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**Response of high-elevation limber pine (*Pinus flexilis*) to
multi-year droughts and 20th-century warming; Sierra
Nevada, California, USA**

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1 Abstract

2 Limber pine stands along the eastern escarpment of the Sierra Nevada, Mono County,
3 California, experienced significant mortality from 1985 to 1995 during a period of sustained low
4 precipitation and high temperature. The stands differ from typical old-growth limber pine forests
5 of this region in being dense, young (<300 years), more even-aged, and located in warmer, drier
6 micro-climates. Tree growth showed high interannual sensitivity. Relative to live trees, dead
7 trees over their lifetimes had higher series sensitivity, grew more variably, and had consistently
8 lower growth. While droughts recurred during the 20th century, tree mortality occurred only in
9 the late 1980s. Positive correlations of growth with minimum temperature and precipitation,
10 negative correlations with maximum temperature, and complex interactions indicate that
11 conditions of significant warmth plus sustained drought increased the likelihood of mortality in
12 the 1985-1995 interval. This resembles a global-change-type drought, where warming combined
13 with drought was the initial stress, trees were further weakened by dwarf mistletoe, and
14 proximally killed by mountain pine beetle. The drought, however, appears to have improved
15 resilience and contributed to longterm persistence of these stands by removing poorly adapted
16 individuals, releasing survivors from competition, and reducing conditions that favor spread of
17 biotic agents: These stands suffered no additional mortality in the subsequent 1999-2004
18 drought. Such events demonstrate that subalpine forest response to global warming is more
19 complex than simple elevational shifts in response to temperature.

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1 **Introduction**

2 Extensive tree mortality associated with recurring droughts is characteristic of western North
3 American montane forests. Most recently the 1999-2004 drought, increasing temperatures, and
4 associated bark beetle infestations are resulting in millions of hectares of forest dieback in
5 lodgepole pine (*Pinus contorta*) in British Columbia, Canada (Ministry of Forests 2006), pinyon
6 pine (*Pinus edulis* and *P. monophylla*) and ponderosa pine (*P. ponderosa*) in the Colorado
7 Plateau region (Breshears et al. 2005), Engelmann spruce (*Picea engelmannii*) in the
8 southwestern ranges (Logan and Powell 2001, 2005), and mixed conifer forests of southern
9 California (Jones et al. 2004). Previous significant droughts and forest mortality events centered
10 on the late 1980s in California (DeMars et al. 1988; Ferrell et al. 1994; Macomber and
11 Woodcock 1994), 1970s in the northern Rockies (Logan and Powell 2001), and 1950s westwide
12 (Allen and Breshears 1998). Droughts and associated impacts on forest growth and mortality
13 have occurred repeatedly during previous centuries as well, as documented by tree-ring
14 reconstructions from throughout western North America (Grissino-Mayer 1996; Gray et al. 2003;
15 Cook et al. 2004).

16 The duration of droughts and interaction with temperature affect forest response. Single dry
17 years are less likely to result in high mortality than multiple years of low precipitation (Guarin
18 and Taylor 2005), and multi-decadal periods (30-60 years) are documented to have resulted in
19 significant regional mortality historically (Swetnam and Betancourt 1998; Gray et al. 2006).
20 High temperatures during droughts increase the likelihood of mortality (Breshears et al. 2005;
21 Guarin and Taylor 2005) as do wet intervals preceding multi-year droughts. While direct water
22 stress is well known to be linked with forest health (Allen and Breshears 1998; Fensham and
23 Holman 1999; Guarin and Taylor 2005), vulnerability of trees varies with other factors as well.

1 Tree death is often proximally caused by insects or pathogen infestation (Mattson and Haack
2 1987; Waring and Cobb 1992; Allen and Breshears 1998, Guarin and Taylor 2005), and the level
3 of stress and success of insect attack depend on conditions of stand structure. Conditions that
4 increase vulnerability of forests include dense and even-age stand structure (Innes 1992; Ferrell
5 et al. 1994; Dolph et al. 1995); aspect and elevation also are related to forest health (Guarin and
6 Taylor 2005; Van Mantgem et al. 2006). Species respond individualistically to drought and
7 insect attack (Kern 1996; Green 2005; Guarin and Taylor 2005) and within-species genetic
8 variation and age-related factors condition response also (Ogle 2000, Suarez et al. 2004;
9 Gutschick and BassiriRad 2003).

10 Whereas forest mortality has been widely documented at low to middle montane elevations in
11 western North America, subalpine forests have been far less affected. Conditions at high
12 elevations generally are more resistant to extensive insect and disease outbreaks than at lower
13 elevations. These include sparse stand structure; dry, rocky substrates; low relative humidity;
14 freezing temperatures; high wind velocities; persistent snowpacks; and high resin concentrations
15 in wood. The most extensive dieback in subalpine forests of western North America in recent
16 decades is occurring in whitebark pine (*Pinus albicaulis*) forests of the Rocky Mountains,
17 Intermountain Ranges (Kendall and Arno 1990; Kendall 1994), and Coast Range of British
18 Columbia (Campbell and Antos 2000) as a result of white pine blister rust caused by the non-
19 native fungus, *Cronartium ribicola*. Whereas drought increases stress to the pines, making them
20 more susceptible to rust, the primary cause of rapid spread and death is not directly climate but to
21 lack of resistance in pines to the exotic disease. In addition to whitebark pine, blister rust has
22 caused extensive mortality in limber pine (*Pinus flexilis*) in the northern and central Rocky

1 Mountains, and adjacent Idaho ranges, where up to 75% of trees in a stand are infected and over
2 30% have died (Kendall et al. 1996; Kendall and Schirokauer 1997).

3 Aside from blister rust, only small amounts of mortality and occasional dead clusters of trees
4 have been noted in recent decades in whitebark pine and limber pine forests in the subalpine
5 zones of western North America. In the 1930s evidence points to an unusual and extensive
6 outbreak of mountain pine beetle (*Dendroctonus ponderosae*) above its normal elevational and
7 climatic limit on whitebark pine at Railroad Ridge, over 2900 m in the White Cloud Mountains
8 of central Idaho (Ciesla and Furniss 1975; Perkins and Swetnam 1996). A similar outbreak on
9 whitebark pine is ongoing at present. First noted at Railroad Ridge in 2003, it is progressing at a
10 rapid rate and causing widespread mortality (Logan 2004). The likely reason for the 1930s and
11 current beetle outbreak is linked by model- and empirical-based evidence to warming of greater
12 than 2°C, which creates an environment favorable for beetles to overwinter at higher elevations
13 (Logan and Powell 2001, 2005; Hicke et al. 2006). Observations of mortality related to
14 mountain pine beetle are being reported for other mountains of the West, although these have
15 generally been in stands at less than 2500 m (Waring and Six 2005; Kegley et al. 2001; Goheen
16 et al. 2002).

17 In this paper we present results from a study of high-elevation limber pine forests in the
18 eastern Sierra Nevada, where extensive mortality was evident. We ask the questions: when did
19 the trees die? What are the correlations of growth with climate? How did growth vary in
20 relation to climate among live and dead trees over their lives? How do the stands differ from
21 typical old-growth stands that escaped mortality? What are the implications for limber pine and
22 subalpine forest response in the future, and how do these implications compare with assumptions
23 about high-elevation forest response under warming climates?

1 **Materials and Methods**

2 **Study area**

3 Limber pine is a wide-ranging species of the British Columbia Coast Range, Canada and the
4 Intermountain, Great Basin and Southwest Ranges, Rocky Mountains, and Sierra Nevada, USA
5 (Fig. 1). While it extends as low into mid-montane forests at 1500 m in the northern parts of its
6 range, limber pine is primarily a subalpine species, reaching 3700 m and often establishing the
7 upper treeline. Our study region was located near the species' northern distribution in the Sierra
8 Nevada (Fig. 1), where limber pine shares the upper elevation tree zone with whitebark pine, and
9 occasionally mountain hemlock (*Tsuga mertensiana*) and western juniper (*Juniperus*
10 *occidentalis*). Stands in this area are disjunct and limited in elevational range (~2450-2990 m),
11 size (small), and aspect (N-NE). Typical stands are characterized by widely separated old-
12 growth trees (often > 100m spacing) dominated by twisted and gnarled, strip-barked individuals
13 800 to over 1500 yrs old, growing on barren, exposed, and steep rocky slopes of blocky granite
14 or metamorphic substrate. Young trees (less than 200 years) and middle-aged trees generally are
15 present in low frequencies; overall the stands are very sparse with little understory vegetation
16 and abundant bare ground. Standing and down deadwood (dating to more than 3500 years old)
17 preserves well in the arid, high-elevation, Sierran habitats of these old-growth limber pine stands.
18 Lightning ignites individual or small clusters of trees, but fire is not an important ecological
19 driver in the old-growth stands.

20 Less commonly stands have denser, nearly closed-canopy conditions (averaging 10-30 m
21 spacing). These comprise pole- to mid-sized, straight-stemmed trees, with few old-growth
22 individuals, little accumulated deadwood, and a small range of size (presumably age) classes.
23 Compared to the old-growth populations, these stands experienced significant mortality during

1 the late 20th century. We studied three stands with high mortality in mature trees, Deschambeau
2 (DES; 2510-2980 m), Clot Cyn (CLO; 2700-2980 m), and Laurel Cyn (LAU; 2450-2960 m)
3 (Fig. 1). While the three populations were similar in overall degree of mortality, at a patch scale
4 of 0.5 ha mortality ranged from 10 - 100%. The stands have north to northeast aspect and are on
5 moderate-steep slopes. Dead trees retained bark and fine branches when sampled in 2005 and
6 2006, and showed signs of past infestation by mountain pine beetle (*Dendroctonus ponderosae*;
7 confirmed during active infestation, and galleries remaining), blue stain fungus (*Ophiostoma*
8 *sp.*), and limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*). These conditions were most
9 severe at the DES and LAU sites. We also studied one population with similar dense and young
10 stand structure but lacking mortality on the north-facing slope of deep, narrow Owens Gorge
11 (OWE; 2040-2150 m; Fig. 1). This locality is unusually low in elevation for limber pine in the
12 region. Typical old-growth stands of limber pine occur near to DES, CLO, and LAU sites at
13 similar elevation range and aspect, and also adjacent to OWE but at higher elevation. These old-
14 growth stands have no evidence of late-20th century mortality.

15 **Tree-ring collections and analysis**

16 We collected increment cores at 0.5 m height on main stems from live and standing dead
17 limber pines at LAU, CLO, and DES stands and live trees at OWE, and prepared cores for ring-
18 width measurement, dating, and analysis using standard tree-ring techniques (Stokes and Smiley
19 1968; Holmes et al. 1986; Cook and Kairiukstis 1990). Live and dead tree chronologies were
20 developed for each site by COFECHA (Holmes et al. 1986), using live trees to establish calendar
21 dates and excluding series that had correlations to the master chronology less than 0.4.

