

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

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**Abstract:** Limber pine (*Pinus flexilis* James) stands along the eastern escarpment of the Sierra Nevada, California, experienced significant mortality from 1985 to 1995 during a period of sustained low precipitation and high temperature. The stands differ from old-growth limber pine forests in being dense, young, more even-aged, and located in warmer, drier microclimates. Tree growth showed high interannual variability. Relative to live trees, dead trees over their lifetimes had higher series sensitivity, grew more variably, and had lower growth. Although droughts recurred during the 20th century, tree mortality occurred only in the late 1980s. Significant correlations and interactions of growth and mortality dates with temperature and precipitation indicate that conditions of warmth plus sustained drought increased the likelihood of mortality in the 1985–1995 interval. This resembles a global-change-type drought, where warming combined with drought was an initial stress, trees were further weakened by dwarf mistletoe (*Arceuthobium cyanocarpum* (A. Nels. ex Rydb.) A. Nels.), and proximally killed by mountain pine beetle (*Dendroctonus ponderosae* Hopkins). However, the thinning effect of the drought-related mortality appears to have promoted resilience and improved near-term health of these stands, which suffered no additional mortality in the subsequent 1999–2004 drought.

**Résumé :** Les peuplements de pin flexible (*Pinus flexilis* James) situés le long de l'escarpement est de la Sierra Nevada, en Californie, ont subi une mortalité appréciable de 1985 à 1995 durant une période marquée par des conditions soutenues de faible précipitation et de température élevée. Ces peuplements diffèrent des vieilles forêts de pin flexible : ils sont denses, jeunes, plutôt équiennes et sous l'influence d'un microclimat plus chaud et plus sec. La croissance des arbres a fortement varié d'une année à l'autre. Comparativement aux arbres vivants, les arbres morts avaient, sur l'ensemble de leur vie, des séries plus sensibles ainsi qu'une croissance plus variable et plus faible. Bien que les sécheresses se soient succédées au cours du 20<sup>e</sup> siècle, la mortalité est survenue seulement à la fin des années 1980. Des corrélations et interactions significatives entre la croissance et le moment où est survenue la mortalité avec la température et la précipitation indiquent que des conditions de chaleur et de sécheresse prolongées ont augmenté les chances de mortalité durant l'intervalle de 1985–1995. Cela ressemble à une sécheresse typique d'un changement global où un réchauffement combiné à la sécheresse a causé un stress initial. Les arbres furent ensuite davantage affaiblis par le faux-gui (*Arceuthobium cyanocarpum* (A. Nels. ex Rydb.) A. Nels.) et tués peu après par le dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins). L'éclaircie causée par la mortalité reliée à la sécheresse apparaît cependant avoir favorisé la résilience et amélioré la santé à court terme de ces peuplements qui n'ont subi aucune mortalité additionnelle lors de la sécheresse de 1999–2004.

[Traduit par la Rédaction]

## Introduction

Extensive tree mortality associated with recurring droughts is characteristic of western North American montane forests. Most recently, the 1999–2004 drought, increasing temperatures, and associated bark beetle infestations are resulting in millions of hectares of forest dieback in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in British Columbia, Canada (B.C. Ministry of Forests and Range 2006), pinyon pine (*Pinus edulis* Engelm. and *Pinus monophylla* Engelm.) and ponderosa pine (*Pinus ponderosa* Dougl. ex

Laws.) in the Colorado Plateau region (Breshears et al. 2005), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the southwestern ranges (Logan and Powell 2001, 2007), and mixed conifer forests of southern California (Jones et al. 2004). Previous significant droughts and forest mortality events centered on the late 1980s in California (Ferrell et al. 1994), 1970s in the northern Rockies (Logan and Powell 2001), and 1950s westwide (Allen and Breshears 1998). Droughts and associated impacts on forest growth and mortality have occurred repeatedly during previous centuries as well, as documented by tree-ring reconstructions from throughout western North America (Cook et al. 2004).

The duration of droughts and interaction with temperature affect forest response. Single dry years are less likely to result in high mortality than multiple years of low precipitation (Guarin and Taylor 2005), and multidecadal periods (30–60 years) are documented to have resulted in significant regional mortality historically (Gray et al. 2003). High temperatures during droughts increase the likelihood of mortal-

Received 15 August 2006. Accepted 7 May 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 6 December 2007.

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ity (Logan and Powell 2001; Breshears et al. 2005; Guarin and Taylor 2005) as do wet intervals preceding multiyear droughts. Although direct water stress is well known to be linked with forest health (Fensham and Holman 1999; Guarin and Taylor 2005), vulnerability of trees varies with other factors as well. Tree death is often proximally caused by insects or pathogen infestation (Mattson and Haack 1987; Waring and Cobb 1992), and the level of stress and success of insect attack depend on conditions of stand structure. Conditions that increase vulnerability of forests include dense and even-age stand structure (Ferrell et al. 1994; Dolph et al. 1995); aspect and elevation also are related to forest health (van Mantgem et al. 2006). Suppressed trees are known to succumb during drought before dominant or codominant trees (Ferrell et al. 1994), and multiple stand stressors (e.g., high density and even-age structure) can contribute to vulnerabilities (Ferrell et al. 1994; Dolph et al. 1995; Fensham and Holman 1999; Guarin and Taylor 2005). Genetic factors also condition vulnerability to environmental stress (Ogle et al. 2000; Suarez et al. 2004; Green 2005). For instance, during the late 1980s drought in the western Sierra Nevada, white fir (*Abies concolor* Gord. & Glend.) Lindl.) experienced significantly higher mortality than other conifers in mixed-species stands (Ferrell et al. 1994). Within species, genetic differences among populations and among trees within populations also affect growth and survival under climate stress (Conkle 1973; Alia et al. 1995). Interactions among genetic and environmental factors of the stand likely precondition vulnerability of stands and trees within stands.

Whereas forest mortality events occur episodically at low to middle montane elevations in western North America, subalpine forests have been far less affected. Conditions at high elevations generally have been less conducive to extensive insect and disease outbreaks than at lower elevations. These include wide spacing among trees, rocky substrates with little shrub or understory, low relative humidity, low temperatures, and persistent snowpacks, which are conditions that suppress build-up of insect populations (Logan and Powell 2001, 2005). The most extensive dieback in subalpine forests of western North America in recent decades is occurring as a result of non-native white pine blister rust (Kendall and Arno 1990). Aside from blister rust, which has not been observed as a significant problem in the eastern Sierra Nevada, observations of scattered mortality related to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are being reported in other subalpine forests of the West, although these generally have been in stands below 2500 m (Logan and Powell 2001, 2005; Goheen et al. 2002; Waring and Six 2005).

