residuals from the entire catchment exhibit a greater dip in recruitment during the early 20th century, and a spike in recruitment during the 1990s (Fig. 6b). The residuals from the entire catchment model generally have a negative correlation with reconstructed winter PDSI, with a significant correlation for the 20- and 25-year forwarded averages (Table 2). The relationship between *P. contorta* recruitment patterns and winter PDSI was weak away from the lakeside.

Recruitment of living *J. occidentalis* showed an increase in successful establishment starting ca. 1850, with a subsequent increase in recruitment beginning ca. 1940 (Fig. 6a). The residuals for each model exhibit decreased recruitment during the mid-1800s and the 1930s and increased recruitment during the 1940s and 1970s (Fig. 6b). Residuals for the entire catchment also show a spike in recruitment during the late 20th century. The residuals from the models show a positive correlation with reconstructed winter PDSI, with a significant correlation for the 15-, 20-, and 25-year forwarded averages for both models (Table 2).

The *P. jeffreyi* histograms were subdivided by lake catchment, as the lake catchments exhibited differing age structure patterns. Recruitment patterns of living *P. jeffreyi* showed an increase in successful establishment at 1900 for both lake catchments (Fig. 6a). The Hidden Lake catchment also exhibited a secondary recruitment spike during the 1960s and 1970s. Hidden Lake residuals showed a depression in recruitment from the 1930s to the 1950s, while the Roosevelt Lake residuals showed an increased recruitment during this time (Fig. 6b). Recruitment patterns in the Hidden Lake catchment displayed a significant positive correlation with reconstructed winter PDSI for the 10-, 15-, 20-, and 25-year forwarded climate averages away from the lakeside, and for the 10- and 15-year forwarded averages away for the entire catchment (Table 2). There were no significant correlations within the Roosevelt Lake catchment.

LAKESIDE MORTALITY EVENT

On average the dead snags along the shoreline of area lakes exhibit mostly decay stage 4 and stage 5 characteristics (absent needles, absent twigs, 1–19 limbs) within the snag decay model

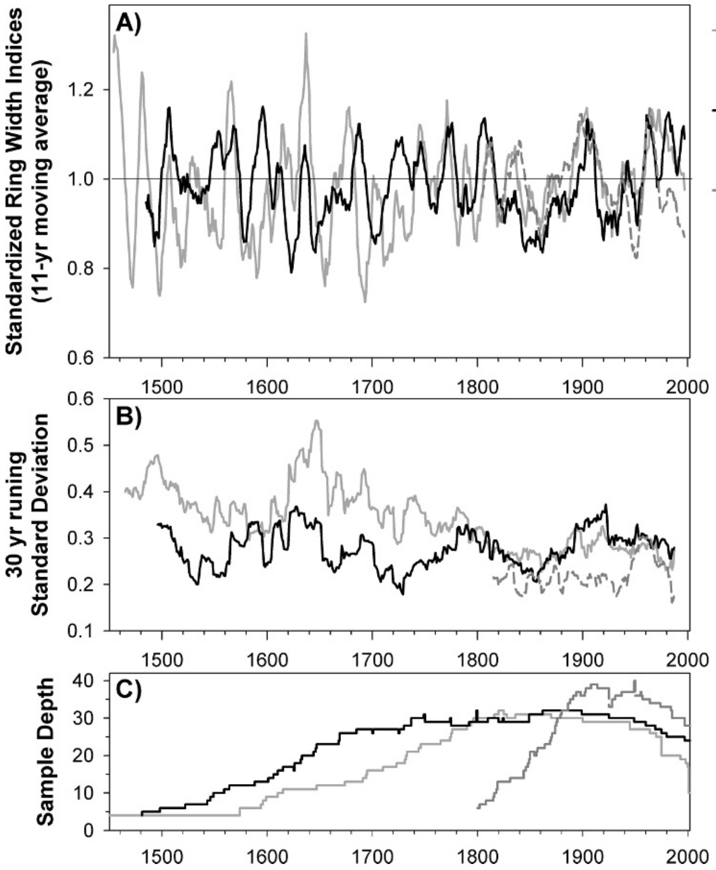

FIGURE 2. (A) 11-year running average standard chronology for each species. (B) 30-year running standard deviations for the chronologies. Variance was adjusted for sample size (Osborn et al., 1997). (C) Sample depth for standard chronologies.