22 Series from the three stands with high mortality (LAU, CLO, and DES) were highly
23 correlated within and among sites, so we combined chronologies from these sites to make

1 composite live and dead chronologies, further eliminating series with low correlations. We kept
2 the live tree chronology from OWE separate due to its low correlation with the other stands,
3 although series within the site were highly correlated. The composite chronologies were
4 imported into ARSTAN40 (Krusic and Cook 2005) for detrending and standardization of ring-
5 widths. Rather than standard methods, we used the RCS detrending algorithm (Briffa et al.
6 1992; Esper et al. 2002), which preserves low-frequency trends in long tree-ring chronologies
7 despite short segment lengths.

8 **Climate and tree-response analysis**

9 Longterm instrumental climate records were compiled from Lake Tahoe, Yosemite Valley,
10 and Sacramento, CA cooperative weather stations (WRCC 2006). Following the approach of
11 Millar et al. (2004), we combined the data from the individual stations into composite records
12 (1910-2005) for mean monthly minimum and maximum temperature, respectively, and annual
13 and water-year (Sept-June) precipitation, respectively. Higher correlations with water-year led
14 us to use that variable rather than annual precipitation. We performed moving-average variance
15 analyses (10-year window) for standard deviations of water-year precipitation (Wolfram 2005).
16 To assess cycles in the time series, we evaluated water-year precipitation and annual streamflow
17 from a composite of four local Sierra Nevada high-elevation river gauges (described in Millar et
18 al. 2004) and ring width with spectral analysis (JMP, Fourier analysis, SAS 2004).

19 As no high-elevation long term instrumental weather stations exist near our sites, we
20 evaluated current climate conditions of the four limber pine study sites and adjacent typical old-
21 growth limber pine stands using the PRISM climate model (Daly et al. 1994). We extracted
22 climate data for annual, January, and July precipitation, respectively; and annual, January, and
23 July minimum and maximum precipitation, respectively, for the period 1961-1990. We used

1 downscaling methods described in Millar et al. (2006) and Hamman and Wang (2005). While
2 PRISM is the best indicator of climate at our stands, the model does not accurately estimate
3 micro-climate at all sites. In a previous study in the same region and time period we tested
4 accuracy by comparing PRISM estimates to nearby weather station records and found root mean
5 squared deviations mostly less than 5% except for average minimum temperature, which was
6 somewhat higher (Millar et al. 2006).

7 To test relationships of climate and ecological responses, we analyzed simple linear
8 correlations (SAS 2004) as well as non-linear relationships. For the latter, we conducted a
9 second-order least squares response-surface model (JMP, SAS 2004) of standardized ring widths
10 versus minimum and maximum annual temperature, respectively, water-year precipitation, as
11 well as standard indices of the Pacific Decadal Oscillation (PDO, Mantua, et al. 1997; indices
12 from JIASO 2006), and Palmer Drought Severity Index (PDSI, Palmer 1965, California Division
13 5, southeastern CA; indices from NOAA 2006) in the analysis. We evaluated the behavior of
14 these variables in second-order response surfaces. Minimum and maximum temperatures and
15 water-year precipitation were the final variables used. We graphed predicted growth using the
16 response-surface model of variables screened, where contour intervals represent standardized
17 growth response, axes are units of standardized deviations from the mean for each climate
18 variable, and in each case, calculations were run under conditions of mean minimum temperature
19 and mean maximum temperature for alternate analyses.

20 To evaluate growth in any single year relative to precipitation in current and previous years
21 we used lag correlation analysis (Wolfram 2005) on annual limber-pine growth in live and dead
22 trees. Heterogeneity of variance (PROC AUTOREG, SAS 2004) and generalized autoregressive
23 conditional heteroscedasticity (GARCH, Chatfield 2004) were used to evaluate changes in

1 growth variances over time, based on a combined dataset from the CLO, DES, and LAU stands.
2 The GARCH model (order 1 and 2) estimates variance in time series based on lagged years, and
3 is dependent on the integral of variance in previous years.
4

5 **Results**

6 **Tree ages, growth, and mortality**

7
8 We collected increment cores from 40 live and 40 dead trees at DES, CLO, and LAU, and 40
9 live trees at OWE. From these, we were able to measure ring widths and accurately date a total
10 of 147 live trees and 84 dead trees (Fig. 2). Individual series from all stands crossdated strongly
11 against chronologies developed from live trees at each site, and series correlations to site
12 chronologies ranged from 0.491 to 0.709 (Table 1). Ring-width series among the LAU, CLO,
13 and DES stands were highly correlated, but OWE had low correlations to the other stands. Ring-
14 width sensitivities (a measure of high-frequency variation, Fritts 1976) were high from the CLO,
15 DES, and LAU stands, ranging from 0.194 to 0.289 for the live trees and 0.218 to 0.313 for the
16 dead trees (Table 1). The OWE series had exceptionally high sensitivity, 0.374. Cores from
17 dead trees were sound, but nearly every core was stained in the sapwood from blue-stain fungi
18 associated with bark beetles. No live trees had blue stain.

19 Compared to typical limber pine forests in the region, the four stands were unusually young
20 (Fig. 2). The oldest series had a pith date of 1607, but most were much younger. The CLO stand
21 had the largest number of older trees, with many pith dates between 1700 and 1800, while the
22 LAU stand was youngest overall, with most pith dates between 1875 and 1920. The DES and
23 OWE stands were intermediate in age and showed more diversity in pith dates than the other
24 stands, concentrated between 1800 and 1920. In the three stands that experienced mortality,

1 while the general age range was similar among live and dead trees (Fig. 2), there were more
2 young trees among the live tree set.

3 Of the trees we sampled, over 90% of the death dates fell between 1985 and 1995 (Figs. 2, 3).
4 The earliest death date was 1959. The stands varied in peak dates of mortality, with LAU
5 earliest (1987), DES (1991) intermediate, and CLO latest (1993) (Fig. 3).

6 Growth rates, as indicated by ring-widths in the composite curve (Fig. 4c), fluctuated over the
7 20th century and showed a consistent increasing trend in live trees (0.0033 std growth units per
8 year ; $p < 0.001$) and a smaller and insignificant positive trend in dead trees (0.0009 std growth
9 units per year; $p = 0.29$). Live and dead trees (prior to their death) grew with similar annual
10 patterns over the century, but the dead trees consistently grew less than live trees, and had greater
11 extremes of minimal growth (Fig. 4c). This pattern of high variability is indicated by the larger
12 ring-series sensitivity of the dead-tree set ($s = 0.240$) than of the live-tree set ($s = 0.211$; Table 1).
13 Ring-growth periodicity over the 300-year chronology had biennial and multi-year cycles, with
14 power at 2.13 and 2.17 yrs (live and dead, respectively) and 15.3 and 13.9 yrs (live and dead,
15 respectively) from Fourier analysis. Compared to climate variables (below), however, none of
16 these shorter-period peaks were dominant.

17 Variance in growth changed over time as indicated by GARCH heterogeneity tests (Fig. 7).
18 Both chronologies significantly fit ARCH, lag 1 and GARCH, lag 1 models, although a GARCH,
19 lag 2 model gave a better fit of the living set. With this latter model, the ARCH terms became
20 non-significant. Interannual variances were low in the 1700s, increased briefly around 1800, and
21 were low during the 1800s. These were significantly greater in the dead set than in the living. In
22 the 20th century variance showed a significant change in pattern with consistently increasing
23 variance over the century, especially in the live tree set.

1 **Climate**

2 Composite regional weather records showed significant increases in minimum temperature (p
3 < 0.001) over the 20th century, with an average warming of 1°C from 1910-2006 (Fig. 4a).
4 Warming trends were minor in maximum temperature, but significant ($p < 0.05$). Water-year
5 precipitation was characterized by high multi-year variability and trends in variability rather than
6 directional changes in mean (Fig. 4b). Dominant peaks in spectral analysis showed strong power
7 at 2.2 years and 15.0 years for water-year precipitation and 2.1 and 15.0 years for annual
8 streamflow (Fig. 5); all other peaks were minor. Multi-year droughts persisted 5-7 years, in
9 some cases with a wet year intervening. Drought periods as recorded by water-year precipitation
10 are indicated at: 1918-1926; 1929-1934; 1944-1951; 1959-1962; 1971-1977; 1984-1992; 1999-
11 2004 (Fig. 4b). While the timing of intervals is consistent and appears to reflect a half-phase in
12 the 15-year precipitation cycle, the pattern of individual droughts differed. Some were severe
13 but short (1929-1934; 1971-1977), others weak but longer (1944-1951), while others were severe
14 but variable inter-annually (1918-1926; 1929-1934). The most persistent drought of the century
15 was 1984-1992, which followed the wettest multi-year period since 1910, namely 1980-1983.
16 Although the 1971-1977 drought was drier on average than that in 1984-1992, the latter period
17 was significantly warmer. Precipitation and minimum temperature in 1992 were in the 20% and
18 97.5% quantiles, respectively, for the period of record. Variability of precipitation as indicated
19 by moving window analysis of standard deviations showed decadal-length patterns of 10-20
20 years duration (Fig. 6). For the 90-year period, standard deviations were lowest during 1920-
21 1930; low again around 1945, and highest from 1976-1986, which is in the interval preceding the
22 late 1980s drought.

1 Estimates from PRISM of 1961-1990 climate for the limber pine study sites and adjacent old-
2 growth limber pine stands are given in Table 2. The three study stands with mortality (CLO,
3 DES, and LAU) differ among themselves slightly in precipitation and more significantly in
4 temperature, with LAU overall warmest and driest, and CLO coolest and wettest. Compared to
5 adjacent old-growth stands, these younger stands are much drier (difference of > 200-400 mm
6 water-year precipitation) and warmer (difference 2-4°C annual maximum temperature and 1-2°C
7 annual minimum temperature). Winter precipitation differs in particular between the young and
8 old-growth stands, as do winter maximum temperatures. The PRISM model indicates the OWE
9 stand, which occurs at anomalously low elevation and experienced no mortality, to have less than
10 half the precipitation and to be significantly warmer than the other limber pine stands (Table 1).
11 Given the very narrow, deep condition of the Owens Gorge, it is likely that the PRISM model,
12 even downscaled, is not able to accurately represent what might be cool-air drainage from
13 adjacent Rock Creek Canyon and Crowley Lake at this site.