During the late 1980s, forest managers observed stands of high-elevation pine dying along the eastern Sierra Nevada escarpment in California. The mortality wave continued for several years and appeared limited to limber pine (*Pinus flexilis* James), a rare subalpine species with highly disjunct range in that part of the Sierra. In this paper, we present results from a study that investigated the mortality event in limber pine forests of the eastern Sierra Nevada. We asked the following questions: what was the time interval during which trees died; how did tree growth and dates of mortality correlate with climate variability; and were there differences

in growth over time between surviving trees and those that died that suggest differential adaptation to climate? We addressed these questions with a dendroecological study of three stands that experienced high mortality and one stand in a comparable location and condition that had no elevated mortality. Our objective was not to assess structural differences among stands that contribute to mortality but to statistically remove stand-level influences and to examine the regional influence (climate) on tree growth and mortality. We assessed age and growth (ring width) of live and dead trees over their lifespans and dated the year of death of dead trees. Assembling regional instrumental weather records, we investigated correlations between growth, death dates, and climate indicators to assess the potential role of climate in influencing high-elevation forest mortality.

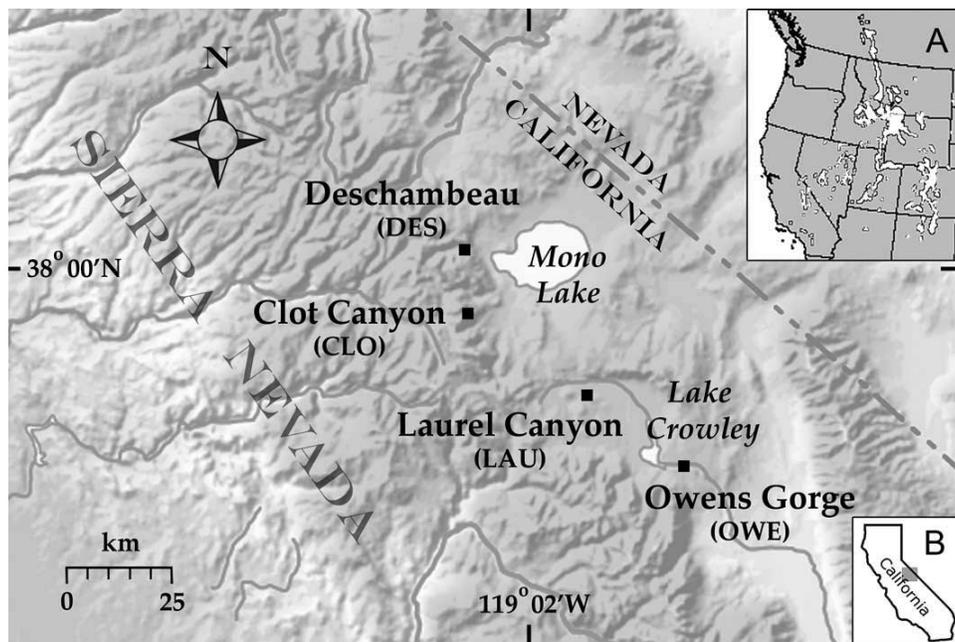
## Materials and methods

### Study area

Limber pine is a wide-ranging species of the British Columbia Coast Range, Canada, and the Intermountain, Great Basin, and Southwest Ranges, Rocky Mountains, and Sierra Nevada, USA (Fig. 1). Although it extends as low into mid-montane forests as 1500 m in the northern parts of its range in Canada, limber pine is primarily a subalpine species, reaching 3700 m and often establishing the upper treeline. Our study region was located near the species' northern distribution in the Sierra Nevada (Fig. 1), where limber pine shares the upper elevation tree zone with whitebark pine (*Pinus albicaulis* Engelm.) and, occasionally, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and western juniper (*Juniperus occidentalis* Hook.). Stands in this area are disjunct and limited in elevational range (2450–2990 m), size (<175 ha), and aspect (north to northeast). Typical stands are characterized by widely separated, old-growth trees dominated by twisted, often strip-barked individuals 800 to >1500 years old growing on steep, rocky slopes of granitic or metamorphic substrate. Trees less than ~200 years old generally are present only in low frequencies; overall, the stands are sparse with little understory vegetation and abundant bare ground. Lightning occasionally ignites individuals or small clusters of trees, but fire is not an important ecological driver in the old-growth stands. Deadwood commonly persists more than three millennia in these cold, arid environments and is evidence for stand persistence for such duration (unpublished study).

Less commonly, limber pine stands in the eastern Sierra Nevada have dense, closed-canopy conditions. These consist of pole- to mid-sized, straight-stemmed trees, with few old-growth individuals, little accumulated deadwood, and a small range of size (presumably age) classes. Compared with the old-growth populations in this region, these stands experienced obvious mortality during the late 20th century. We studied three stands with high mortality in mature trees: Deschambeau Creek (DES; 2510–2980 m; 155 ha), Clot Canyon (CLO; 2700–2980 m; 40 ha), and Laurel Canyon (LAU; 2450–2960 m; 55 ha) (Fig. 1). The stands have north to northeast aspects and are on moderate to steep slopes. Dead trees retained bark and fine branches when sampled in 2005 and 2006 and showed signs of past infestation by mountain pine beetle (confirmed during active infestation,

**Fig. 1.** Location of four study sites in eastern North America (main image). Inset A: distribution of *Pinus flexilis* in western North America; inset B: location of the study area in the eastern Sierra Nevada.



and galleries remaining), blue stain fungus (*Ophiostoma* sp.), and limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* (A. Nels. ex Rydb.) A. Nels.). These conditions were most severe at the DES and LAU sites. We also studied one population that had similar dense and young stand structure but lacked mortality. It was located on the north-facing slope of deep, narrow Owens Gorge (OWE; 2040–2150 m, 40 ha) (Fig. 1) at an unusually low elevation for limber pine in the region. Typical old-growth stands of limber pine occur near to DES, CLO, and LAU sites at similar elevation range and aspect and, also, adjacent to OWE but at much higher elevation. These old-growth stands showed no sign of late 20th century mortality.

#### Tree-ring collections and analysis

We measured stem diameters and collected increment cores at 0.5 m height on main stems from 40 live and 40 dead trees at DES, CLO, and LAU and 40 live trees at OWE and prepared cores for ring-width measurement, dating, and analysis using standard tree-ring techniques (Stokes and Smiley 1968; Holmes et al. 1986; Cook and Kairiukstis 1990). Pith and bark dates were obtained for all series that could be dated. Cross-dating was done by live and dead tree chronologies developed for each site by COFECHA (Holmes et al. 1986) using live trees to establish calendar dates and excluding series that had correlations to the master chronology of  $<0.4$ .

Series from the three stands with high mortality (LAU, CLO, and DES) were highly correlated within and among sites, so we combined chronologies from these sites to make composite live and dead chronologies, further eliminating series with low correlations. We kept the live tree chronology from OWE separate because of its low correlation with the other stands, although series within the site were highly correlated. The combined (live and dead) raw ring-width data prescreened by COFECHA were imported

into ARSTAN40 (Krusic and Cook 2005) for detrending and standardization of ring widths using biweight robust averaging to remove exogenous factors, such as density, and to maximize correlations with climate (Cook 1985). Rather than standard methods, we used the regional curve standardization detrending algorithm (Briffa et al. 1992; Esper et al. 2002) for its skill in preserving low-frequency trends in long tree-ring chronologies despite short segment lengths. In subsequent analyses of growth, we used standardized ring width to improve comparisons among trees of different ages and growing under different stand structural conditions. Detrending removes age- and local-stand related effects that would confound the climate signal and has been recommended as a better indicator of growth than raw ring widths (Biondi 1999; Campbell et al. 2007).

