



Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA

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Abstract

Tree mortality is an important process causing forest structural and compositional change. In this study, we investigate the influence of drought and topography on recent patterns of tree mortality in old-growth mixed conifer forests in Yosemite National Park, located in the Sierra Nevada Mountains of northern California, USA. The surveyed stands have experienced a century of fire exclusion and are dominated by associations of *Pinus ponderosa*, *Calocedrus decurrens* and *Abies concolor*. The average age of trees in the stands was 88 years. We sought answers to the following questions: (1) Do periods of high tree mortality correspond with drought? (2) Do spatial and temporal patterns of high tree mortality vary by slope aspect? and (3) Do different tree species exhibit similar temporal and spatial patterns of tree mortality? We identified temporal patterns of tree mortality on three north- and south-facing slopes by determining the death date of trees using dendrochronology. Tree death date frequency was then compared by slope aspect and to Palmer Drought Severity Index (PDSI), and April snowpack depth as measures of growing season water availability. The frequency of tree death dates was negatively correlated with annual and seasonal PDSI and April snowpack depth, and more trees died in years with below normal PDSI and snowpack. Correlations between tree mortality and drought were evident only for multi-year periods (2–5 years). Temporal patterns of tree death were similar on north- and south-facing slopes and among species, but the density of dead trees was higher on north than south slopes. Dense stand conditions caused by fire suppression, and the coincident outbreak of bark beetles during drought, may have limited any buffering effect of topography on tree mortality. Drought induced tree mortality in mixed conifer forests in Yosemite National Park highlights the importance of both historical legacies such as fire suppression and exogenous controls such as climate as drivers of vegetation change.

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1. Introduction

Tree mortality plays a key role in the functional and structural dynamics of forest ecosystems, both as a mechanism for the release of carbon and nutrients, and

as an agent of forest structural and compositional change (Franklin et al., 1987). While the causes of tree death related to discrete events such as fire or wind-throw may be identified easily, longer periods of elevated tree mortality are usually associated with complex interactions between endogenous factors such as stand characteristics and genetics, and exogenous factors like site conditions, climate, insects and pathogens, which operate over a range of scales (Allen and Breshears, 1998; Mueller-Dombois, 1987, 1992; Savage, 1994).

Climate is an exogenous, regional-scale environmental control that influences vegetation development and establishes a context for local stand-level growth responses of trees (Lertzman and Fall, 1998). Climatic variation is thought to be an important factor influencing temporal and spatial patterns of tree death in forested ecosystems in both direct and indirect ways. For example, extended drought has been linked directly to tree death in tropical and temperate forests (Allen and Breshears, 1998; Villalba and Veblen, 1998; Fensham and Holman, 1999; Williamson et al., 2000). Indirectly, drought has been linked to tree death by acting as a trigger for insect or pathogen outbreaks (Ferrell et al., 1994; Ferrell, 1996; Speer et al., 2001). Extended periods of warm, dry conditions can induce a state of physiological stress, which reduces the ability of trees to withstand insect attacks. Consequently, drought often makes conifers more vulnerable to the attack of cambium-eating insects and this vulnerability may be expressed by an episode of high tree mortality (Mattson and Haack, 1987; Ferrell et al., 1994).

Montane forests in the western United States that once experienced frequent low and moderate severity fires have been dramatically altered by nearly a century of fire exclusion. For example, prior to Euro-American settlement, fires burned every 5–10 years in California's mixed conifer forests (Kilgore and Taylor, 1979; Caprio and Swetnam, 1995; Beaty and Taylor, 2001; Taylor and Skinner, 2003). Since the early 20th century a policy of excluding fires has been implemented in these forests (Skinner and Chang, 1996) and the reduction in the frequency and extent of fire has caused an increase in forest density, and a compositional shift to more fire sensitive species (Vankat and Major, 1978; Parsons and DeBenedetti, 1979; Minnich et al., 1995; Taylor, 2000; Taylor and

Skinner, 2003). Unusually high forest densities caused by fire suppression are thought to exacerbate the effect of drought on tree mortality because of increased competition for soil moisture that increases water stress in trees (Innes, 1992; Dolph et al., 1995). Consequently, drought may trigger rapid vegetation change because mortality processes are quick and episodic compared to vegetation changes caused by new establishment which are slow and gradual (Franklin et al., 1987). Retrospective studies that examine the influence of climate on vegetation dynamics (e.g., Overpeck et al., 1990) provide an important basis for understanding how ecosystems respond to climatic variation, including climate changes predicted by models that incorporate increased greenhouse gas emissions from the combustion of fossil fuels (e.g., Leung and Ghan, 1999; Dettinger et al., 2004).