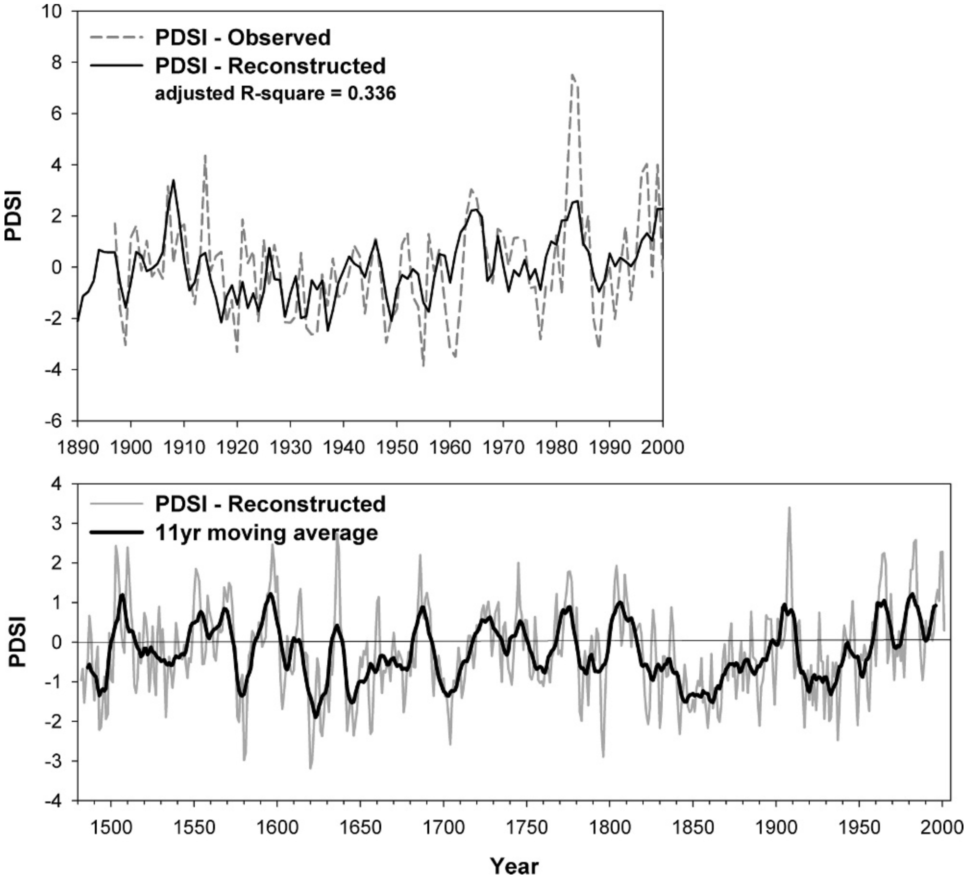

FIGURE 3. Reconstructed October to February Palmer Drought Severity Index (PDSI) using standardized *P. jeffreyi* chronology. (A) Reconstructed versus observed PDSI (1895–2002). (B) Reconstructed winter PDSI with an 11-year moving average.

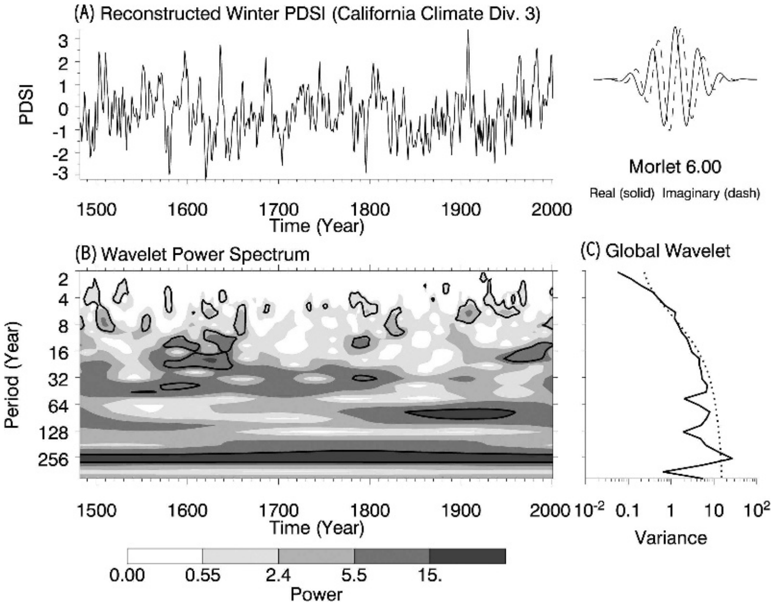

FIGURE 4. (A) Reconstructed winter PDSI. (B) The Morlet 6.00 wavelet power spectrum. The contour levels are chosen such that 75%, 50%, 25%, and 5% of the wavelet power is above each level, respectively. Black contour is the 10% significance level, using a red-noise (autoregressive lag1) background spectrum. (C) The global wavelet power spectrum (black line). The dashed line is the significance for the global wavelet spectrum, assuming the same significance level and background spectrum as in (B).

designed by Raphael and Morrison (1987). As these trees were likely killed by water immersion and are mostly 20 to 50 cm diameter, it is likely that the snags decayed to stage 4 within 10–20 years and to stage 5 by 20–30 years. After they reach these decay stages, they can remain standing for 20–30 years (Raphael and Morrison, 1987; Morrison and Raphael, 1993), placing the mortality event at some point in the latter half of the 20th century. Living tree recruitment at the lakeside nodes offers a clearer picture of when this event likely occurred. Successful recruitment began in the 1950s (Fig. 7). Recruitment increased by ca. 1970, especially for shade-intolerant *P. contorta* seedlings (Bartolome, 1983). Recruitment of *P. contorta* again increased by 1980.

The series intercorrelation for the cross-dated dead tree COFECHA chronology was 0.354 ($p \leq 0.01$), and mean sensitivity was 0.234 using 31 of the most well-preserved series. Using marker rings and fire scars, this floating chronology was matched with several living trees to place the mortality event between 1952 and 1978 (Fig. 7). The snags do not show a clear pattern in recruitment date.