As an indicator of responsiveness to environment, we calculated ring-width sensitivity as the mean of the individual series chronologies (Fritts 1976). Sensitivity is a measure of relative year to year ring-width variability, i.e., the high-frequency response in growth to environmental variables such as climate, and ranges from 0 (all rings equal width; trees are complacent to environmental change) to 2.0 (every other ring missing; tree growth is highly responsive to environmental change). We tested differences in sensitivities between live and dead tree classes and among stands in a mixed model ANOVA, with classes as fixed and stands as random effects.

#### Climate and tree-response analysis

Long-term instrumental climate records were compiled from Lake Tahoe, Yosemite Valley, and Sacramento, California, cooperative weather stations (WRCC 2006). Following the approach of Millar et al. (2004), we statistically combined the data from the individual stations into composite records (1910–2005) for mean monthly minimum and maximum temperature, respectively, and annual and wet-

season (September–April) precipitation, respectively. Higher correlations of tree growth with wet-season precipitation led us to use that variable rather than annual precipitation. We performed moving-average variance analyses (10-year window; Wolfram Research Inc. 2005) using standard deviations of wet-season precipitation derived from variances in interannual deviations in each 10-year window.

Because no high-elevation long-term instrumental weather stations exist near our sites, we evaluated current climate conditions of the four limber pine study sites and adjacent old-growth limber pine stands using the PRISM climate model (Daly et al. 1994). We extracted climate data for annual, January, and July temperature and annual, January, and July minimum and maximum precipitation for the period 1961–1990. We used downscaling methods described in Millar et al. (2006) and Hamann and Wang (2005). Although PRISM is the best indicator of climate at our stands, the model does not accurately estimate microclimate at all sites. In a previous study in the same region and time period, we tested accuracy by comparing PRISM estimates to nearby weather station records and found root mean square deviations mostly less than 5% (Millar et al. 2006).

To test relationships of climate and ecological responses, we analyzed simple linear correlations (SAS Institute Inc. 2004) as well as nonlinear relationships. For the latter, we conducted a second-order, least-squares, response-surface model (JMP; SAS Institute Inc. 2004) of standardized ring widths versus minimum and maximum annual temperature, wet-season precipitation, as well as standard indices of the Palmer drought severity index (PDSI; Palmer 1965, California Division 5, southeastern California; indices from NOAA 2006 for 1900–2006). We evaluated the behavior of these variables in second-order response-surface models of the form  $(x + y + \dots) + (x + y + \dots)^2$ , where redundant interaction terms were omitted. Living and dead classes were included in a mixed-effect, least-squares model with interactions between class effects and surface model terms to test heterogeneity of slopes between the effects.

Minimum and maximum temperatures and wet-season precipitation were the final variables used. We graphed predicted growth using the response-surface model of variables screened, where contour intervals represent standardized growth response, axes are units of standardized deviations from the mean for each climate variable, and in each case, calculations were run under conditions of mean minimum temperature and mean maximum temperature for alternate analyses.

Heterogeneity of variance (PROC AUTOREG; SAS Institute Inc. 2004) was modeled by generalized autoregressive conditional heteroscedasticity (GARCH; Chatfield 2004) to evaluate changes in growth variances over time, based on combined data sets from the CLO, DES, and LAU stands. The ARCH model (orders 1 and 2) estimates variance in time series based on lagged years, whereas the GARCH model is dependent on the integral of variance in previous years.

## Results

### Stand structure, tree ages, growth, and mortality

Limber pine constituted 100% of the conifers in all stands

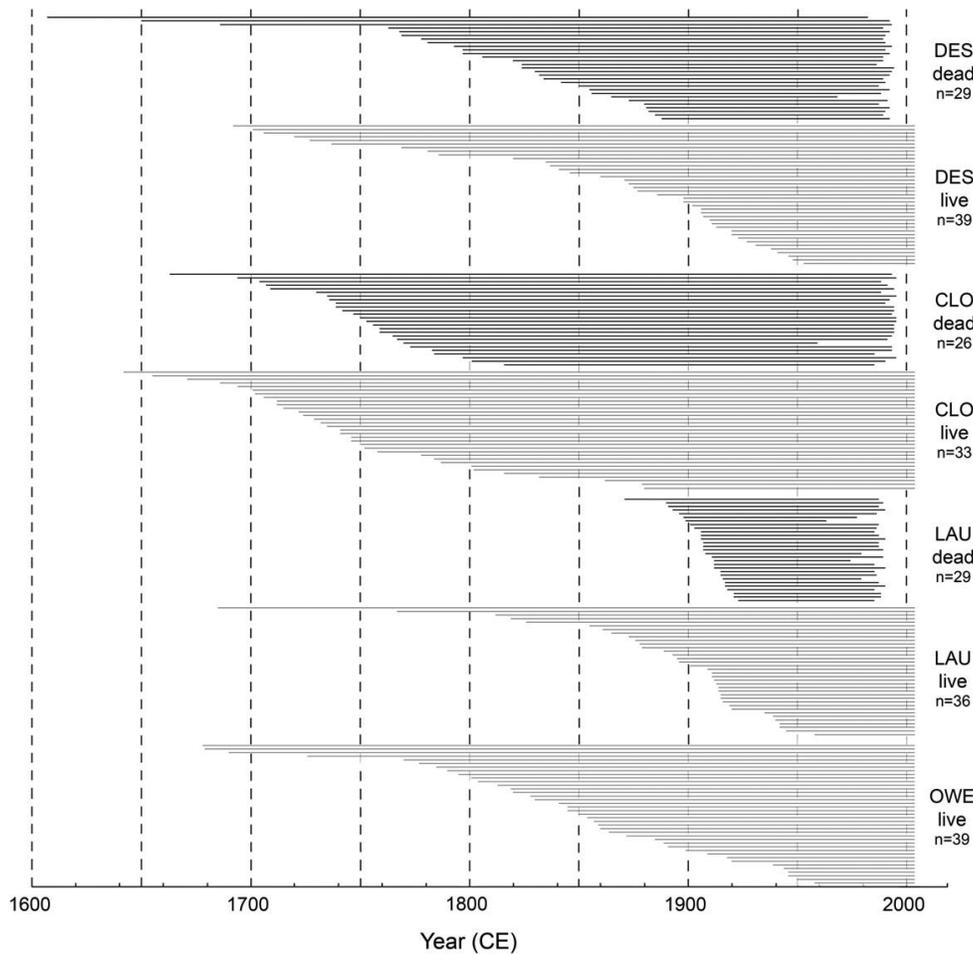
except DES. In the highest 10% elevation (>2930 m) at DES, limber pine was mixed with whitebark pine, which constituted <15% of the stand. Whitebark pine had no signs of 20th century mortality. At LAU, occasional aspen (*Populus tremuloides* Michx.) and desert mahogany (*Cercocarpus ledifolius* Nutt.) occurred between limber pine patches. Limber pine averaged 5–20 m spacing within stands and, at LAU, within patches. At LAU, trees were clustered in patches 0.5–1 ha in size, which were scattered over the extent of the stand and separated by shrubland. Live trees were mixed regularly with dead trees in each stand, although there were occasional patches of high mortality. The overall range at the stand level was 50%–75% mortality in pole and mature trees (>10 cm diameter). Trees with diameters <10 cm experienced no obvious mortality. The mean diameter of all trees was 37.7 cm. A direct comparison of diameters of live and dead trees taken in 2005 was not indicative of the relative size of trees during the mortality period. Surviving trees grew an additional 15–20 years (see death dates below) beyond the time the other group of trees died. Thus, the nonsignificantly larger diameters in 2005 of live trees (40.6 cm) than dead trees (32.1 cm; reflecting diameters prior to 2005) suggests only what was obvious from field observations: the dead trees were not suppressed but rather shared dominance with the surviving trees at least through the late 20th century.