14 **Climate interactions with growth and mortality**

15 Mortality in three of the limber pine stands occurred during the 1984 – 1992 drought and no
16 mortality was associated with earlier or later droughts in the 20th century. Trees died at slightly
17 different times during the drought, with the LAU stand responding earliest, DES intermediate,
18 and CLO peaking at the end and slightly after the drought (Fig. 3).

19 Annual growth in the combined live and dead tree set was significantly and positively
20 correlated with water-year precipitation, and with annual, May, and July minimum temperature,
21 respectively (Table 3). In the dead tree set, correlations were lower with temperature than
22 among the live trees, especially in summer. With annual maximum temperature, correlations of

1 growth were negative overall, but not significant. A plot of the correlation curves for maximum
2 temperature shows positive slope at low temperature and negative at high temperature.

3 These correlations are reflected in growth over the 20th century, which declined during the
4 multi-year periods of low precipitation, including the 1920-1930s and late 1980-early 1990s, and
5 increased in intervals of high precipitation, such as the early 1940s and early 1980s (Fig 4c). In
6 all situations, the highest correlations between precipitation and growth were in the current water
7 year; lower but significant positive correlations occurred to 1-2 yrs prior precipitation, and
8 negative correlations to ~8-9 yrs prior precipitation. This lag is evident during 1984-1986, when
9 growth remained high despite low precipitation (Fig. 4c).

10 Annual growth was also positively and significantly correlated with PDSI (Table 3),
11 corroborating better growth during years of high available soil moisture (positive PDSI indices)
12 and poorer growth in dry conditions (negative PDSI). This correlation was twice as strong in the
13 dead tree set as for the live trees, indicating the role of low soil moisture in stressing trees that
14 later died. Ring-width growth correlations with PDO were very low and non-significant.

15 Interactions of growth with climate were significant and complex, and differed among the
16 dead and live tree sets (Fig. 8). Growth in live trees increased with both increasing minimum
17 temperatures and precipitation; trees were most responsive to precipitation changes at low
18 temperature and most responsive to temperature changes at low precipitation (Fig. 8a). Dead
19 trees responded to precipitation similarly at low minimum temperatures, but their interactions
20 were more complex at intermediate and high temperatures (Fig. 8b). With low precipitation,
21 growth was better at low and high minimum temperatures, while with high precipitation, growth
22 was best at low minimum temperatures.

1 Interactions with maximum temperatures were also complex but similar among live and dead
2 trees (Figs. 8c and 8d). The greatest growth occurred at intermediate maximum temperatures
3 and with intermediate to high precipitation. Lowest growth occurred at high maximum
4 temperatures and low precipitation. Growth was relatively insensitive to changes in maximum
5 temperatures at intermediate precipitation and more sensitive under low precipitation.

6

7 **Discussion**

8

9 Drought-related forest dieback has been common and increasing in western North America
10 during the late 20th century (Breshears et al. 2005, Allen and Breshears 1998). Except for
11 situations associated with exotic pathogens such as white-pine blister-rust and where fire
12 suppression is problematic, however, high-elevation forests have remained relatively healthy. A
13 significant mortality event occurred from 1985 to 1995 in low diversity, dense, young (80-300 yr
14 old) limber pine stands in the subalpine zone of the eastern Sierra Nevada escarpment. Nearby
15 old-growth stands with low density, and a single low-elevation stand in an unusual micro-site,
16 did not experience mortality. Neither young nor old stands experienced significant mortality
17 during the recent 1999-2004 drought that has affected millions of hectares elsewhere in the West
18 (Breshears et al. 2005; Jones et al. 2004; Logan and Powell 2001; Ministry of Forests 2006).
19 Mortality also did not occur in the young limber pine stands during earlier low precipitation
20 periods of the 20th century in the Sierra Nevada, namely 1918-1926, 1929-1934, 1944-1951,
21 1959-1962, or 1971-1977.

22 During the late 1980s and early 1990s other montane species of mid-elevations (< 2500 m) in
23 California also experienced high mortality. Significant dieback occurred in true fir species
24 (*Abies sp.*) in the Lake Tahoe Basin and along the eastern Sierran slope near Lake Tahoe

1 (Berryman and Ferrell 1988; Ferrell et al. 1994; Ferrell 1996), up to 15% mortality occurred in
2 fir and pine (*Pinus ponderosa* and *P. jeffreyi*) of northern Sierran forests (Macomber and
3 Woodcock 1994; CFPC 1970-1997), and up to 14% mortality in mixed-conifer forests of
4 southern California (Savage 1994). In a study of diverse mid-elevation forests throughout
5 Yosemite National Park, Guarin and Taylor (2005) found a significant mortality episode
6 concentrated between 1986 and 1992 reflected in all species studied. There was little evidence
7 of mortality at other times during the 20th century in the Yosemite study.

8 Climatic and stand structure factors associated with the 1984-1992 period are implicated in
9 the limber pine mortality episode. As indicated from instrumental weather stations, this interval
10 was the most persistent drought in the Sierra Nevada during the 20th century. The intensity of
11 the drought is reflected in proxies of distant San Francisco Bay salinity, which represent Sierran
12 snowpack depths and river runoff. In that system, the persistent 1987-1992 episode was
13 unmatched over the prior 400 years (Stahle et al. 2001). In the Sierra Nevada, precipitation,
14 PDSI, and April snowpack were all below average for the years 1987-1992, except for 1991.
15 This drought also occurred during a period of greater warmth than any of the previous 20th
16 century droughts, with annual minimum and maximum temperatures significantly above century
17 means. In limber pine, growth was positively correlated with precipitation, minimum
18 temperature, and maximum temperature at low temperatures. This reflects a typical response of
19 high-elevation trees to grow better with more water, warmer nights (minimum temperatures), and
20 relatively warmer days (maximum temperature). Negative correlations of growth with minimum
21 and maximum temperatures at high temperatures, as well as complex interactions of growth with
22 temperature and precipitation, however, suggest that as daytime and summer temperatures
23 increased during the 20th century, limber pine growth declined. Trees that died were less able to

1 respond resiliently to precipitation under increasing minimum temperatures than trees that lived.
2 Thus climatic stress in limber pine appears to have passed critical thresholds in these stands
3 leading to mortality in the late 1980s. This pattern was described by Breshears et al. (2005) as
4 global-change-type drought, implicated in forest dieback in Yosemite National Park (Guarin and
5 Taylor 2005) and massive mortality events throughout the west during 1999-2004.

6 Another climatic conditioning factor for mortality might have been the wet years that
7 preceded the 1984-1992 drought, supported by negative correlation in the 8-9 year lag. In the
8 eastern Sierra, the most extreme El-Niño of the century occurred in 1982-1983, and mean
9 precipitation in other years prior to the drought was well above the mean. Although this was a
10 wet interval, like the dry late 1980s it was also very warm relative to the 20th-century mean as
11 well. This sequence of high precipitation years followed by drought has been linked to other
12 forest mortality episodes, in particular a wet interval preceding the massive diebacks during the
13 1999-2004 drought (Breshears et al. 2005).

14 While significant mortality occurred in the limber pine stands only in the late 1980s-early
15 1990s drought, growth suppressions occurred cyclically with low precipitation through the 20th
16 century. The dominant quasi-biennial (2.1, 2.2 yr) and 15.0 year cycles arising in the water-year
17 precipitation, streamflow, and annual tree growth are reminiscent of the periodicities of the
18 Asian monsoon tropospheric biennial oscillation (TBO), which has power in this time scale (2.1 -
19 2.2 yrs and 15 yrs; Meehl 1997; Chang and Li 2000). The TBO has been implicated in climate
20 variability of the west coast of North America through interactions with the El Niño/Southern
21 Oscillation. Some investigators view the two oscillations mechanistically as phases of one
22 system, while others consider them to be separate modes with distinct mechanisms. Nonlinear
23 interactions of two modes may explain complexity of the climate fluctuations in the quasi-

1 biennial and 15 year time period (Chang and Li 2000) that we are seeing in the Sierra climate
2 and tree-ring records over the past century. Alternately, the recurring patterns in precipitation
3 and growth on 15-20 year intervals may reflect the location of central California in the dipole
4 action of the PDO (Mike Dettinger, USGS, pers. comm. 2006). In our data, however, we found
5 no statistical evidence including spectral decomposition to suggest this.

6 In addition to climate, other factors appear to have conditioned the limber pine stands to
7 extreme stress. High tree density is a common attribute of forest stands throughout California
8 and western U.S. that experience mortality, especially during droughts (Berryman and Ferrell
9 1988; Innes 1992; Ferrell et al. 1994; Savage, 1994; Macomber and Woodcock 1994; Dolph et
10 al. 1995; Ferrell 1996; Allen and Breshears 1998; Breshears et al. 2005). In Yosemite National
11 Park, mixed-conifer forests growing on north slopes were more likely to have died in the 1980s
12 drought than forests on other aspects; the north slope forests had the highest density of all stands
13 studied (Guarin and Taylor 2005). Whereas nearly all limber pine in the Mono-Mammoth
14 region of the Sierra Nevada occur on north slopes, only those stands that were relatively young,
15 even-aged, and dense had trees that died in this interval.

16 Dense stands combined with climate stress of high temperature and low precipitation also are
17 most likely to promote bark beetle epidemics (Mitchell et al. 1983; Schmid and Mata 1992).
18 Increasing temperatures are related to mountain pine beetle movement upslope, as well as to
19 promoting a switch from semivoltine to univoltine life cycles (Logan and Powell 2001; 2005).
20 Logan and Powell have shown that a 2°C increase in temperature is enough to cause such a
21 switch in voltinism. In the eastern Sierra, increases in minimum temperature exceeded this
22 threshold in the late 20th century (Millar et al. 2004). These conditions may have facilitated bark
23 beetles epidemics. Furthermore, bark beetle infestations were in the region on mid-elevation

1 lodgepole pine forests during the 1970s and 1980s drought. Stand structure of the limber pine
2 forests we studied also favors spread of the dwarf mistletoe parasite, which is among the most
3 damaging of native biotic threats to limber pine. Mistletoe weakens trees by competing for water
4 and nutrients, both directly and indirectly through influence on ectomycorrhizal communities of
5 the host (Taylor and Mathiason, 1999; Raleigh et al., 2005). The combination of climate, closed-
6 canopy, low-diversity stands, mistletoe, bark beetles, and blue stain fungus created a complex,
7 multi-factor stress situation in these limber pine forests that predisposed the trees to die.