Discussion

RING-WIDTH CHRONOLOGY

The *P. jeffreyi* ring-width chronology was favored over the *J. occidentalis* chronology for climate reconstruction for a number of reasons. The *P. jeffreyi* chronology regularly exhibited higher correlations with all climate variables. Furthermore, the *J. occidentalis* chronology became unstable toward the beginning of the record (Fig. 2b). As the record becomes older, sample-size-adjusted 30-year running standard deviation creeps upward and the chronology becomes less stable. Finally, *J. occidentalis* ring-

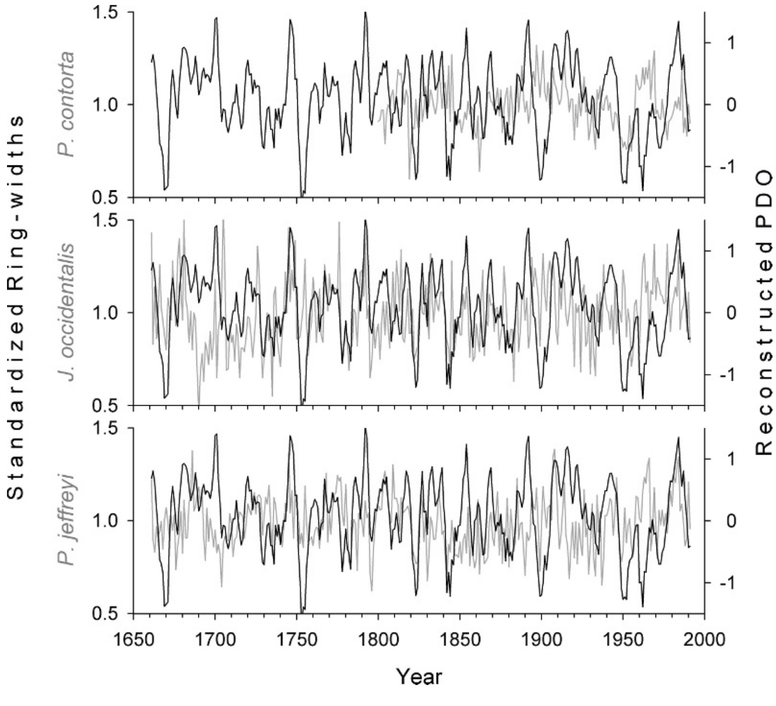

FIGURE 5. Comparison of reconstructed North Pacific Decadal Oscillation (PDO) (black; Biondi et al., 2001) and standard tree ring chronologies (gray). Graphs cover the time span of reconstructed PDO (1661–1991).