Of the trees sampled in the field, we were able to measure ring widths and accurately cross-date a total of 147 live trees and 84 dead trees from the four sites (Fig. 2). Cores from dead trees were comparably as sound as live trees, but every dead-tree core was stained in the sapwood from blue-stain fungi associated with bark beetles. No live trees showed evidence of blue stain. Individual tree-ring series from dead trees at all stands cross-dated strongly against chronologies developed from live trees at each site, and series correlations to site chronologies ranged from 0.491 to 0.709 (Table 1). Ring-width series among the LAU, CLO, and DES stands were highly correlated, but OWE had low correlations to the other stands.

Compared with typical limber pine stands in the region, the four stands we studied were unusually small diameter, even-aged, and young; the oldest series had a pith date of 1607 (Figs. 2 and 3A). The age of live trees at the four stands in 2005 was  $181 \pm 83$  years (mean  $\pm$  SD). Mean age in 1985 of trees that survived and trees that would subsequently die was not significantly different in the combined data set (dead,  $163 \pm 88$  years; live,  $152 \pm 79$  years) or within stands. Trees at CLO were oldest (age of live trees in 2005,  $255 \pm 60$  years), followed by DES ( $147 \pm 78$  years), OWE ( $142 \pm 52$  years), and LAU ( $113 \pm 54$  years) (Figs. 2 and 3A). Of the trees we sampled, over 90% of the death dates fell between 1985 and 1995. The earliest death date was 1959.

Relative growth of live and dead trees, as indicated by ring widths in the composite curve (Fig. 3B), fluctuated at interannual and multiyear scales over the 20th century and had a small but consistent positive century-long trend ( $p < 0.001$  for live trees;  $p = 0.29$  for dead trees). Although live and dead tree growth (prior to their death) had similar patterns in interannual growth variability during the 20th century, dead trees consistently and significantly ( $p < 0.0001$ )

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



**Table 1.** Tree-ring series sensitivity values (*s*), correlations among cores (*r*) in chronologies, and number of trees in the series (*N*) by site and composites of live and dead tree sets.

Class	Site*	<i>n</i>	<i>s</i>	<i>r</i>
Live	CLO	23	0.194	0.526
	DES	18	0.289	0.525
	LAU	20	0.242	0.511
	Composite	59	0.211	0.466
Dead	CLO	26	0.218	0.491
	DES	28	0.238	0.582
	LAU	29	0.313	0.709
	Composite	82	0.240	0.512
Live	OWE	20	0.374	0.704

**Note:** Only highly correlated series were used in the composite and series with greater than 100 years in the individual sites. The OWE site was analyzed separately because of its distinct location, growth behavior, and lack of mortality.

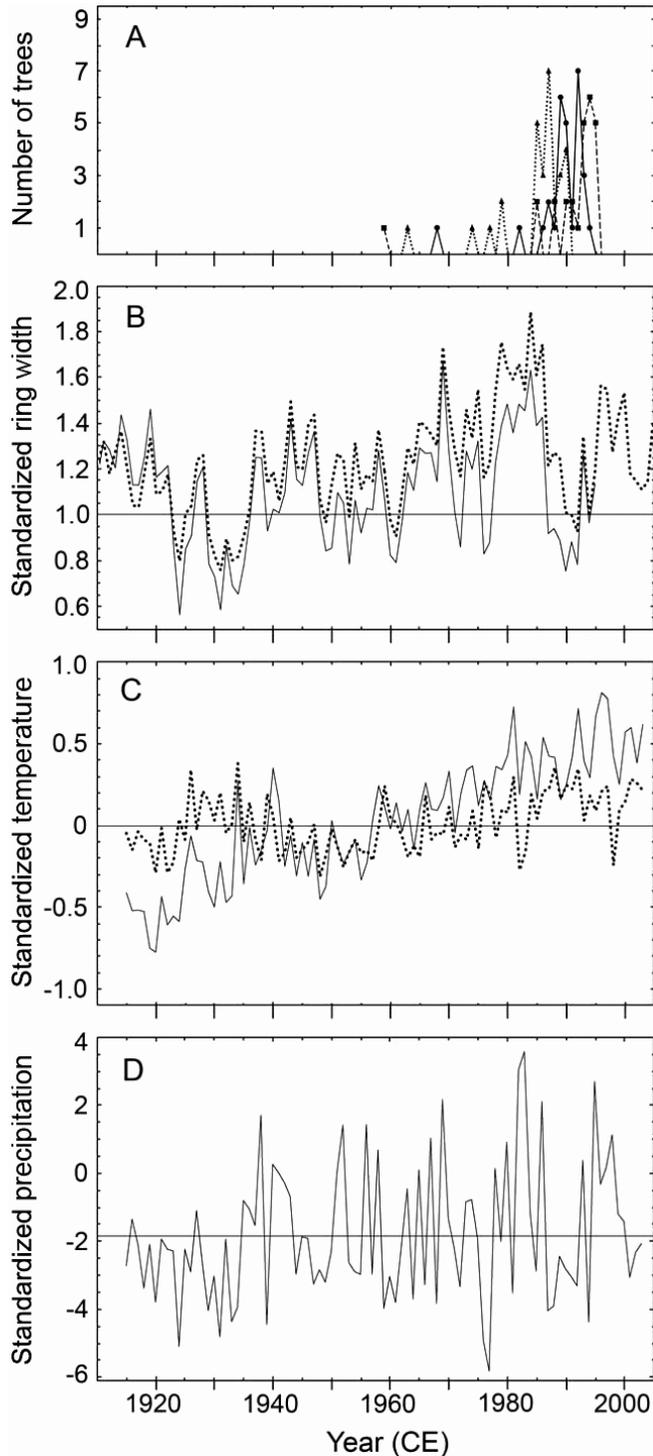
\*DES, Deschambeau Creek; CLO, Clot Canyon; LAU, Laurel Canyon; OWE, Owens Gorge.

grew less than live trees on an annual basis and had greater extremes of minimal growth (Fig. 3B).

However, relative growth of live versus dead trees over 300 years varied by century (Fig. 4A). In contrast to the 20th century, dead trees grew significantly greater ( $p < 0.001$ ) than live trees in the 19th and especially 18th centuries. Not until the early 1920s did the rank switch, and live tree growth began to consistently exceed dead trees. Interannual variances estimated by GARCH also show trends in autocorrelated, low-frequency variability (Fig. 4B). Overall, variances were low in the 1700s, increased briefly around 1800, and were low during the remaining 1800s. These were significantly greater in the dead trees than in the living ( $p < 0.001$ ), reflecting the growth and sensitivity in dead trees during this period. In the 20th century, variance changed in pattern and consistently increased over the century, although live and dead trees were not significantly different in variance.