8 The dates of mortality among the LAU, CLO, and DES stands showed a progression from
9 early in the drought to late. The mortality episode peaked earliest in LAU, where no trees died
10 after 1990; the peak was later in DES with no trees dying after 1992; and in CLO, mortality
11 started late and did not stop until 1995, well after return to greater precipitation. These minor
12 differences among stands are likely related to their environmental situation, as confirmed by
13 PRISM climate relations. The LAU stand is the southernmost, has trees concentrated at lowest
14 elevation of the three stands, is the most exposed, being on an expansive open slope of Long
15 Valley, and correspondingly had the warmest and driest climate of the three stands from the
16 PRISM model. The DES stand is northernmost, and is situated in a minor canyon at the head of
17 large Lee Vining Canyon, where elevation and topographic features provide cooler conditions
18 and more protection from direct exposure than at LAU. The CLO stand, although between the
19 two in latitude, has trees concentrated at the highest elevations, and is located at the base of a
20 large cirque of Mt Lewis. This site is also situated farther into the center of the range and nearer
21 the Sierran crest than the other stands. Cool-air drainage from the persistent snowfield in the
22 cirque and storms over the crest likely create a cooler environment than the other stands; PRISM
23 indicated its location to be the coolest and wettest of the three. Thus the pattern of mortality

1 among the stands indicate the onset of stress earliest in the warm, dry conditions at LAU, and
2 latest at cooler, wetter CLO, where a lag in stress was evident. Why mortality didn't continue
3 until the end of the drought at LAU is not clear, but potentially all the weakest trees had died by
4 1992, and the remainder were healthy enough to endure the continuing drought conditions.

5 Lack of mortality in the OWE stand was surprising, given its similar stand structure to the
6 other three young stands, its southernmost location of the four stands studied, and its elevation
7 well below the normal lower range limit for limber pine in California or the Great Basin. The
8 OWE stand is much warmer and drier than the other three as indicated by PRISM. Despite the
9 PRISM estimates, its location on the steep north face of narrow, rocky Owens Gorge directly
10 below the outlet of Crowley Lake and Rock Creek Canyon, which drains air from the Sierra
11 crest, suggests that cool air likely pools there. This is corroborated by values of PRISM tiles to
12 the north and west. Moreover, twice in summer in the Owens Gorge stand we observed yellow-
13 bellied marmots (*Marmota flaviventris*), typical of high-elevation habitats, foraging at the site.
14 Similarly, Unita chipmunk (*Eutamias umbrinus*), another high-elevation vertebrate, has been
15 observed in the Owens Gorge limber pine stands (Derham Giuliani, emeritus California Dept
16 Fish and Game, pers. comm. 2006). These observations anecdotally suggest that the north-
17 facing portion of the Owens Gorge is an anomalously cool microsite. Surprisingly high tree-ring
18 sensitivity at this site, however, indicates that even though the trees grow well during cool and
19 wet years the location of the stand is marginal, and the trees are highly reactive to changes in
20 conditions. The ages of trees at OWE, with >90% less than 250 years, and no indication of
21 deadwood on this site, suggests that it is a recently colonized stand. Between 90 and 200 years
22 ago, Little Ice Age conditions were among the coolest and wettest of the prior centuries and
23 much wetter and cooler than the 20th century (Graumlich 1993; Stine 1994, 1996). Colonization

1 may have occurred fortuitously during this favorable period. If fire were to burn this site in the
2 future, or other biotically induced mortality to occur, it seems unlikely that limber pine would
3 regenerate there.

4 Compared to adjacent old-growth limber pine stands characteristic of the species throughout
5 the Sierra Nevada and White Mountains, the three stands with mortality as well as the OWE
6 stand are in much drier and warmer locations as indicated by the PRISM model. Although they
7 are not located at geographic range limits, the four stands appear to be marginal climatically for
8 the species in this region as indicated also by their unusually high series sensitivity values.
9 Further, unlike typical old-growth stands of limber pine that have evidence of multi-millennial
10 site persistence, the four stands we studied all seem to have originated as an episodic
11 colonization event. As at OWE, the other three stands also date to the late Little Ice Age. In
12 addition to being cooler and wetter than the mid-late 20th century, this was also a time of lowest
13 interannual climate variability. Low variability combined with cool, wet conditions would be
14 conducive to stand recruitment and establishment. Heightened stress of increasing temperature
15 and greater variance in precipitation later in the 20th century, coupled with the persistent 1980s
16 drought and bark beetle/mistletoe interactions, apparently stimulated synchronous death in these
17 relatively new and increasingly marginal stand locations. High variability in interannual growth
18 at all stands suggests increasing susceptibility to climate. This was also seen in pinyon pine
19 forests in northern Arizona, where dead trees exhibited 1.5 times greater variation in growth than
20 live trees, especially during the 10-15 years before they died (Ogle et al. 2000) and in other
21 situations (Gutschick and BassiriRad 2003; Suarez et al. 2004).

22 Despite high mortality in the overstory, the result of the mortality event was not a stand
23 extirpation but a thinning episode. Not only did many pole-sized trees live through the drought,

1 but also scattered young (less than 50-75 years) trees survived in the understory of each stand.
2 These trees were too small to suffer bark beetle or mistletoe infestation during the 1980s, and
3 remain (as of 2006) healthy and vigorous. The stand structure of surviving live trees is sparse (>
4 ~75 m spacing) and reminiscent of typical old-growth stands. The thinning effect therefore
5 appears to have been one that improved longterm health of the stands. That none of these sites
6 experienced mortality in the subsequent 1999-2004 drought suggests that the conditions may
7 now be more favorable to growth than prior to the 1980s drought. More generally, it is possible
8 that droughts and warm periods and the tree mortality they induce through time create favorable
9 stand conditions over the long term in limber pine where persistence can exceed three millennia
10 at a site despite significant climate and biotic variability. In California pine stands supporting
11 outbreaks of western pine beetle (*Dendroctonus brevicomis*), ability for a group kill event drops
12 to near zero as spacing among live and dead trees increases over 10 m (David Schultz, USDA
13 Forest Service, pers. comm. 2006). The sparseness of typical old-growth limber stands similarly
14 is less likely to favor build-up or spread of bark beetle or mistletoe, and this appears to be the
15 stand structure being created at the CLO, DES, and LAU stands.

16 In addition to favorable cultural conditions resulting from mortality, drought-induced culling
17 may have genetic selection effects as well. Selective mortality in the late 1980s drought would
18 not only cull weak individuals generally but especially those that were poorly adapted
19 genetically to warm and dry conditions. Given that the stands appear to be Little Ice Age
20 colonizations, the trees in the founding cohort were likely adapted to conditions of the 1700-
21 1800s and increasingly less adapted as 20th-century climates changed. Genetic differences
22 between the live trees and those that died at the CLO, DES, and LAU stands are implicated by
23 differences in their growth rate, growth sensitivity, and susceptibility to bark beetles and blue

1 stain fungus. During the 18th-19th centuries of the Little Ice Age, the dead trees grew faster than
2 the live trees, whereas in the 20th century, the opposite was true, with low growth in the dead tree
3 set especially pronounced during extreme low-growth years. This suggests different adaptive
4 modes with a lack of fitness among the dead trees to 20th century conditions compared to the live
5 tree set. While live trees were able to take advantage of increasing minimum temperatures
6 during wet periods of the 20th century, the dead trees, prior to their death, did not. Further, the
7 dead tree set showed relatively greater interannual growth variability than the live trees during
8 the Little Ice Age, possibly reflecting a greater response to climate. Finally, the dead trees were
9 the only ones that showed evidence of blue stain, which results from a fungus introduced by bark
10 beetles during early attack and which weakens trees for beetle aggregation. Trees that survived
11 apparently also were strong enough to resist mistletoe weakening, bark beetle attack, and blue-
12 stain fungus effects. While other factors could condition these trees to lower growth, greater
13 sensitivity, and pest susceptibility, genetic differences seem likely. The thinning effect of the late
14 1980s drought, thus, likely removed climatically sensitive trees and Little-Ice-Age adapted
15 genotypes from the stand, resulting in trees of progressively older ages having lower sensitivity,
16 greater resilience, and closer adaptation to warming conditions. The high sensitivity of the OWE
17 stand may result from having experienced little genetic selection through mortality and selection
18 over its relatively short lifetime.

19 The movement of forest mortality related to complex climate and native biotic factors into
20 high-elevation forests is another late-20th/early 21st-century global-warming phenomenon
21 important to monitor. Subalpine and alpine zones are considered at higher risk in general for
22 early and more intense effects of global warming than lower elevations (e.g., Hayhoe et al.
23 2005); models show heightened suitability for mountain pine beetle outbreaks at increasingly

1 high elevations in the early 21st century (Logan and Powell 2001; Hicke et al. 2006). Whereas
2 significant mortality in high-elevation whitebark pine forests has resulted from non-native white-
3 pine blister-rust, increasingly mountain pine beetle related mortality is also being observed
4 (Kegley et al. 2001; Goheen et al. 2002; Logan, 2004; Logan and Powell 2001, 2005; Waring
5 and Six 2005). In California, high-elevation reports of mortality in whitebark pine and other 5-
6 needle white pines that implicate bark beetles and drought but little to no white-pine blister-rust
7 include: 1.1% mortality in the central eastern Sierra Nevada (northern Mono, Alpine, and El
8 Dorado Counties) but none in the southern Sierra Nevada (Patricia Maloney, University of
9 California, Davis, pers. comm. 2006); mortality in old-growth whitebark pine and foxtail pine
10 (*Pinus balfouriana*) in the Marble Mountains (Dave Schultz and Deems Burton, U.S. Forest
11 Service, pers. comm. 2006), on western white pine (*Pinus monticola*) and whitebark pine in the
12 Eddy Mountains, NW California, and whitebark pine near Sonora Pass, Sierra Nevada, the
13 Southern Warner Mtns (NE California), and Goosenest Mtn (N California) (Dave Schultz, U.S.
14 Forest Service, pers. comm. 2006).

15

16 **Conclusions**

17 In this study we document a significant forest mortality event occurring from 1985-1995 in
18 high-elevation limber pine stands of the eastern escarpment, Sierra Nevada, California.
19 Increasing 20th-century temperature interacting with a sustained multi-year drought appears to
20 have severely stressed these stands, pre-conditioning them to infestation from mountain pine
21 beetle and dwarf mistletoe, which were the proximal causes for death. While droughts have
22 recurred at quasi-regular basis through the past century in the eastern Sierra, high temperatures
23 are novel during this period, leading to “global-change-type” drought situations that have killed

1 forests throughout the west in the 1980s and subsequent droughts (Breshears et al. 2005). Dense
2 even-aged stand conditions, a history of Little Ice Age recruitment, and stand locations at
3 temperature and precipitation margins of the species further predisposed these stands to climatic
4 thresholds imposed during the late 20th century. While the dense young stands experienced high
5 mortality, typical diverse and sparse old-growth limber pine forests, which are more common in
6 the Sierra, had no observable mortality during the droughts. The thinning effect of the 1984-1992
7 drought appears to have created higher resilience and greater genetic adaptation in the surviving
8 trees, as no mortality was experienced in the subsequent 1999-2004 drought in the young stands
9 and surviving trees are healthy.