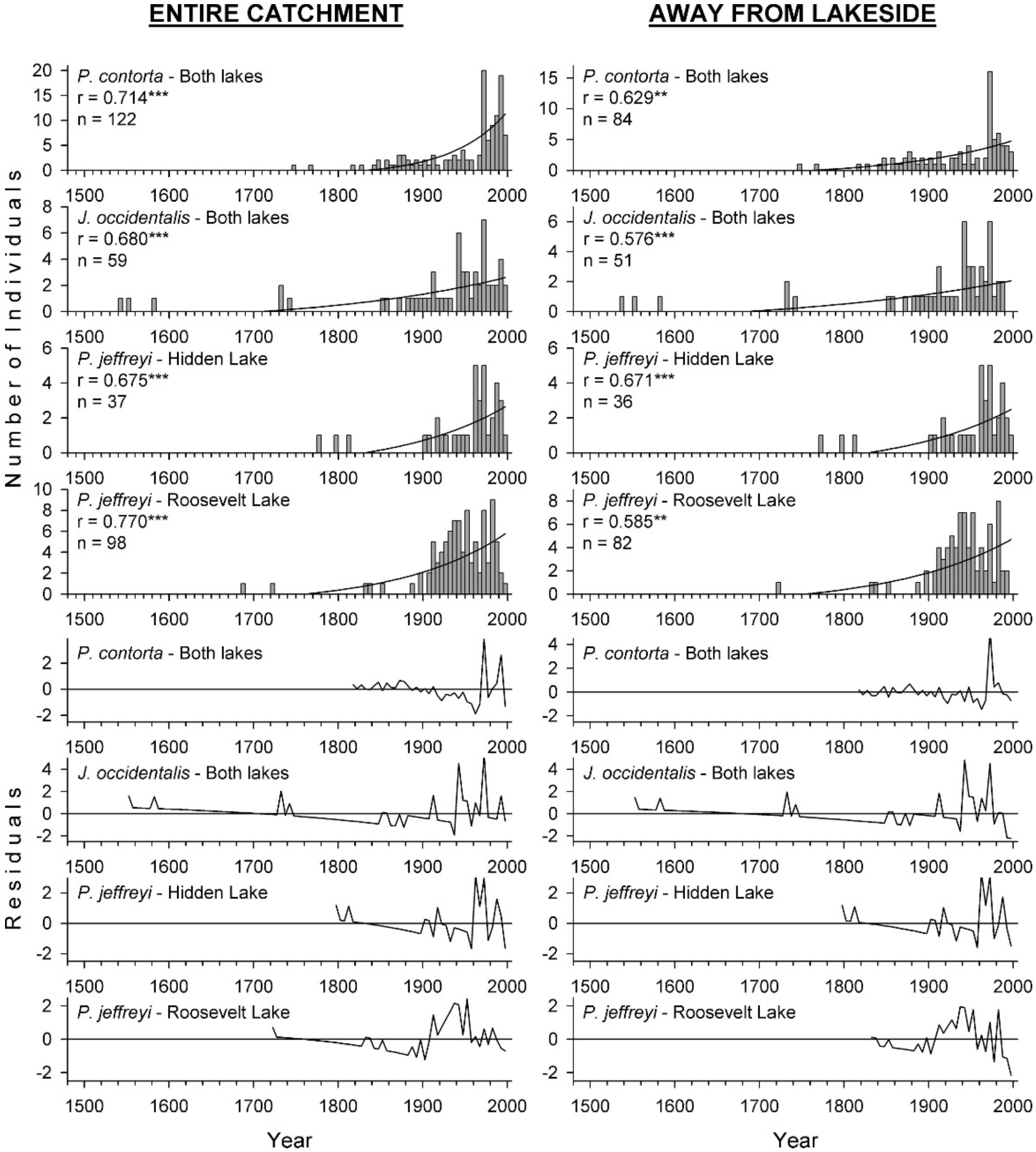

FIGURE 6. Recruitment patterns compared to the winter PDSI reconstruction. Figure shows 5-year age groups for the entire catchment, as well as 5-year age groups for those nodes away from the lakesides. (A) Age structure histograms and the corresponding exponential model to predict age structure given constant mortality and recruitment. (B) Standardized residuals from the exponential model. ** $p \leq 0.01$, *** $p \leq 0.001$.

width series are known to be a poor predictor of climate patterns, as their annual growth can be heavily influenced by other factors (Grissino-Mayer et al., 1997).

The *P. jeffreyi* ring-width chronology proved to be a good predictor of PDSI values for the previous winter (October to February). However, annual ring growth patterns only accounted for 33.6% of the variance in the winter PDSI reconstruction, meaning that other factors also influence radial growth, and the reconstruction is prone to some uncertainty. These confounding influences include other climatic factors, fire, pathogens, competition while in the understory, and possible human impacts (McBride, 1988). Furthermore, typical of many dendroclimatic reconstructions, the tree-ring model does not capture the full amplitude of annual variations (Loaiciga et al., 1993).

Although the *P. jeffreyi* ring-width series only explains a third of the variation in winter PDSI, the reconstruction can be used to ascertain intervals of large or persistent droughts over the past 520 years. There were substantial droughts in the record centered at ca. 1490, ca. 1580, ca. 1620, ca. 1645, ca. 1700, mid 1800s, and the 1930s, with lesser droughts from 1510 to 1545, the late 1750s, and 1780–1800. The drought in the late 16th century generally coincides with a mega-drought that has been recorded in tree ring records over much of North America (Stahle et al., 2000). Other major droughts in the record coincide with the lowest flows in a tree ring–based Sacramento River flow reconstruction (e.g. 1580s, 1650s, 1840s, and 1930s) (Meko et al., 2001). Correlation with this record is 0.225 (Pearson correlation coefficient; $p \leq 0.01$). The reconstruction also matches some general trends of the bristlecone pine precipitation reconstruction from the White Mountains in eastern California and western Nevada: a prolonged drought during the first half of the 16th century, a more intense drought centered at ca. 1580, a highly fluctuating record through most of the 18th century, and a dry interval during the 1930s (Pearson correlation coefficient = 0.100, $p \leq 0.05$; Hughes and Graumlich, 1996). Finally, the reconstruction correlates (Pearson correlation coefficient = 0.247, $p \leq 0.001$) with the nearest grid-point (37.5°N, 120°W) of a 2000-yr tree ring reconstructed summer PDSI record (Cook et al., 2004) when the summer PDSI record is lagged one year.

As the wavelet analysis has shown, the chronology has both a ~7 year periodicity throughout the record and a 60–80 year periodicity after ca. 1750. This could be due to the influence of both ENSO and PDO on winter precipitation in the region. The PDO has been shown to have a frequency domain of 60 to 70 years starting at 1650 (Mann et al., 1995), with a stronger signal along western North American beginning in the late 1700s (MacDonald and Case, 2005; Benson et al., 2003; Gedalof et al., 2002; Gedalof and Smith, 2001; Biondi et al., 2001). Although ENSO exerts an influence on winter PDSI through the reconstruction, the PDO has been shown to have an overarching influence on ENSO patterns for the multi-decadal to century time scales (McCabe and Dettinger, 1999). This is supported by the significant correlation of the *P. jeffreyi* and *J. occidentalis* chronologies with long-term PDO values. The lack of correlation with ENSO could be due to the overriding influence of the PDO in the region, or to local stand dynamics dampening the signal.

TABLE 2

Pearson correlation coefficients between recruitment residuals from exponential modeling and reconstructed PDSI.

	Pearson Correlations	
Climate averaging	Entire catchment	Away from lakeside
P. contorta (both lakes)		
5-year	–0.189	–0.038
10-year	–0.267	–0.028
15-year	–0.245	0.121
20-year	–0.290*	0.123
25-year	–0.331*	0.071
J. occidentalis (both lakes)		
5-year	0.154	0.131
10-year	0.167	0.133
15-year	0.186*	0.192*
20-year	0.253**	0.264**
25-year	0.286**	0.300**
P. jeffreyi (Hidden Lake)		
5-year	0.179	0.189
10-year	0.334*	0.329*
15-year	0.315*	0.334*
20-year	0.266	0.286*
25-year	0.273	0.295*
P. jeffreyi (Roosevelt Lake)		
5-year	0.120	0.063
10-year	0.090	–0.020
15-year	0.176	0.054
20-year	0.181	0.102
25-year	0.159	0.044

$*p \leq 0.05$, $**p \leq 0.01$.