Ring-width sensitivities over the entire record were high for the CLO, DES, and LAU stands, ranging from 0.194 to 0.289 for the live trees and 0.218 to 0.313 for the dead trees (Table 1). The OWE series had the highest sensitivity (0.374), which differed significantly ( $p = 0.05$ ) in pairwise comparisons with the other stands, which did not differ

**Fig. 3.** Mortality, growth, and climate from 1910 to 2005, eastern Sierra Nevada. (A) Number of trees that died per year at three stands (DES, broken line; CLO, solid line; LAU, dotted line) showing cluster of dates between 1985 and 1995. (B) Limber pine growth (ring width) using composite data from the CLO, DES, and LAU sites: dead trees (solid line) and live trees (dotted line). (C) Trends in minimum monthly temperature (solid line) and maximum monthly temperature (dotted line) in the composite record derived from three regional weather stations. (D) Trends in wet-season precipitation derived from the same composite climate record.



among themselves. The combined dead tree group had a higher, although nonsignificant, ring-width sensitivity (0.240) compared with the live-tree set (0.211) (Table 1), reflecting the greater growth variability in this group (Fig. 3B).

**Climate**

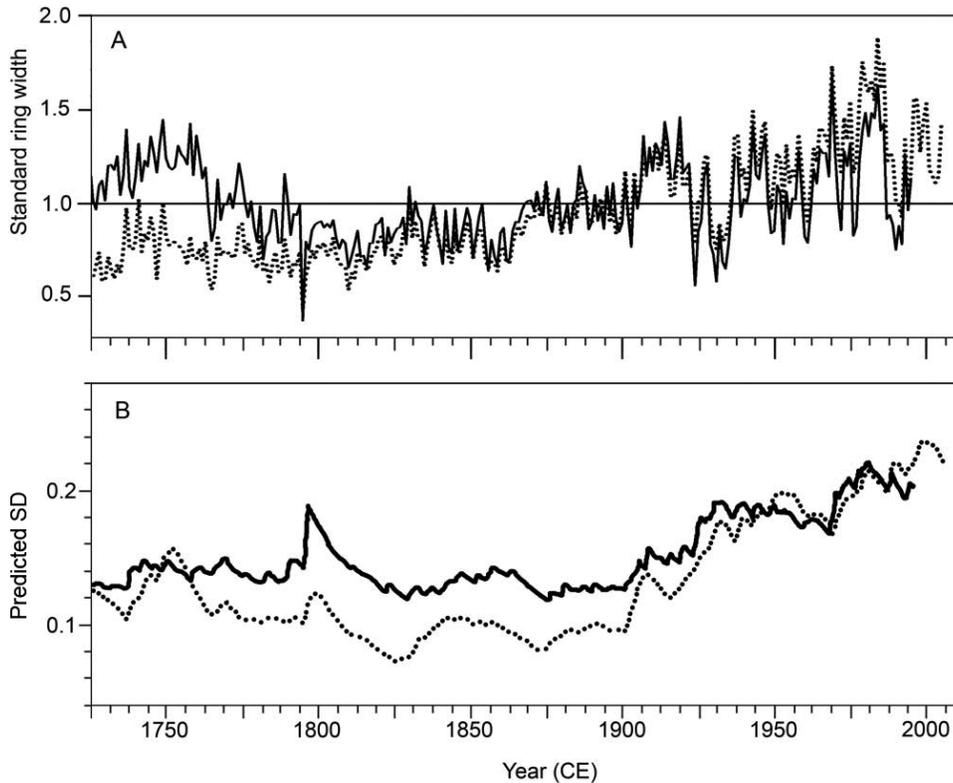
Composite regional weather records showed significant increases in minimum temperature ( $p < 0.001$ ) over the 20th century, with a mean warming of 1 °C from 1910 to 2006 (Fig. 3C). Warming trends were minor in maximum temperature but significant ( $p < 0.05$ ). Wet-season precipitation was characterized by high multiyear variability and trends in variability rather than directional changes in mean (Fig. 3D). A spectral decomposition indicated significant peaks at periods of 2.2 and 15 years ( $p < 0.05$ ). Multiyear droughts persisted 5–7 years, in some cases with a wet year intervening. Drought periods as recorded by wet-season precipitation are indicated in 1918–1926, 1929–1934, 1944–1951, 1959–1962, 1971–1977, 1984–1992, and 1999–2004 (Fig. 3D). Although the timing of intervals is consistent and intervals persist about 6–8 years, the pattern of individual droughts differed. Some were severe but short (1929–1934 and 1971–1977), others were weak but longer (1944–1951), and others were severe but variable interannually (1918–1926 and 1929–1934). The second most persistent drought of the century was 1984–1992, which followed the wettest multiyear period since 1910, namely 1980–1983 that includes the most severe El Niño event of the century. Although the 1971–1977 drought was drier on average than that of 1984–1992, the latter interval was significantly warmer. Precipitation and minimum temperature in 1992 were in the 20% and 97.5% percentiles, respectively, for the period of record. Variability of precipitation as indicated by moving window analysis of standard deviations showed decadal-length patterns of 10–20 years duration (Fig. 5). For the 90 year period, standard deviations were lowest during 1920–1930; low again around 1945, and highest from 1976–1986, which is in the interval preceding the late 1980s drought. These indicate low and high phases of inter-annual variability during the century.

Estimates from PRISM of 1961–1990 climate for the limber pine study sites and adjacent old-growth limber pine stands are given in Table 2. The three study stands with mortality (CLO, DES, and LAU) differ slightly in precipitation and more in temperature, with LAU warmest and driest overall and CLO coolest and wettest. However, compared with adjacent old-growth stands, these younger stands are much drier (difference of >200–400 mm wet-season precipitation) and warmer (difference 2–4 °C annual maximum temperature and 1–2 °C annual minimum temperature). In particular, winter precipitation differs between the young and old-growth stands, as do winter maximum temperatures. The PRISM model indicates that the OWE stand, which occurs at anomalously low elevation and experienced no mortality, has less than one-half the precipitation and is much warmer than the other limber pine stands (Table 2).

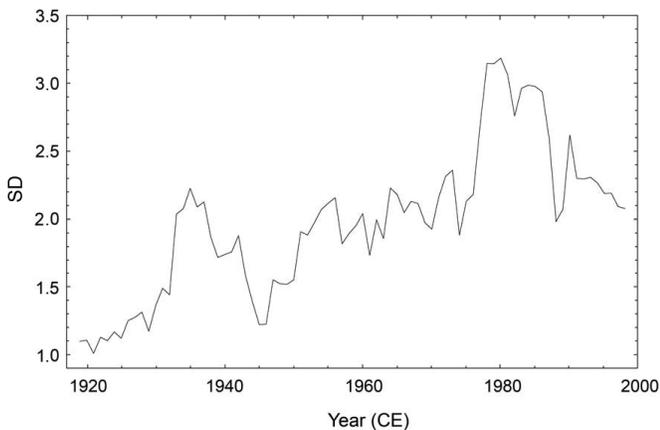
**Climate interactions with growth and mortality**

Mortality in three of the limber pine stands occurred during the 1984–1992 drought, and no mortality was associated with earlier or later droughts in the 20th century. Trees died

**Fig. 4.** Growth and variance in annual growth of live (dotted line) and dead (solid line) limber pine from 1700 to 2005 (minimum 10 trees/decade through the period of record) using the composite of the CLO, DES, and LAU sites and the GARCH method of analysis. (A) Limber pine growth (ring width). (B) Change in variance of tree growth for live and dead tree sets showing a significant change of pattern and increasing variance in the 20th century.