10 The results documented here and implications for the role of drought in improving stand
11 resilience are further demonstration of the complex response of subalpine forests to global
12 warming. Typically subalpine forests are modeled in future scenario projections to shift
13 continuously up in elevation, with consequences of massive extirpation as they run out of
14 suitable habitat at summits (e.g., Shafer et al. 2001; Hayhoe et al. 2005). In other Sierran studies
15 we have been documenting that forest response to climate variability is far more complex, with
16 reversible disturbance and colonization events, shifts among aspects and not just elevation,
17 changes in growth habit rather than population shift, and even retreat downslope into cooler
18 ravines off exposed windswept slopes (Millar et al. 2004; Millar et al. 2006). The processes of
19 mortality in the sensitive limber pine stands described in this paper are another example of such
20 complexity. The limber pine stands we studied are likely to persist into the future, despite the
21 heavy mortality they experienced, and even with increasing temperatures and recurring droughts.
22 Healthy advanced regeneration under the dead overstory, as well as pole-sized survivors of the
23 1980s-1990s drought, persist at present, with above average growth and no sign of stress or

1 mortality. We suggest that the mortality pulse during the 1982-1994 drought served to improve
2 the resilience and adaptation of these stands, and that this mechanism may function in other
3 subalpine species and situations as well.

4

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11

Literature Cited

Allen, C.D. and D.D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone:
rapid landscape response to climate variation. *Proceedings of the National Academy of
Sciences (USA)* **95**: 14839-14842.

Berryman, A.A. and G.T. Ferrell. 1988. The fir engraver beetle in the western states. *In*
Dynamics of forest insect populations. Edited by A.A. Berryman. Plenum Press, NY. pp.
555-577.

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H.
Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional
vegetation die-off in response to global-change-type drought. *Proceedings of the National
Academy of Sciences (USA)* **102**: 15144-15148.

- Briffa, K.R., Jones, P.D., Bartholin, T.S., Eckstein, D., Schweingruber, F.H, Karlen, W., Zetterberg, P. and Eronen, M. 1992. Fennoscandian summers from A.D.500: temperature changes on short and long timescales. *Climate Dynamics* **7**: 111-119.
- Campbell, E.M. and J.A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Forest Research* **30**: 1051-1059.
- CFPC (California Forest Pest Council). 1970-1997. Forest pest conditions in California annual reports, 1970-1997. California Forest Pest Council, Sacramento, California.
- Chang, C.P. and T. Li. 2000. A Theory for the tropical tropospheric biennial oscillation *Journal of the Atmospheric Sciences* **57**(14): 2209–2224.
- Chatfield, C. 2004. *The analysis of time series: An introduction*. 6th Ed. Chapman&Hall/CRC.
- Ciesla, W.M., and M.M. Furniss. 1974. Idaho's haunted forests. *American Forests* **81**: 32-35.
- Cook, E.R., and L.A. Kairukstis (eds). 1990. *Methods of dendrochronology*. Dordrecht, Netherlands: Kluwer. 394 pp.
- Cook, E.R., C.A. Woodhouse, C.M. Eakin, and D.M. Meko. 2004. Long-term aridity changes in the western United States. *Science* **306**: 1015-1018.
- Daly, C., R.P. Neilson, D.L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* **33**: 140-158.
- DeMars, C.J., G.T. Ferrell, and W.J. Orosina. 1988. Host-insect/disease interactions in drought-stressed white fir stands at Lake Tahoe, California. *In* Integrated control of Scolytid bark beetles. Proceedings of the IUFRO Working Party and XVII International Congress of

- Entomology Symposium, 4 July 1988. *Edited by* T.L. Payne and H. Saarenmaa. Virginia Polytechnic Institute. Pp 135-146.
- Dolph, K.S., S.R. Mori, and W.W. Oliver. 1995. Long-term response of old-growth stands to varying levels of partial cutting in the eastside pine type. *Western Journal of Applied Forestry* **10**: 101-108.
- Esper, J., E.R. Cook, and F.H. Schweingruber. 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* **295**: 2250-2253.
- Fensham, R.J. and J.E. Holman. 1999. Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *Journal of Applied Ecology* **36**: 1035-1050.
- Ferrell, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options*. Centers for Water and Wildland Resources. University of California, Davis, Water Resources Center Report No. 37. pp. 1177-1192.
- Ferrell, G.T., W.J. Otrasina, and C.J. Demars. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus entralis*, in California. *Canadian Journal of Forest Research* **24**: 302-305.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, New York.
- Goheen, E.M., D.J. Goheen, K. Marshall, R.S. Danchok, J.A. Petrick, and D.E. White. 2002. The status of whitebark pine along the Pacific Crest National Scenic Trail on the Umpqua National Forest. USDA Forest Service. General Technical Report, PNW-GTR-530. 21 pp.
- Graumlich, L.G. 1993. A 1000-yr record of temperature and precipitation in the Sierra Nevada. *Quaternary Research* **39**: 249-255.

- Gray, S.T., J.L. Betancourt, C.L. Fastie, and S.T. Jackson. 2003. Patterns and sources of multidecadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. *Geophysical Research Letters* **30**: X1-X6.
- Gray, S.T., J.L. Betancourt, S.T. Jackson, and R.G. Eddy. 2006. Role of multidecadal climate variability in a range extension of pinyon pine. *Ecology* **87**(5): 1124-1130.
- Green, D.S. 2005. Adaptive strategies in seedlings of three co-occurring ecologically distinct northern coniferous tree species across an elevational gradient. *Canadian Journal of Forest Research* **35**: 910-917.
- Grissino-Mayer, H.D. 1996. A 2129-year reconstruction of precipitation for northwestern New Mexico, USA. In *Tree Rings, Environment, and Humanity*, J.S. Dean, D.M. Meko, and T.W. Swetnam (eds.) pp191-204. *Radiocarbon*. Tucson, AZ.
- Guarin, A., and A.H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *Forest Ecology and Management* **218**: 229-244.
- Gutschick, V.P. and H. BassiriRad. 2003. Extreme events as shaping physiology, ecology, and evolution of plants; toward a unified definition and evaluation of their consequences. *New Phytologist* **160**: 21-42.
- Hamann, A. and T.L. Wang. 2005. Models of climatic normals for geneecology and climate change studies in British Columbia. *Agricultural & Forest Meteorology* **128**: 211-221.
- Hayhoe, K., D. Cayan, C.B. Field, and 16 others. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Science*, **101**: 12422-12427.

- Hicke, J.A., J.A. Logan, J. Powell, and D.S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research-Biosciences*. In press
- Holmes, R.L., R.K. Adams, and H.C. Fritts. 1986. Tree-ring chronologies of western North America: California, Eastern Oregon, and Northern Great Basin with procedures used in the chronology development work including user's manuals for computer programs COFECHA and ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Chronology Series VI.
- Innes, J.L. 1992. Forest decline. *Progress in Physical Geography* **16**: 1-64.
- JISAO (Joint Institute for the Study of the Atmosphere and Ocean). 2006. University of Washington and NOAA. Monthly PDO indices available at:
<http://www.jisao.washington.edu/pdo/>
- Jones, M.E., T.D. Paine, M.E. Fenn, and M.A. Poth. 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *Forest Ecology and Management* **200**: 67-76.
- Kegley, S., J. Schwandt, and K. Gibson. 2001. Forest health assessment of whitebark pine on Pyramid Pass, Russell Mountain, and Burton Ridge in the Selkirk Mountains on the Idaho Panhandle National Forest. USDA Forest Service. FHP Report **01-8**: 11 pp.
- Kendall, K.C. 1994. Whitebark pine conservation in North American national parks. *In* Proceedings-International workshop on subalpine stone pines and their environment: The status of our knowledge. *Edited by* W. Schmidt and F.K. Holtmeier USDA Forest Service, Intermountain Research Station, Ogden, UT. General Technical Report INT-GTR-309. pp. 302-307.

- Kendall, K.C. and S.A. Arno. 1990. Whitebark pine -- An important but endangered wildlife resource. Proc. Whitebark Pine Symposium. USDA Forest Service General Tech. Rep. INT-270. pp. 264-273.
- Kendall, K. C. and D. Schirokauer. 1997. Alien threats and restoration dilemmas in whitebark and limber pine communities. Proceedings of the George Wright Society Conference on Research and Resource Management in Parks and on Public Lands. **Vol 9**. pp. 218-225
- Kendall, K. C., D. Ayers, and D. Schirokauer. 1996. Limber pine status from Alberta to Wyoming. Nutcracker Notes 7:23-24. USDA Forest Service, Intermountain Research Station, IFSL. Missoula, MT.
- Kern, R.A. 1996. A comparative study of growth and survival of Sierran conifers. Doctoral Dissertation Thesis. Duke University, Durham N.C.
- Krusic, P. and E. Cook. 2005 ARSTAN40 for MAC OS X. Available at:
<http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html>
- Logan, J.A. 2004. Climate change altered disturbance regimes in high-elevation pine ecosystems. Abstracts and presentations of the American Geophysical Union Meeting 13-17 December 2004, San Francisco, CA. Available at:
<http://www.fs.fed.us/psw/cirmount/meetings/agu/agu2004.shtml>
- Logan, J.A. and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*: **47**(3): 160-172.
- Logan, J.A. and J.A. Powell. 2005. Ecological consequences of climate change altered forest insect disturbance regimes. *In* Climate change in western North America: evidence and environmental effects. *Edited by* F. H. Wagner. Allen Press.