RECRUITMENT PATTERNS

Although it has been shown that recruitment patterns in this area are influenced by variations in winter PDSI, this is not the only controlling factor in determining establishment and survival of the three conifers. Competition in the more dense stands can

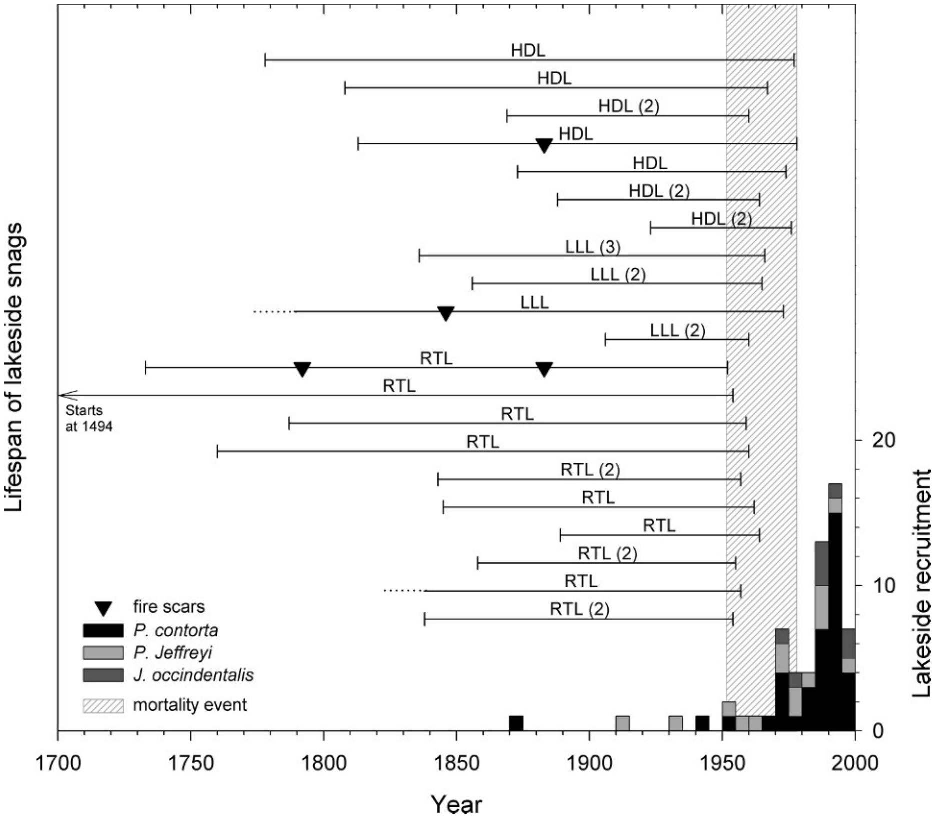

FIGURE 7. Mortality patterns for dead trees around the lake edges. Length of horizontal lines show lifespan of trees. Dashed lines indicate rotted tree core and uncertain recruitment date. Numbers in parentheses indicate whether more than one radius was measured from each tree. Histogram shows 5-year age classes of living trees at lakeside nodes using combined Roosevelt Lake and Hidden Lake catchment populations. (HDL = Hidden Lake, RTL = Red Top Lake, LLL = Lane Lake).

lower the variance of the recruitment/climate correlations. This is especially true in the dense *P. contorta* and closed canopy *P. jeffreyi* stands, where shade-intolerant species recruitment can be thwarted during times when climate is otherwise conducive to survival (Bartolome, 1983). Insect outbreaks and fire can also have a large influence on recruitment and survival of each species (Laudenslayer, 1988; McBride, 1988; Bartolome, 1988). Finally, other climate factors including summer heat and spring rains may influence recruitment patterns (Laudenslayer, 1988). Given all of this possible dampening of the recruitment residuals versus winter PDSI correlation, many relationships still proved significant.

The recruitment patterns of *P. contorta* have an inverse correlation with winter PDSI, so that this species shows positive pulses in recruitment during extended time intervals (15 to 25 years) with dry winters. This may be because *P. contorta* thrives after fire, which can be promoted during extended dry climatic interludes (Critchfield, 1980). It may also be because *P. contorta* is mostly found on flat land and poorly drained soils within the catchments, and would thus benefit from more favorable moisture conditions during droughts than those species that are found on more open slopes.

The recruitment patterns of *J. occidentalis* showed a strong positive correlation with winter PDSI. Because *J. occidentalis* is mostly found on dry open slopes within the lake catchments, water is likely the limiting factor to their survival (Royce and Barbour, 2001). Thus, during persistently wetter conditions, this species shows a pulse in hillside recruitment. Additionally, they do not compete well when in close association with other conifers (Grissino-Mayer et al., 1997). Therefore, young *J. occidentalis* that are found within the *P. contorta* forest around Hidden Lake may be out-competed during dry periods.

As with *J. occidentalis*, *P. jeffreyi* recruitment showed a positive correlation with winter PDSI within the Hidden Lake catchment. All but one of the *P. jeffreyi* in the Hidden Lake catchment are on south-facing slopes, and may thus be under more water stress than those that surround Roosevelt Lake. However, when the Roosevelt Lake population was separated by slope aspect, there was no discernable pattern for the south-facing slope. Intraspecific competition may be dampening the signal in this catchment, as most of the trees on the south-facing slope are in a dense, closed-canopy *P. jeffreyi* stand. As with the closed-canopy *P. contorta* stand at Hidden Lake, these trees may be benefiting from poorly drained soil.