**Fig. 5.** Variation in wet-season precipitation from 1920 to 2005 derived from composite precipitation records, eastern Sierra Nevada.



at slightly different times during the drought, with the LAU stand responding earliest and CLO peaking latest, slightly after the drought (Fig. 3A).

Annual 20th century growth in the combined live and dead tree set was significantly and positively correlated with wet-season precipitation and with annual, May, and July minimum temperature, respectively (Table 3). In the dead tree set, correlations were significantly lower with temperature than among the live trees, especially in summer. With annual maximum temperature, correlations of growth were negative overall, but not significant, in the live trees.

These correlations are reflected in growth over the 20th century, which declined during the multiyear periods of low precipitation, including the 1920s, 1930s, and late 1980 to the early 1990s, and increased in intervals of high precipitation, such as the early 1940s and early 1980s (Fig. 3B). Annual growth was also positively and significantly correlated with PDSI (Table 3), corroborating better growth during years of high soil moisture (positive PDSI indices) and poorer growth in dry conditions (negative PDSI). In the dead trees, this correlation was twice that for the live trees, suggesting a role of low soil moisture in stressing trees that later died.

Interactions of 20th century growth with climate were significant and complex (Fig. 6). In the mixed model response-surface analysis, overall growth (pooled data set) had a significant interaction between precipitation and temperature ( $p < 0.01$ ) and between survival class and minimum temperature ( $p < 0.01$ ). Growth in live trees increased with both increasing minimum temperatures and precipitation; trees were most responsive to precipitation changes at low temperature and most responsive to temperature changes at low precipitation (Fig. 6A). Dead trees responded to precipitation similarly at low minimum temperatures, but their interactions were more complex at intermediate and high temperatures (Fig. 6B). With low precipitation, growth was better at low and high minimum temperatures, whereas growth was less responsive to increases in precipitation at high minimum temperatures.

Growth overall was significantly related to precipitation

**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. 1994) and downscaled as in Millar et al. (2006).

	Age	Elevation (m)	Precipitation (mm)			Maximum temperature (°C)			Minimum temperature (°C)		
			Annual	January	July	Annual	January	July	Annual	January	July
Laurel Canyon	Y	2615	656.45	103.84	12.23	12.51	3.92	24.11	-3.56	-8.60	4.47
Glass Mountain	O	3057	885.31	163.53	16.14	11.00	2.30	22.16	-4.10	-10.24	4.73
Deschambeau Creek	Y	2682	620.07	133.02	17.68	12.90	2.66	24.82	-3.49	-11.01	5.44
Lundy Canyon	O	3028	876.90	150.60	23.34	8.52	-0.20	20.58	-4.96	-11.58	4.33
Clot Canyon	Y	2813	698.91	143.57	15.67	11.61	1.81	23.40	-3.65	-10.74	5.29
Bloody Canyon	O	3070	1133.31	191.33	28.66	8.31	0.35	19.33	-5.80	-12.71	3.61
Owens Gorge	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

( $p < 0.001$ ) and minimum temperature ( $p < 0.001$ ). There was also a significant interaction between precipitation and pooled temperature ( $p < 0.004$ ) and between survival class (dead or live) and minimum temperature ( $p < 0.01$ ). Interactions with maximum temperatures were also complex but similar among live and dead trees (Figs. 6C and 6D). The greatest growth occurred at intermediate maximum temperatures and with intermediate to high precipitation. Lowest growth occurred at high maximum temperatures and low precipitation. Growth was relatively insensitive to changes in maximum temperatures at intermediate precipitation and more sensitive under low precipitation.

## Discussion

Drought-related forest dieback has been common and increasing in western North America during the late 20th century (Allen and Breshears 1998; Breshears et al. 2005). However, except for situations associated with exotic pathogens and fire suppression, high-elevation forests have remained relatively healthy. A significant mortality event occurred from 1985 to 1995 in low diversity, dense, young limber pine stands in the subalpine zone of the eastern Sierra Nevada escarpment. Higher elevation old-growth stands with very low density did not experience mortality. Neither young nor old stands experienced significant mortality during the recent 1999–2004 drought that has affected millions of hectares elsewhere in the West (Logan and Powell 2001; Breshears et al. 2005; B.C. Ministry of Forests and Range 2006). Mortality also did not occur in the young limber pine stands during earlier low precipitation periods of the 20th century in the Sierra Nevada, namely 1918–1926, 1929–1934, 1944–1951, 1959–1962, or 1971–1977.

During the late 1980s through early 1990s, other montane species of midelevations (<2500 m) in California also experienced high mortality. Significant dieback occurred in true fir species (*Abies* sp.) in the Lake Tahoe Basin and along the eastern Sierran slope near Lake Tahoe (Ferrell et al. 1994), up to 15% mortality occurred in fir and pine (*P. ponderosa* and *Pinus jeffreyi* Grev. & Balf.) of northern Sierran mixed forests (Macomber and Woodcock 1994), and up to 14% mortality in mixed-conifer forests of southern California (Jones et al. 2004). In a study of diverse midelevation forests throughout Yosemite National Park, Guarín and Tay-

lor (2005) found a significant mortality episode concentrated between 1986 and 1992 reflected in all species studied. There was little evidence of mortality at other times during the 20th century in the Yosemite study.

Climatic and stand structure factors associated with the 1984–1992 period are implicated in the limber pine mortality episode. As indicated from instrumental weather stations, this interval rivaled the 1918–1926 event as the most persistent 20th century drought in the Sierra Nevada. The intensity of the drought is indicated in proxies of distant San Francisco Bay salinity, which reflect Sierran snowpack depths and river runoff. In that system, the 1987–1992 episode was unmatched over the prior 400 years (Stahle et al. 2001). In the Sierra Nevada, precipitation, PDSI, and April snowpack were all below average for the years 1987–1992, except for 1991. This drought also occurred during a period of greater warmth than any of the previous 20th century droughts, with annual minimum and maximum temperatures significantly above century means. In limber pine, growth was positively correlated with precipitation, minimum temperature, and maximum temperature. This reflects an expected response of high-elevation trees to grow better with more water, warmer nights (minimum temperatures), and relatively warmer days (maximum temperature). However, negative correlations of growth with minimum and maximum temperatures at high temperatures, as well as complex interactions of growth with temperature and precipitation suggest that, as nighttime and summer temperatures increased during the 20th century, limber pine growth declined during periods of low precipitation. Trees that died were less able to respond resiliently to precipitation under increasing minimum temperatures than trees that lived. Thus, climatic stress in limber pine appears to have passed critical thresholds in these stands that lead to mortality in the late 1980s. This pattern was described for forest dieback events westwide during 1999–2004 by Breshears et al. (2005) as global-change-type drought and implicated locally in Yosemite National Park (Guarín and Taylor 2005) during the previous drought.