- Macomber, S.A. and C.E. Woodcock. 1994. Mapping and monitoring conifer mortality using remote sensing in the Lake Tahoe Basin. *Remote Sensing of Environment* **50**: 255-266.
- Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of American Meteorology. Soc.* **78**: 1069-1079.
- Mattson, W.J. and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* **37**: 110-118.
- Meehl, G.A. 1997. The South Asian monsoon and the tropospheric oscillation (TBO). *Journal of Climate* **10**: 1921-1943.
- Millar, C.I., R.D. Westfall, D.L. Delany, J.C. King, and L.C. Graumlich. 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**: 181-200.
- Millar, C.I., J.C. King, R.D. Westfall, H.A. Alden, and D.L. Delany. 2006. Late Holocene forest dynamics, volcanism, and climate change at Whitewing Mountain and San Joaquin Ridge, Mono County, Sierra Nevada, CA, USA. *Quaternary Research*. In Press.
- Ministry of Forests. 2006. Mountain pine beetle action plan. Province of British Columbia. Mountain pine beetles in British Columbia. Survey information available at:
http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/#action
- Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases vigor and resistance to mountain pine beetle. *Forest Science* **29**: 204-211
- NOAA. 2006. Palmer Drought Severity and soil moisture indices available from
<http://www.drought.noaa.gov/>

- Oogle, K., T.G. Whitham, and N.S. Cobb. 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* **81**: 3237-3243.
- Palmer, W. C., 1965. Meteorological drought. Research Paper No. 45, U.S. Department of Commerce Weather Bureau, Washington, D.C.
- Perkins, D.L. and T.W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Canadian Journal of Forest Resources* **26**: 2123-2133.
- Raleigh, C., D.R. Vogler, and K. Cullings. 2005. Effects of severe dwarf mistletoe infection on the ectomycorrhizal community of a *Pinus contorta* stand in Yellowstone Park. *Canadian Journal of Botany* **83(9)**: 1174-1189.
- SAS Institute Inc. 2004. SAS Online Doc 9.1.2. Cary, NC: SAS Institute Inc. JMP Statistics and Graphics Guide, version 5. SAS Institute, Cary, NC.
- Savage, M. 1994. Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Canadian Journal of Forest Research* **24**: 1149-1159.
- Schmid, J.M. and S.A. Mata. 1992. Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands. USDA For. Serv., Res. Note RM-515, Rocky Mountain For. and Range Exp. Stn., Ft. Collins, CO. 4 p.
- Shafer, S.L., P.J. Bartlein, and R.S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* **4**: 200-215.
- Stahle, D.W., M.D. Therrell, D.R. Cayan, M.D. Dettinger, and N. Knowles. 2001. Ancient blue oaks reveal human impact on San Francisco Bay salinity. *EOS Transactions, American Geophysical Union* **82**: 141. 144-145.

- Stahle, D.W., M.K. Cleaveland, R.D. Griffin, M.D. Spong, E.K. Fye, R.B. Culpepper and D. Patton. 2006. Decadal drought effects on endangered woodpecker habitat. EOS Transactions, American Geophysical Union **87**: 121-125.
- Stine, S. 1994. Extreme and persistent drought in California and Patagonia during Medieval time. Nature **369**: 546-549.
- Stine, S. 1996. Climate, 1650-1850. Sierra Nevada Ecosystem Project: Final report to Congress. Vol. II: Assessments and Scientific Basis for Management Options. Wildland Resources Center Report **37**: 25-31.
- Stokes, M.A., Smiley, T.L. 1968. An Introduction to Tree-Ring Dating. Chicago, University of Chicago Press: 73 pp.
- Suarez, M., L. Ghermandi, and T. Kitzberger. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. Journal of Ecology **92**: 954-966.
- Swetnam, T.W. and J.L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climatology **11**: 3128-3147.
- Taylor, J.E. and R.L. Mathiason. 1999. Limber pine dwarf mistletoe. USDA Forest Service Forest Insect and Disease Leaflet **171**: 1-8.
- USGS (U.S. Geological Survey). 2006. Water Resources Division. Streamflow data available from http://nwis.waterdata.usgs.gov/ca/nwis/annual/calendar_years
- van Mantgem, P.J., N.L. Stephenson, and J.E. Keeley. 2006. Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecology and Management **225**: 391-399.

Waring, G.L. and N.S. Cobb. 1992. The impact of plant stress on herbivore population dynamics.

In Insect-plant interactions. Vol. 4. *Edited by* Bernays, E. CRC Press. Pp. 167-187.

Waring, K.M. and D.L. Six. 2005. Distribution of bark beetle attacks after whitebark pine

restoration treatments: A case study. *Western Journal of Applied Forestry* **20(2)**: 110-116.

Wolfram Research Inc. 2005. Mathematica. A system for doing mathematics by computer. Vs 5.

Champaign, IL.

WRCC (Western Regional Climate Center). 2006. Instrumental historic weather databases,

available from <http://wrcc.dri.edu>

Table 1. Tree-ring series sensitivity values (s) and correlations among cores (r) in chronologies, by site and composites of live and dead tree sets. OWE site was analyzed separately because of its distinct location and growth behavior, and lack of mortality.

Class	Site	s	r
Live	CLO	0.194	0.526
	DES	0.289	0.525
	LAU	0.242	0.511
	Composite	0.211	0.466
Dead	CLO	0.218	0.491
	DES	0.238	0.582
	LAU	0.313	0.709
	Composite	0.240	0.512
Live	OWE	0.374	0.704

Table 2. Estimates of current (1961-1990) climate for young (Y) limber pine study stands and nearby old-growth (O) limber pine stands, extracted from the PRISM climate model (Daly et al. 2001) and downscaled as in Millar et al. (2006).

	Age	Elev	Annual Precip	January Precip	July Precip	Annual Max Temp °C	January Max Temp °C	July Max Temp °C	Annual Min Temp °C	January Min Temp °C	July Min Temp °C
		<i>m</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>						
LAU	Y	2615	656.45	103.84	12.23	12.51	3.92	24.11	-3.56	-8.60	4.47
Glass Mtn	O	3057	885.31	163.53	16.14	11.00	2.30	22.16	-4.10	-10.24	4.73
DES	Y	2682	620.07	133.02	17.68	12.90	2.66	24.82	-3.49	-11.01	5.44
Lundy Cyn	O	3028	876.90	150.60	23.34	8.52	-0.20	20.58	-4.96	-11.58	4.33
CLO	Y	2813	698.91	143.57	15.67	11.61	1.81	23.40	-3.65	-10.74	5.29
Bloody Cyn	O	3070	1133.31	191.33	28.66	8.31	0.35	19.33	-5.80	-12.71	3.61
OWE	Y	2060	292.91	47.41	14.55	16.27	6.78	28.19	-1.11	-7.15	7.70
Wheeler Crest	O	3050	477.30	74.57	10.16	10.34	2.76	21.38	-4.05	-9.68	4.74

Table 3. Correlation coefficients of standardized tree-ring widths (Std RW) for live and dead trees at the CLO, DES, and LAU stands with water-year precipitation (WY ppt), minimum annual temperature (Tmin), May minimum temperature (TminM), July minimum temperature (TminJ), annual maximum temperature (Tmax), the Palmer Drought Severity Index (California Zone 5; PDSI), and the Pacific Decadal Oscillator (PDO). Correlations of Tmax and PDO are not significant; all others have $p < 0.05$.

	WY ppt	Tmin	TminM	TminJ	Tmax	PDSI	PDO
Live Trees: Std RW	0.52	0.48	0.40	0.31	-0.01	0.27	0.10
Dead Trees: Std RW	0.57	0.22	0.19	0.07	-0.21	0.46	0.08

Figure Captions

Figure 1. Location of the four study sites in the eastern Sierra Nevada. Inset: distribution of *Pinus flexilis* in western North America.

Figure 2. Individual tree-ring-series ages for four limber pine stands in the eastern Sierra Nevada. Birth (pith) dates at left and death (bark) dates at right. Gray lines are live trees, black lines are dead trees. Sample numbers for dead and live trees are indicated.

Figure 3. Frequency of limber pine death dates at three stands (DES, CLO, LAU), showing cluster of dates between 1985 and 1995.

Figure 4. Climate, mortality, and growth from 1910 to 2005, eastern Sierra Nevada. **A.** Trends in minimum monthly temperature (solid line) and maximum monthly temperature (dotted line) in the composite record derived from three regional weather stations. **B.** Trends in water-year precipitation (solid line), derived from the same composite climate record. **C.** Growth of secondary rings in limber pine, composite of CLO, DES, and LAU sites; dead trees (solid line), live trees (dotted line).

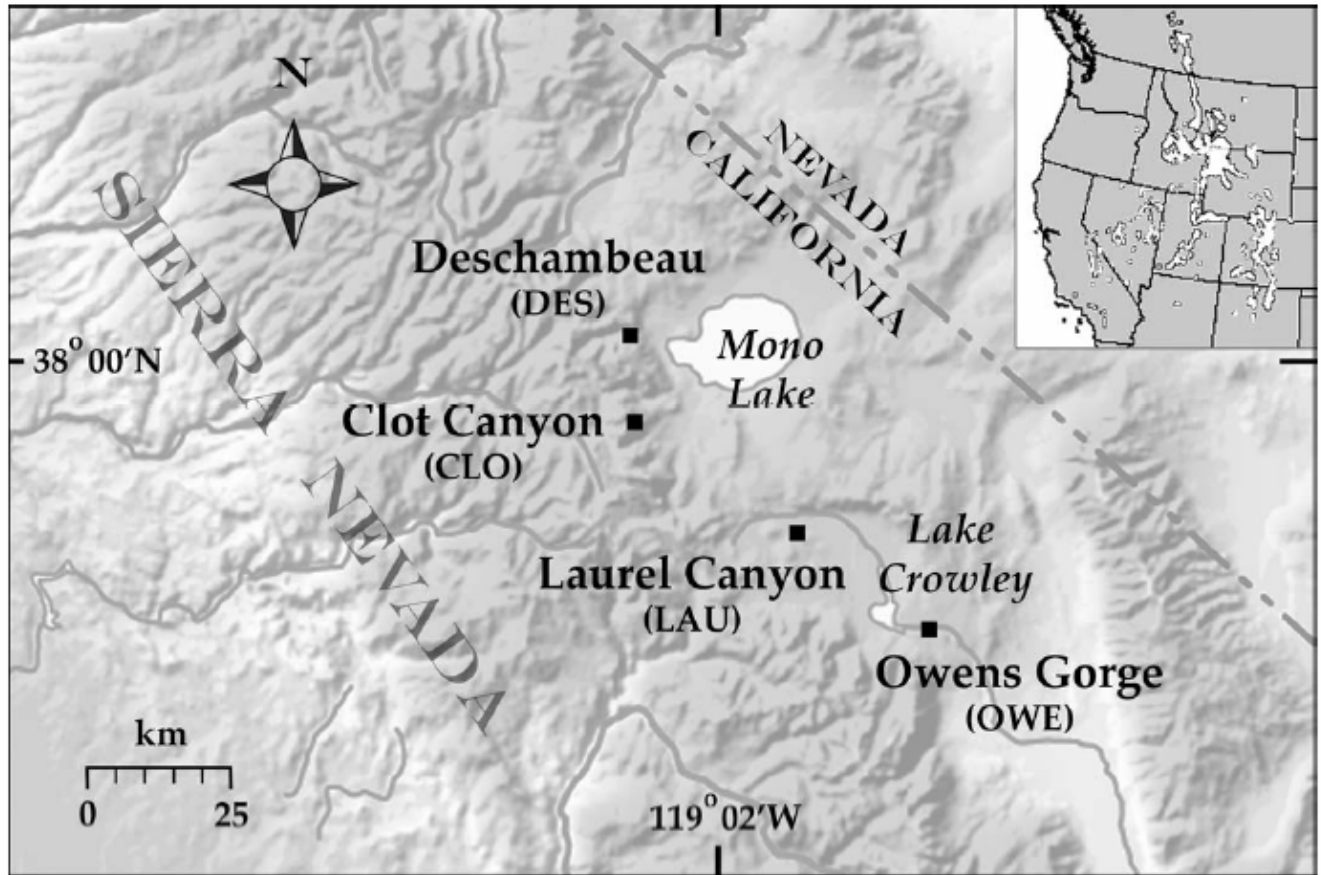
Figure 5. Fourier analysis of water year precipitation (solid line) and annual streamflow from composite Sierra climate and river gauge stations. Significant spectral peaks occur at 2.20 and 15.00 years (precipitation) and 2.14 and 15.00 (streamflow).