LAKESIDE MORTALITY EVENT

Timing of mortality was dependent upon the lake catchment. Trees surrounding Red Top Lake died the earliest (1952–1964), as this is a small, shallow lake that likely overflowed more easily than the other lakes. Trees at Lane Lake died in the middle of this event (1960–1973), and mortality occurred around Hidden Lake during the later part of this event (1960–1978). No dead trees from Roosevelt Lake were preserved well enough for accurate dating, due to tree clearing for recreational users.

The mortality event that occurred along the shores of area lakes between 1952 and 1978 may be related to early snowmelt over much of the western United States and Canada during the last 50 years. Wilby and Dettinger (2000) have shown that in the Sierra Nevada, earlier rains on warmer snowpack could result in more flooding events dependent on the shape of the water basin. This earlier snowmelt could be due to global warming (Mote, 2003; Stewart et al., 2004) or natural climate variability, including the PDO (Cayan et al., 2001, 2004). The mortality event could also be due to generally wetter conditions in the Sierra Nevada after the 1930s (Haston and Michaelsen, 1994; Graumlich, 1993). These dead trees are likely still becoming inundated with water annually or during wetter years, evidenced by watermarks on all of the snags and hydrophytic vegetation around the snags' bases. *P. contorta* (the dominant lakeside snag species) can survive short intervals in waterlogged conditions, but has been shown to suffer in a more consistently waterlogged environment (Coutts and Philipson, 1978). Finally, since snags do not exhibit any discernable pattern in recruitment date, the sites were likely conducive to tree establishment for many years (from at least the mid-19th century) until the 1950–1978 mortality event.

Conclusions

The *P. jeffreyi* reconstruction has proven to be a good measure of winter PDSI, and has succeeded in showing known drought events, as well as other drought events, through the last 520 years. The periodicity of the drought events and correlation with a 400-year North Pacific PDO reconstruction show that winter PDSI is influenced by both PDO and ENSO through most of the reconstruction. *J. occidentalis* did not prove to be a good measure of climate phenomena (Grissino-Mayer et al., 1997), and *P. contorta* did not possess a long enough record for a useful climate reconstruction. Therefore, it is recommended that *P. jeffreyi* be used for climate reconstructions in low-elevation sites along the eastern Sierra Nevada where possible. Although there are other longer climate reconstructions in the region, this model succeeds in teasing out species-specific responses to moisture stress through time. In addition, most longer reconstructions are from high-altitude regions where the impacts of temperature and moisture can confound interpretation (Scuderi, 1993; Graumlich, 1993; Lloyd and Graumlich, 1997).

Given all of the possible confounding factors that could weaken the climate signal in recruitment patterns, all three tree species showed some correlation with multi-decadal winter PDSI patterns. This is likely due to the moisture-stressed location of the study site—lower elevation, on the eastern slope of the Sierra Nevada near the Great Basin boundary. *J. occidentalis* from both catchments and *P. jeffreyi* from one of the lake catchments showed positive pulses in recruitment with persistently high winter moisture. Conversely, *P. contorta* showed positive pulses in recruitment during prolonged multi-decadal droughts. The differing responses of each species to winter PDSI patterns could provide range managers with the data needed to predict long-term ecosystem response to global climate change. However, more work needs to be done to determine the effects of other factors on species-specific recruitment.

Finally, area lakes seem to have undergone a fundamental shift to higher maximum levels beginning ca. 1950. The lake level rise, as evidenced by a ring of dead standing trees around area lakes, could be from warmer winters and earlier snowmelt due to global warming. This mortality event may be an early impact of global warming and changing hydrological conditions in the Sierra Nevada. The results of all three aspects of this study suggest that moisture availability has been a critical and relatively variable factor that has exerted a strong influence on Sierra Nevada forest pattern and process through time.

Acknowledgments

This research was conducted in the Toiyabe National Forest. We would like to thank everybody at the Bridgeport Ranger

Station, Bridgeport, California, for their assistance in conducting this study. We would also like to thank Valerie Ledwith, Kevin McDonald, David Porinchu, Paul Richardson, and Joanne Situ for their help with field and laboratory research. Funding for this research was provided by National Science Foundation, Geography and Regional Sciences (Grant no. BCS-0135748 and BCS-9905350).

References Cited

Ågren, J., and Zackrisson, O., 1990: Age and size structure of *Pinus sylvestris* populations on mires in central and northern Sweden. *Journal of Ecology*, 78: 1049–1062.

Baker, W. L., 1992: Structure, disturbance, and change in the bristlecone pine forests of Colorado, U.S.A. *Arctic and Alpine Research*, 24: 17–26.

Bartolome, J. W., 1983: Overstory-understory relationships: lodgepole pine forest. *In* Bartlett, E. T., and Betters, D. R. (eds.), *Overstory-Understory Relationships in Western Forests*. Ft. Collins, Colorado: Colorado State University, Western Regional Resources Publication No. 1: 1–4.

Bartolome, J. W., 2002: Lodgepole pine. *In* Mayer, K. E., and Laudenslayer, W. F., Jr. (eds.), *A Guide to Wildlife Habitats of California*. Sacramento: California Department of Forestry and Fire Protection, 44–45.