In addition to climate, other factors appear to have conditioned the limber pine stands to extreme stress. High tree density is a common attribute of forest stands throughout California and western United States that experience mortality, especially during droughts (Ferrell et al. 1994; Ma-

**Table 3.** Correlation coefficients of standardized tree-ring widths for live and dead trees at the CLO, DES, and LAU stands with wet-season precipitation, annual minimum temperature, May minimum temperature, July minimum temperature, annual maximum temperature, and the Palmer drought severity index (California Zone 5; PDSI).

Standardized ring width	Wet-season precipitation	Minimum temperature	May minimum temperature	July minimum temperature	Maximum temperature	PDSI
Live trees	0.52	0.48	0.40	0.31	-0.01	0.27
Dead trees	0.57	0.22	0.19	0.07	-0.21	0.46

**Note:** Correlations are significant ( $p < 0.05$ ) except annual maximum temperature, which is nonsignificant.

comber and Woodcock 1994; Jones et al. 2004; Breshears et al. 2005; Campbell et al. 2007). In Yosemite National Park, mixed-conifer forests growing on north slopes were more likely to have died in the 1980s drought than forests on other aspects; the north slope forests had the highest density of all stands studied (Guarin and Taylor 2005). Whereas nearly all limber pine in the Mono–Mammoth region of the Sierra Nevada occur on north slopes, only those stands that were relatively young, even aged, and dense had trees that died in this interval.

Dense stands combined with climate stress of high temperature and low precipitation also are most likely to promote bark beetle epidemics (Schmid and Mata 1992). Increasing temperatures are related to mountain pine beetle movement upslope, as well as to promoting a switch from semivoltine to univoltine life cycles (Logan and Powell 2001, 2007). Logan and Powell (2007) have shown that a 2 °C increase in temperature is enough to cause such a switch in voltinism. In the eastern Sierra, increases in minimum temperature exceeded this threshold in the late 20th century (Millar et al. 2004). These conditions may have facilitated bark beetle epidemics at higher elevations than previously observed. Furthermore, bark beetle infestations were already in the eastern Sierra Nevada region on midelevation lodgepole pine forests during the 1970s and 1980s drought. Stand structure of the limber pine forests we studied also favors spread of the dwarf mistletoe parasite, which is among the most damaging of native biotic threats to limber pine. Mistletoe weakens trees by competing for water and nutrients, both directly and indirectly through influence on ectomycorrhizal communities of the host (Taylor and Mathiason 1999). The combination of climate; closed-canopy, low-diversity stands; mistletoe; bark beetles; and blue stain fungus seems to have created a complex, multifactor stress situation in these limber pine forests that predisposed trees to die.

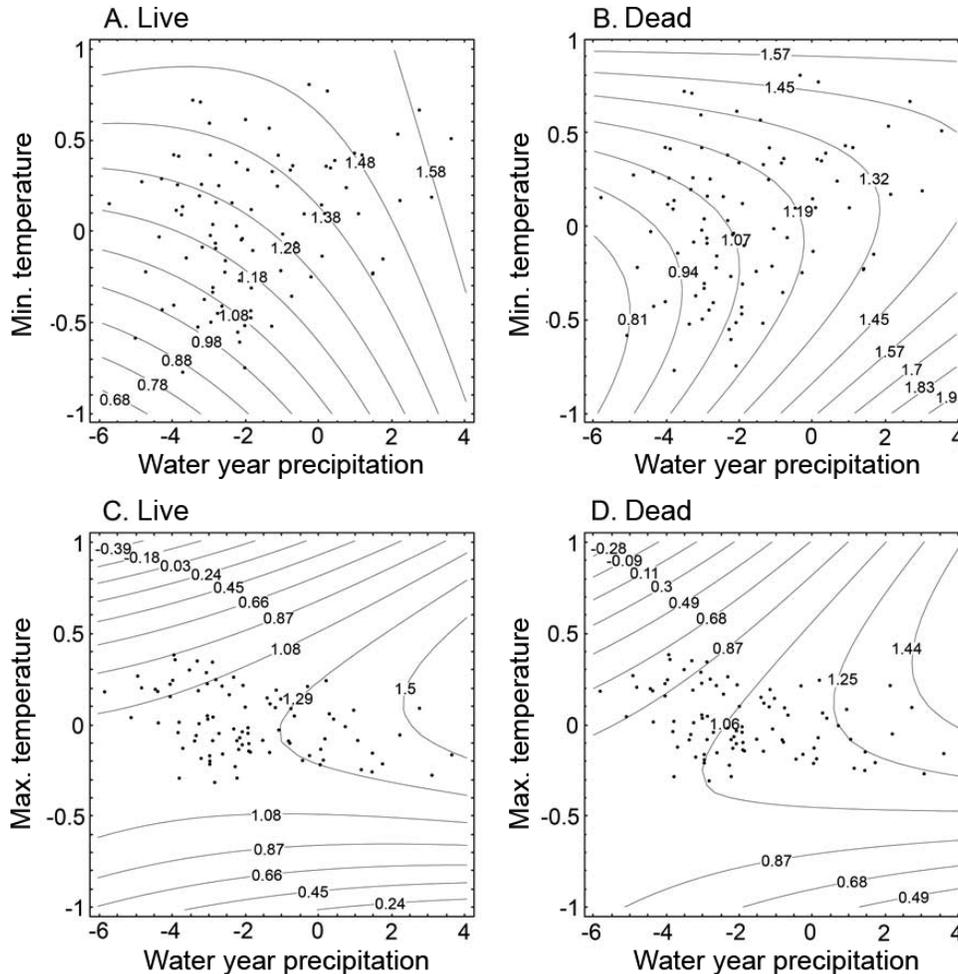
Given similar stand and age structures at LAU, CLO, and DES, minor differences among stands in dates of mortality are likely related to their environmental situation, as indicated by their PRISM climate conditions. The pattern of mortality among the stands indicate the onset of stress earliest in the warm, dry conditions at LAU and latest at cooler, wetter CLO, where a lag in stress was evident. Lack of mortality in the OWE stand was surprising, given its similar stand structure to the other three young stands and its elevation well below the normal lower range limit for limber pine in California or the Great Basin. Despite PRISM estimates of the OWE stand being warmer and drier than the other three, its location on the north face of narrow, rocky Owens Gorge directly below the outlet of Crowley Lake and Rock

Creek Canyon, which drain air from the Sierra crest, suggests that cool air likely pools there. This is corroborated by values of PRISM tiles to the north and west and, further, by anomalously low-elevation records of subalpine animal species that use this habitat. Taken together, these observations suggest that the north-facing portion of the Owens Gorge is an exceptionally cool microsite and that the PRISM model misrepresents its climate values.