Figure 6. Variation in water-year precipitation from 1920-2005, derived from composite precipitation records, eastern Sierra Nevada.

Figure 7. Change in variance of tree growth for live and dead tree sets over 20th century, showing significant change of pattern and increasing variance in the 20th century. Combined dataset from LAU, CLO, and DES stands. GARCH method of analysis.

Figure 8. Contour maps showing effects of second-order interactions between tree growth and climate. **A.** Live tree response to water year precipitation and minimum temperature. **B.** Dead tree response to water year precipitation and minimum temperature. **C.** Live tree response to water year precipitation and maximum temperature. **D.** Dead tree response to water year precipitation and maximum temperature. In each case, tree growth increases as contours increase. Contour intervals are in units of standardized tree-ring growth. Main axis units are standard deviations from the mean of each variable. Scatter of dots in each graph is the set of recorded points from the composite 20th-century instrumental weather record. Maximum temperature is held at mean in A. and B.; minimum temperature at mean in C. and D.

FIGURE 1



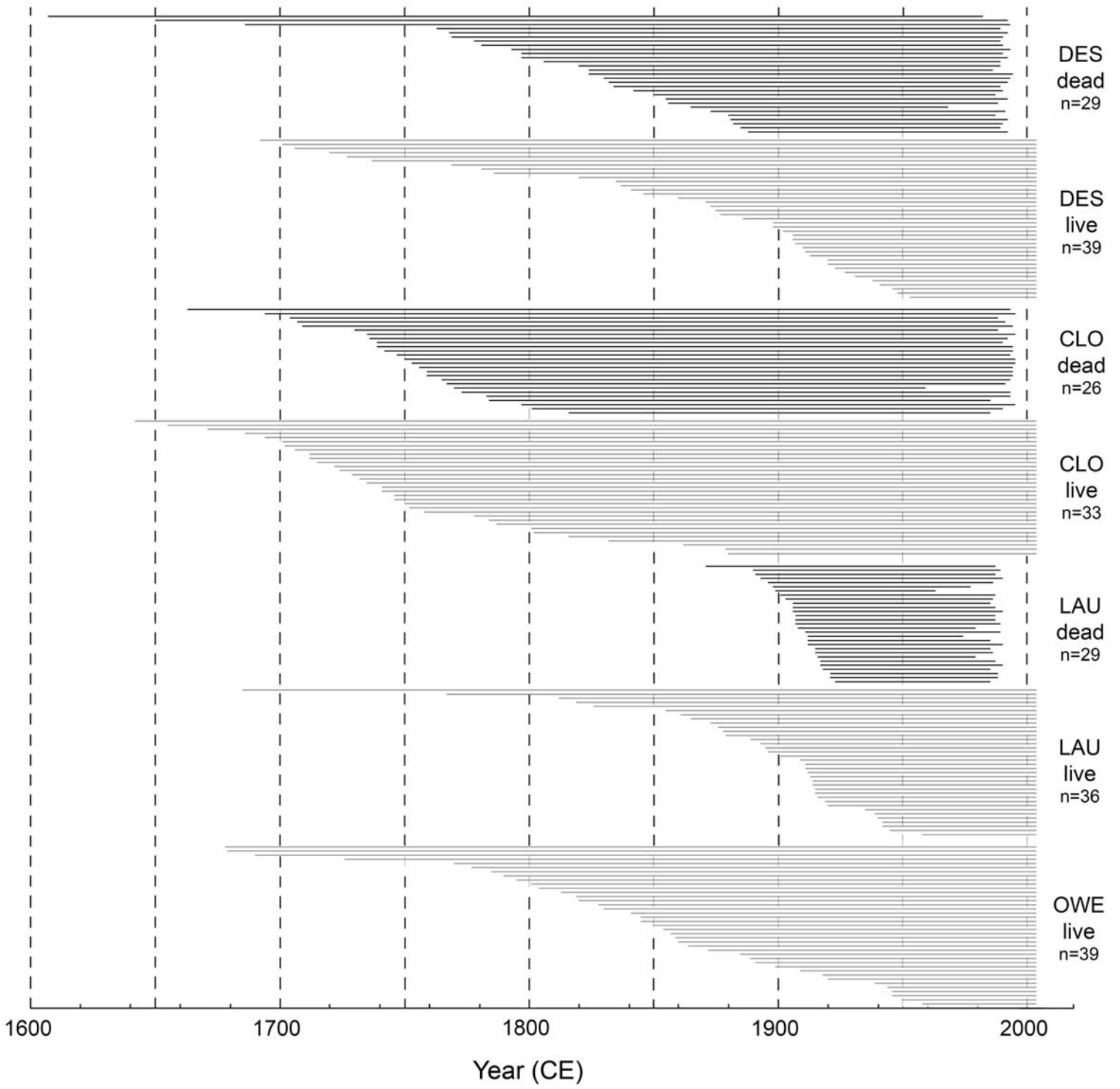


FIGURE 3

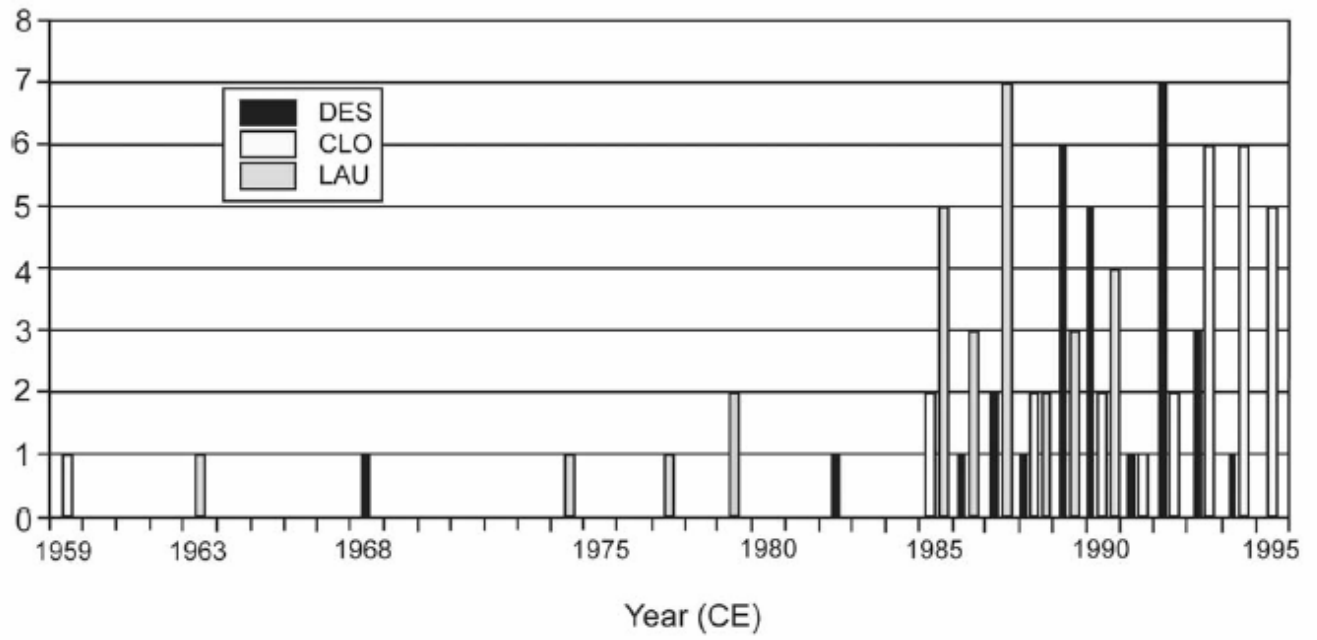


FIGURE 4

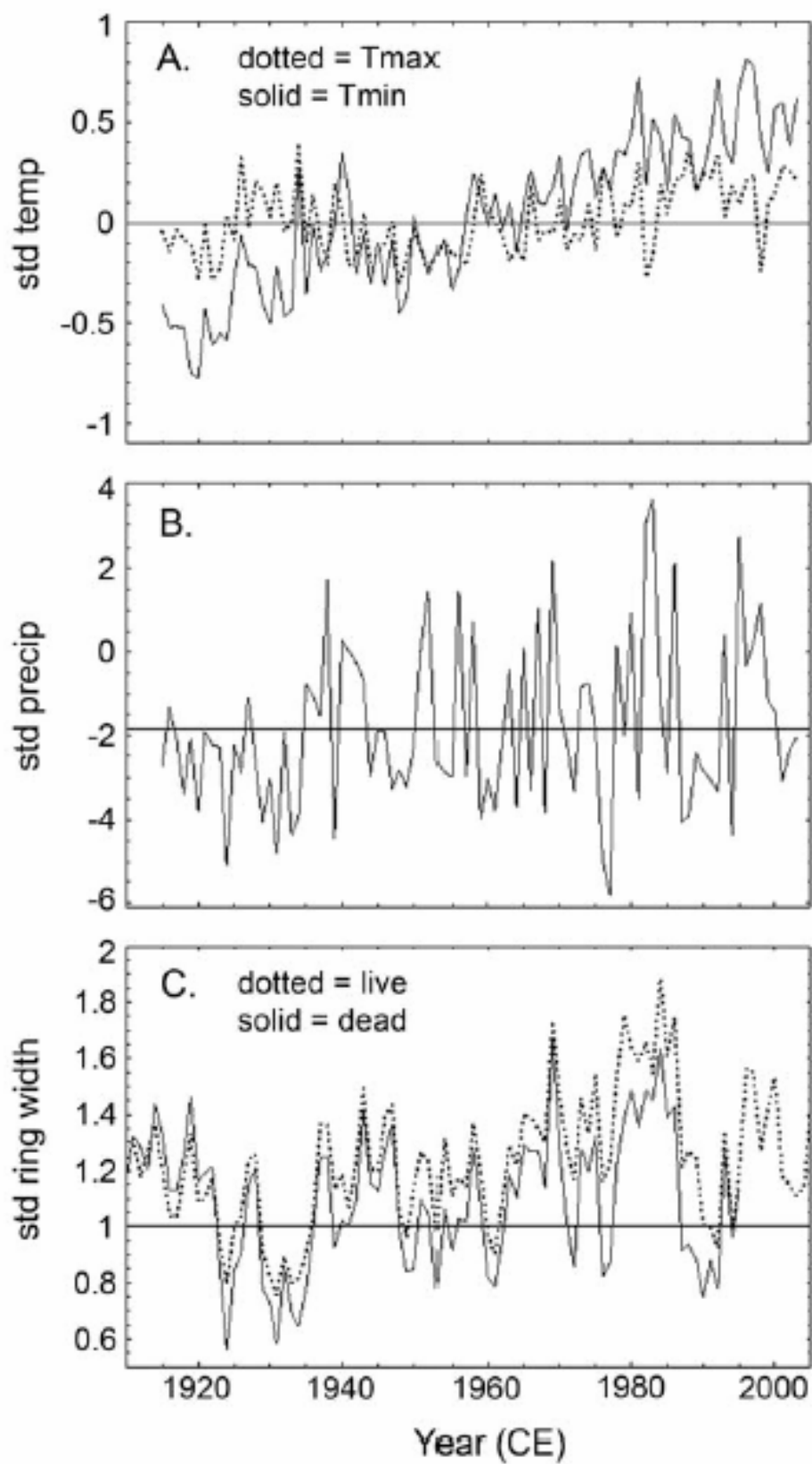


FIGURE 5

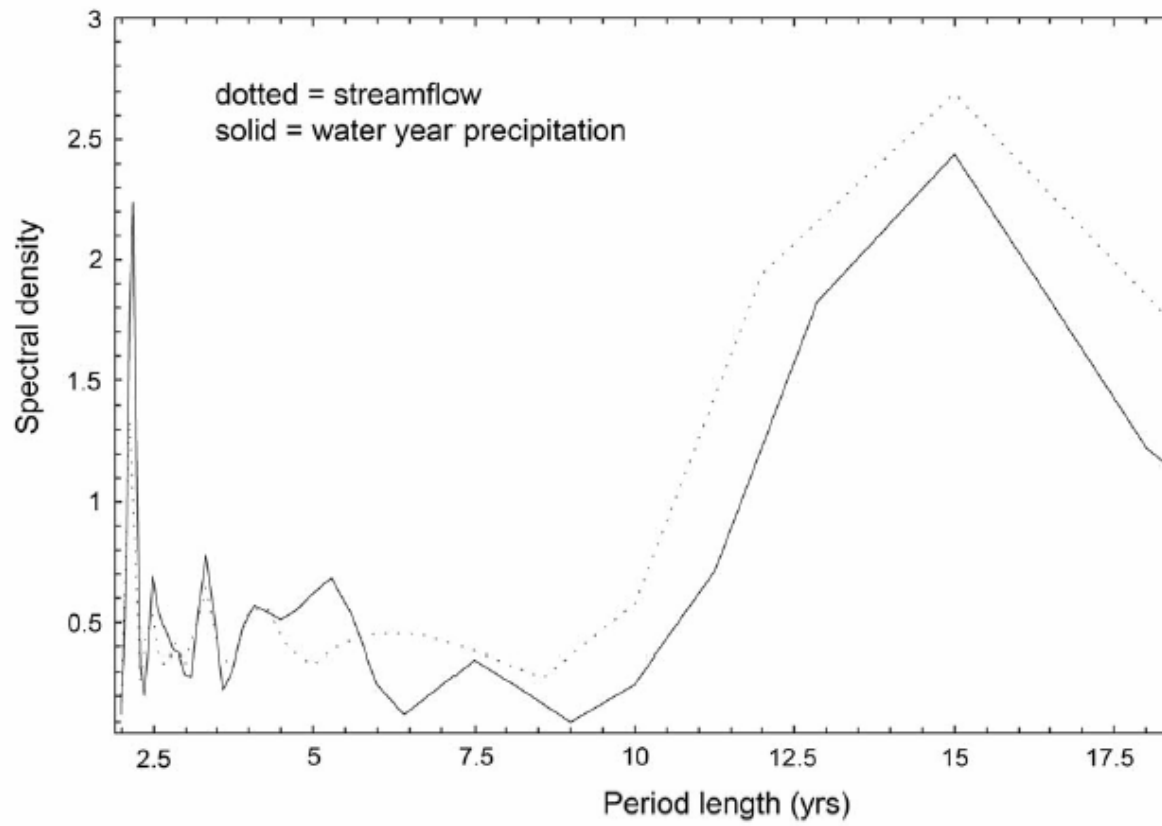


FIGURE 6

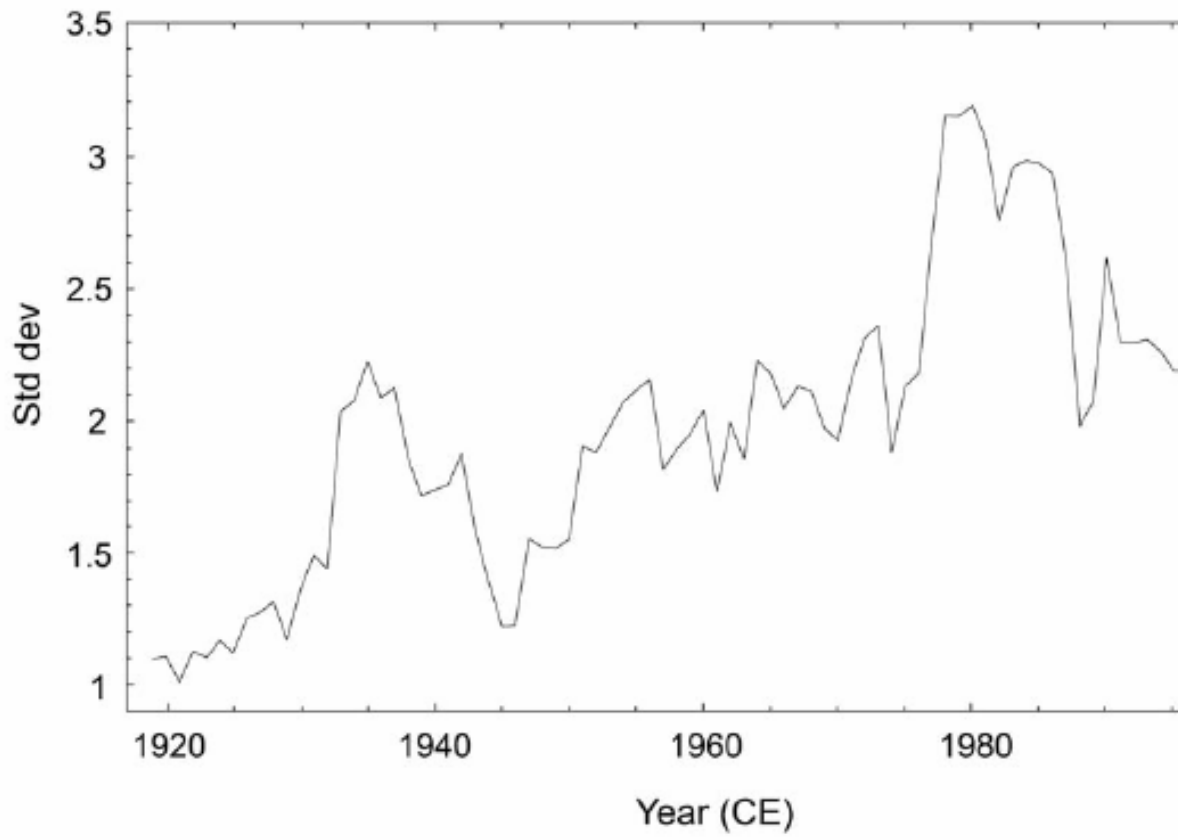


FIGURE 7

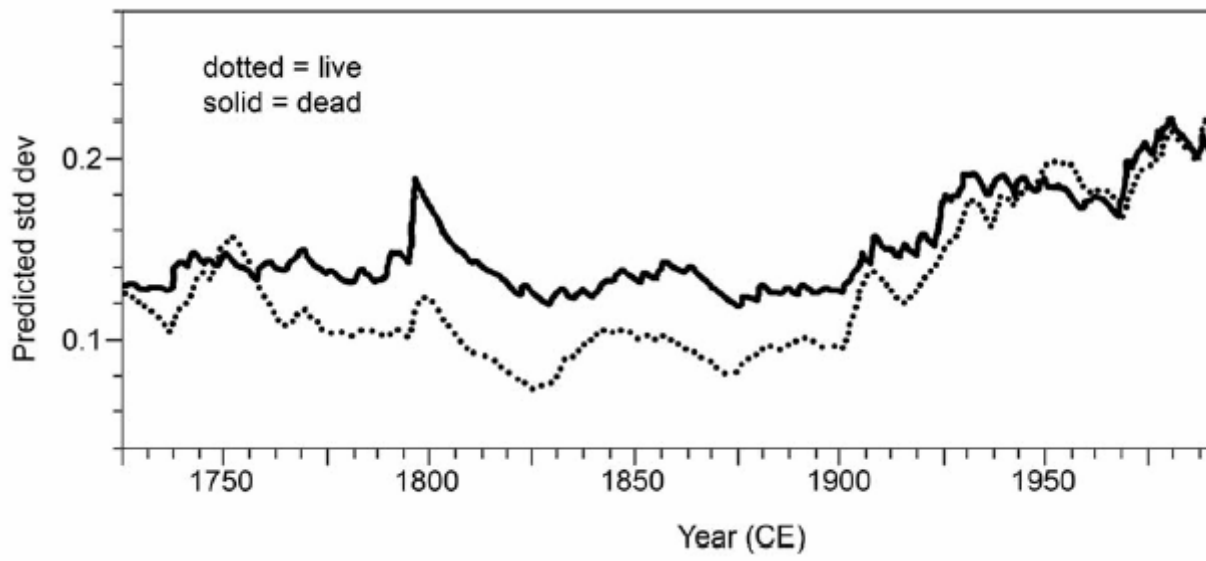


FIGURE 8