Benson, L., Linsley, B., Smoot, J., Mensing, S., Lund, S., Stine, S., and Sarna-Wojcicki, A., 2003: Influence of the Pacific Decadal Oscillation on the climate of the Sierra Nevada, California and Nevada. *Quaternary Research*, 59: 151–159.

Biondi, F., 2001: A 400-year tree-ring chronology from the tropical treeline of North America. *AMBIO: A Journal of the Human Environment*, 30(3): 162–166.

Biondi, F., Gershunov, A., and Cayan, D. R., 2001: North Pacific decadal climate variability since 1661. *Journal of Climate*, 14: 5–10.

Blake, E. W., 2006: *Soil Survey of Toiyabe National Forest Area, California*. United States Department of Agriculture: Washington, D.C.: Natural Resources Conservation Service.

Blasing, T. J., Duvick, D. N., and West, D. C., 1981: Dendroclimatic calibration and verification using regionally averaged and single station precipitation data. *Tree-Ring Bulletin*, 41: 37–43.

Bonham, C. D., 1989: *Measurements of Terrestrial Vegetation*. New York: John Wiley and Sons, 159–164.

Cayan, D. R., Kammerdiener, S., Dettinger, M. D., Caprio, J. M., and Peterson, D. H., 2001: Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society*, 82: 399–415.

Cayan, D. R., Stewart, I. T., and Dettinger, M. D., 2004: Earlier snowmelt streamflow in western North America—A response to Pacific decadal variability or climate change? *Eos Transactions*, AGU 85(47), Fall Meeting Supplement, Abstract H24B-05.

Cook, E. R., Briffa, K. R., Meko, D. M., Graybill, D. A., and Funkhouser, G., 1995: The 'segment length curse' in long tree-ring chronology development for paleoclimatic studies. *The Holocene*, 5: 229–237.

Cook, E. R., Meko, D. M., Stahle, D. W., and Cleaveland, M. K., 2004: *North American summer PDSI reconstructions*. Boulder, Colorado: NOAA/NGDC Paleoclimatology Program, IGBP Pages/World Data Center for Paleoclimatology Data Contribution Series # 2004-045.

Coutts, M. P., and Philipson, J. J., 1978: Tolerance of tree roots to waterlogging. I. Survival of Sitka spruce and lodgepole pine. *New Phytolology*, 80: 63–69.

Critchfield, W. B., 1980: Genetics of lodgepole pine. United States Department of Agriculture, United States Forest Service, Research Paper WC-37.

Diaz, H. F., and Markgraf V. (eds.), 2000: *El Niño and the Southern Oscillation: Multiscale variability, Global and Regional Impacts*. Cambridge, U.K.: Cambridge University Press, 496 pp.

Fritts, H. C., 1976: *Tree Rings and Climate*. New York: Academic Press, 567 pp.

Gedalof, Z., and Smith, D. J., 2001: Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophysical Research Letters*, 28(8): 1515–1518.

Gedalof, Z., Mantua, N. J., and Peterson, D. L., 2002: A multi-century perspective of variability in the Pacific Decadal Oscillation: new insights from tree rings and coral. *Geophysical Research Letters*, 29: doi: 10.1029/GL015824.

Graumlich, L. J., 1993: A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research*, 39: 249–255.

Gray, S. T., Betancourt, J. L., Fastie, C. L., and Jackson, S. T., 2003: Patterns and sources of multidecadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. *Geophysical Research Letters*, 30(6): GL016154.

Grissino-Mayer, H. D., Arabas, K. B., Losleben, M., McCarthy, B. C., Mensing, S., Pringle, P. T., Splechtna, B., and Van Norman, K., 1997: Relationships between climate and growth of western juniper (*Juniperus occidentalis* Hook.) in the eastern Oregon Cascades. *In* Brown, P. M., and Krusic, P. J. (eds.), *Eighth North American Dendroecological Fieldweek, H.J. Andrews Experimental Forest, Blue River, Oregon, Final Report*, 1–17. (http://dendrolab.indstate.edu/nadef/).

Haston, L., and Michaelsen, J., 1994: Long-term central coastal California precipitation variability and relationships to El Niño–Southern Oscillation. *Journal of Climate*, 7: 1373–1387.

Hett, J. M., and Loucks, O. R., 1976: Age structure models of balsam fir and eastern hemlock. *Journal of Ecology*, 64: 1029–1044.

Hidalgo, H. G., Piechota, T. C., and Dracup, J. A., 2000: Alternative principle components regression procedures for dendrohydrological reconstructions. *Water Resources Research*, 36(11): 3241–3249.

Holmes, R., 1986: Quality control of crossdating and measuring: a users manual for program COFECHA. *In* Holmes, R. L., Adams, R. K., and Fritts, H. C. (eds.), *Tree-ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin*. Tucson: University of Arizona.

Holmes, R., 1992: Dendrochronology Program Library, Version 1992-1. Tucson: University of Arizona, Laboratory of Tree-Ring Research.

Hughes, M. K., and Graumlich, L. J., 1996: Climatic variations and forcing mechanisms of the last 2000 years. *In* Bradley, R. S., Jones, P. D., and Jouzel, J. (eds.), *Multi-Millennial Dendroclimatic Studies from the Western United States*. NATO Advanced Study Workshop Series, NATO Advanced Study Institute, Volume 141: 109–124.

Kitzberger, T., Steinaker, D. F., and Veblen, T. T., 2000: Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology*, 81(7): 1914–1924.