Compared with adjacent old-growth limber pine stands characteristic of the species throughout the Sierra Nevada, the three stands with mortality as well as the OWE stand are in much drier and warmer locations, as indicated by the PRISM model, and lower in elevation. Although they are not located at geographic range limits, the four stands appear to be marginal climatically for the species in this region as indicated also by their high series sensitivity values, which considerably exceed a mean of 0.193 we estimated from local old-growth limber-pine stands (unpublished studies). Further, unlike typical old-growth stands of limber pine that have multimillennial site persistence and high age-class diversity, the four stands we studied appear to have originated as a recent and episodic colonization event during the late Little Ice Age. Between 90 and 200 years ago, Little Ice Age conditions were among the coolest and wettest of the prior centuries in the eastern Sierra Nevada, much wetter and cooler than the 20th century, and a period of lowest interannual climate variability relative to the last 1000 years (Graumlich 1993). Low variability combined with cool, wet conditions would be conducive to stand recruitment and establishment at these marginal locations. Heightened stress of increasing temperature and greater variance in precipitation over the 20th century, coupled with the persistent 1980s drought and bark beetle–mistletoe interactions, appear to have contributed to the mortality event in these relatively young and increasingly marginal stand locations.

Differences in growth between surviving trees and trees that died suggest possible adaptive differences within stands. Although clearly not a controlled environment, trees that died and trees that survived were not significantly different in age, diameter, elevational distribution, or location within stand or patches within stands at LAU, CLO, and DES. Nonsignificant differences in diameter suggest the two groups of trees shared similar size-class positions within stands. However, superior relative growth of the dead-tree group in the first two centuries of stand establishment suggests that those trees were better adapted to cool, wet conditions of the Little Ice Age. A switch in rank to live trees consistently outgrowing dead trees after the early 1920s coincides with warming and drying trends through the rest of the 20th century (Stine 1996; Graumlich 1993). The extreme

**Fig. 6.** 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. The data points in each graph are the recorded points from the composite 20th century instrumental weather record. Maximum temperature is held at the mean in Figs. 6A and 6B, and minimum temperature is held at the mean in Figs. 6C and 6D.



low growth of the dead-tree group during warmest and driest years of the 20th century, the higher relative ring-width sensitivity, and the differential susceptibility to bark beetles and blue-stain fungus further suggest adaptive differences among trees within stands.

Higher variability in interannual growth of all trees during the 20th century relative to earlier centuries at all stands suggests increasing susceptibility to climate. This was also seen in pinyon pine forests in northern Arizona, where dead trees exhibited 1.5 times greater variation in growth than live trees, especially during the 10–15 years before they died (Ogle et al. 2000) and in other regions where dead trees grew more variably prior to death than live trees (Gutschick and BassiriRad 2003; Suarez et al. 2004).

Despite high mortality in the overstory, the result of the mortality event was not a stand extirpation but a thinning event. Scattered young (less than 10 cm) trees in the understorey of each stand survived. These trees apparently were too small to suffer bark beetle or mistletoe infestation during

the 1980s and remain (as of 2007) healthy and vigorous. Further, the stand structure of surviving mature trees is now much sparser (a minimum spacing of greater than ~75 m) after the mortality event. Growth also improved after the drought, suggesting potential stand release and (or) climate effects (Fig. 3B). The thinning effect therefore appears to have improved health of the stands, as suggested by the lack of mortality in these stands during the 1999–2004 drought. Stand structure being created at the CLO, DES, and LAU stands may be moving toward the sparseness of typical old-growth limber stands in the region, which have so far remained resistant to mortality events.

The movement of forest mortality related to complex climate and native biotic factors into high-elevation forests is an important late 20th to early 21st century global-warming phenomenon. Subalpine and alpine zones are considered at higher risk in general for early and more intense effects of global warming than lower elevations (e.g., Hayhoe et al. 2004); models show heightened suitability for mountain

pine beetle outbreaks at increasingly high elevations in the early 21st century (Logan and Powell 2001; Hicke et al. 2006). Whereas significant mortality in high-elevation whitebark pine forests has resulted from non-native white pine blister rust, increasingly mountain pine beetle related mortality is also being observed (Logan and Powell 2001, 2005; Goheen et al. 2002; Waring and Six 2005). In California, high-elevation reports of mortality in whitebark pine and other five-needle white pines that implicate bark beetles and drought include the central eastern Sierra Nevada (northern Mono, Alpine, and El Dorado counties) but not southern Sierra Nevada (Patricia Maloney, University of California, Davis, Calif., personal communication, 2006); the Marble Mountains (Dave Schultz and Deems Burton, US Forest Service, personal communication, 2006); the Eddy Mountains, northwestern California, southern Warner Mountains (northeastern California), and Goosenest Mountain (northern California) (Dave Schultz, US Forest Service, personal communication, 2006).

### Conclusions

In this study, we document a significant forest mortality event occurring from 1985 to 1995 in subalpine limber pine stands of the eastern escarpment, Sierra Nevada, California. Increasing 20th century temperature interacting with a sustained multiyear drought appears to have severely stressed these stands, preconditioning them to infestation from mountain pine beetle and dwarf mistletoe, which were the proximal causes for death. Although droughts have recurred on quasi-regular basis through the past century in the eastern Sierra, persistent high temperatures were novel during this period, leading to global-change-type drought situations that have killed forests throughout the West in the 1980s and subsequent droughts (Breshears et al. 2005). Dense even-aged stand conditions, a history of Little Ice Age recruitment, and stand locations at temperature and precipitation margins of the species further predisposed these stands to climatic thresholds imposed during the late 20th century. Although the dense young stands experienced high mortality, typical diverse and sparse old-growth limber pine forests, which are more common in the Sierra, had no observable mortality during the droughts. The thinning effect of the 1984–1992 drought appears to have created higher resilience and greater adaptation in the surviving trees, because no mortality was experienced in the subsequent 1999–2004 drought in the young stands and surviving trees remain healthy.

The results documented here and implications for the role of drought in improving stand resilience are further demonstration of the complex response of subalpine forests to global warming. Typically, subalpine forests are modeled in future scenario projections to shift continuously up in elevation, with consequences of massive extirpation as they run out of suitable habitat at summits (e.g., Shafer et al. 2001; Hayhoe et al. 2004). In other Sierran studies, we have been documenting that forest response to climate variability is more complex, with reversible disturbance and colonization events, shifts among aspects and not just elevation, changes in growth habit rather than population shift, and even retreat downslope into cooler ravines off exposed windswept slopes (Millar et al. 2004, 2006). The processes of mortality in the

sensitive limber pine stands described in this paper are another example of such complexity and suggest that mortality events are not necessarily detrimental to long-term population fitness. The limber pine stands we studied are likely to persist into the future, despite the heavy mortality they experienced, even with increasing temperatures and recurring droughts. Healthy advanced regeneration under the dead overstory, as well as pole-sized survivors of the 1980s and 1990s drought, persist at present, with above-average growth and no sign of stress or mortality. We suggest that the mortality pulse during the 1982–1994 drought served to improve the resilience and adaptation of these stands and that this mechanism may function in other subalpine species and situations as well.

### Acknowledgements

We thank Jeff Hicke, Patricia Maloney, and David Schultz for sharing observations and reviewing the draft manuscript; two anonymous reviewers for comments on the submitted manuscript; Deems Burton, Jesse Logan, and Detlev Vogler for discussions of high-elevation beetle behavior; Mike Dettinger, Dan Cayan, and Kelly Redmond for discussions about climate mechanisms; and John Wentz for confirming the biotic agents during active infestations.

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