Kozlowski, T. T., Kramer, P. J., and Pallardy, S. G., 1991: *The Physiological Ecology of Woody Plants*. San Diego: Academic Press.

Latif, M., and Barnett, T. P., 1994: Causes of decadal climate variability over the North Pacific and North America. *Science*, 266: 634–637.

Laudenslayer, W. F., Jr., 2002: Juniper. *In* Mayer, K. E., and Laudenslayer, W. F., Jr. (eds.), *A Guide to Wildlife Habitats of California*. Sacramento: California Department of Forestry and Fire Protection, 64–65.

Légère, A., and Payette, S., 1981: Ecology of a black spruce (*Picea mariana*) clonal population in the hemiarctic zone, northern Québec: population dynamics and spatial development. *Arctic and Alpine Research*, 13: 261–276.

Lloyd, A. H., and Graumlich, L. J., 1997: Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, 78: 1199–1210.

Loaiciga, E. M., Haston, L., and Michaelsen, J., 1993: Dendrohydrology and long-term hydrologic phenomena. *Review of Geophysics*, 31: 151–171.

MacDonald, G. M., and Case, R. A., 2005: Variations in the Pacific Decadal Oscillation over the past millennium. *Geophysical Research Letters*, 32: L08703.

Mann, M. E., Park, J., and Bradley, R. S., 1995: Global interdecadal and century-scale climate oscillations during the past five centuries. *Nature*, 378: 266–270.

McBride, J. R., 2002: Jeffrey pine. *In* Mayer, K. E., and Laudenslayer, W. F., Jr. (eds.), *A Guide to Wildlife Habitats of California*. Sacramento: California Department of Forestry and Fire Protection, 54–55.

McCabe, G. J., and Dettinger, M. D., 1999: Decadal variations in the strength of ENSO teleconnections with precipitation in the western United States. *International Journal of Climatology*, 19: 1399–1410.

Meko, D. M., Therrell, M. D., Baisan, C. H., and Hughes, M. K., 2001: Sacramento River flow reconstructed to A.D. 869 from tree rings. *Journal of the American Water Resources Association*, 37(4): 1029–1040.

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. *Arctic, Antarctic, and Alpine Research*, 36(2): 181–200.

Mitchell, K., 2001: *Data Analysis by Point-Centered Quarter Method*. Geneva, New York: Department of Mathematics and Computer Science, Hobart and William Smith Colleges, 14 pp.

Morrison, M. L., and Raphael, M. G., 1993: Modeling the dynamics of snags. *Ecological Applications*, 3(2): 322–330.

Mote, P. W., 2003: Trends in snow water equivalent in the Pacific Northwest and their climatic causes. *Geophysical Research Letters*, 30: GL0172588.

North, M., Hurteau, M., Fiegener, R., and Barbour, M., 2005: Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. *Forest Science*, 51(3): 187–197.

Osborn, T. J., Briffa, K. R., and Jones, P. D., 1997: Adjusting variance for sample-size in tree-ring chronologies and other regional mean timeseries. *Dendrochronologia*, 15: 89–99.

Palmer, W. C., 1965: *Meteorological Drought*. Washington, DC: U.S. Weather Bureau, Research Paper 45: 58 pp.

Raphael, M. N., and Mills, G., 1996: The role of mid-latitude Pacific cyclones in the winter precipitation of California. *Professional Geographer*, 48(3): 251–262.

Raphael, M. G., and Morrison, M. L., 1987: Decay and dynamics of snags in the Sierra Nevada, California. *Forest Science*, 33(3): 774–783.

Royce, E. B., and Barbour, M. G., 2001: Mediterranean climate effects I: Conifer water use across a Sierra Nevada ecotone. *American Journal of Botany*, 88(5): 911–918.

Scuderi, L. A., 1993: A 2000-year tree ring record of annual temperatures in the Sierra Nevada Mountains. *Science*, 259: 1433–1436.

Stahle, D. W., Cook, E. R., Cleaveland, M. K., Therrell, M. D., Meko, D. M., Grissino-Mayer, H. D., Watson, E., and Luckman, B. H., 2000: Tree-ring data document 16th century megadrought over North America. *EOS Transactions, American Geophysical Union*, 81(12): 121–125.

Stewart, I., Cayan, D. R., and Dettinger, M. D., 2004: Changes in snowmelt runoff timing in western North America under a "Business as Usual" climate change scenario. *Climatic Change*, 62: 217–232.

Stokes, M. A., and Smiley, T. L., 1968: *An Introduction to Tree Ring Dating*. Chicago: University of Chicago Press, 73 pp.

Swetnam, T. W., and Betancourt, J. L., 1998: Mesoscale disturbance and ecological response to decadal climate variability in the American Southwest. *Journal of Climate*, 11: 3128–3147.

Szeicz, J. M., and MacDonald, G. M., 1995: Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology*, 83: 873–885.

Torrence, C., and Compo, G. P., 1998: A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society*, 79: 61–78.

Wigley, T. M. L., Briffa, K. R., and Jones, P. D., 1984: On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23: 201–213.

Wilby, R. L., and Dettinger, M. D., 2000: Streamflow changes in the Sierra Nevada, California, simulated using a statistically downscaled general circulation model scenario of climate change. *In* MacLaren, S., and Kniveton, D. (eds.), *Linking Climate Change to Land Surface Change*. Dordrecht, Netherlands: Kluwer Academic Publishers, 1–20.

Ms accepted May 2007