The regional-scale control of climate on temporal patterns of tree mortality may be mediated by local-scale controls, such as topographic variation, that influence site-level water availability (Stephenson, 1990). Topographic characteristics such as slope position and slope aspect are known to strongly influence site moisture conditions (Stephenson, 1990, 1998), and climatically triggered tree dieback may vary accordingly (Jane and Green, 1983; Allen and Breshears, 1998; Powers et al., 1999). Slope aspect, in particular, is a key topographic variable influencing site moisture availability in the mountainous western United States (Parker, 1982; Stephenson, 1990). South-facing slopes receive more solar radiation, experience greater evapotranspiration, and have less plant available soil moisture compared to north-facing slopes. Consequently, spatial and temporal variations in site moisture conditions may influence the spatial pattern and severity of drought induced tree mortality. Yet, few studies have evaluated the potential mediating effects of topography on widespread tree mortality (Akashi and Mueller-Dombois, 1995; Powers et al., 1999).

High interannual variability in precipitation is a hallmark of California's Mediterranean climate (Mittchell and Blier, 1997), and tree mortality in Californian mixed conifer forests in the San Bernardino Mountains and Sierra Nevada appear to be associated with prolonged drought and drought-related insect outbreaks (CFPC, 1970–1997; Maccom-

ber and Woodcock, 1994; Savage, 1994, 1997). In this study, we evaluate the effect of topography on the spatial patterns of climatically related tree mortality in two mixed conifer forests in Yosemite National Park (hereafter Yosemite). Our goal was to determine if local-scale controls on site moisture availability, in particular slope aspect, mediate regional climatic-related tree mortality. Specifically, we sought answers to the following questions: (1) Do periods of high tree mortality correspond with periods of drought? (2) Do spatial and temporal patterns of high tree mortality vary by slope aspect? and (3) Do different tree species exhibit similar temporal and spatial patterns of tree mortality? We hypothesized that widespread tree mortality was associated with drought, but that the timing and extent of tree death would be influenced by slope aspect. In particular, we expected decreased or delayed mortality on north-facing slopes compared to south-facing slopes because of higher soil moisture availability on north-facing slopes.

1.1. Study area and stands

The influence of drought and topography on temporal and spatial patterns of tree mortality was examined in mixed conifer forests in Yosemite, a 3000 km² protected area in the central Sierra Nevada, in northern California, USA (latitude 37.58° N, longitude 119.66° W). Terrain in the park is rugged and varied and elevations range from 610 to 4000 m. The climate is Mediterranean and is characterized by warm, dry summers and cold, wet winters. Mean monthly temperatures in Yosemite, at 1200 m of elevation, range from 32 °C in July to –3 °C in January. Average annual precipitation is 945 mm, 85% of which falls between November and March as snow (NCDC, 2003). Soils in Yosemite are derived mainly from Mesozoic-aged granitic bedrock, and soil depth is variable depending on local site conditions (Hill, 1975; Huber, 1987).

Forests in the study area were composed of any of six conifer species: ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*P. lambertiana* Dougl.), incense cedar (*Calocedrus decurrens* Torr. Florin), white fir (*Abies concolor* Gord. and Glend.), Jeffrey pine (*P. jeffreyi* Grev. and Balf.), and Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], which may co-occur and share dominance in a stand depending on

local site conditions and stand history (Barbour, 1988). In general, south-facing stands were dominated by an association of *P. ponderosa* and *C. decurrens*, while forests on north-facing sites were predominantly *A. concolor*, *C. decurrens*, and *P. lambertiana*. The sub-canopy hardwoods black oak (*Quercus kelloggii* Newb.) and canyon live oak (*Q. chrysolepsis* Liebm.) were present in the understory of most stands.

To examine the mediating role of topography on recent episodes of tree mortality, stands on paired north- and south-facing slopes were chosen in two watersheds 7.5 km apart: Alder Creek (hereafter AC) and South Fork Merced River (hereafter SFM). For each slope aspect, we then chose three 5 ha stands on comparable elevations and slope configurations but separated by at least 1 km to serve as replicates. The south-facing stands were AC1, AC2, and SFM1, and the north-facing stands were AC3, SFM2, and SFM3. Stands were chosen subjectively to represent wide areas of tree mortality in the two watershed based on evidence of tree mortality (standing dead trees, fallen boles). Many of the dead trees were standing (42%), and fallen boles were in variable states of decay (Maser et al., 1979). Tree mortality in the stands appeared to be relatively recent because over 80% of the trees had some bark attached.

2. Methods

2.1. Forest structure and composition

Forest structure and composition were determined on each site using the point-centered quarter method (Cottam and Curtis, 1956), a commonly used sampling method in forestry to characterize stand structure (Krebs, 1989). Thirty points were sampled at each site along three to six parallel transects and points were sampled every 25 m along each transect. Due to the irregular shape of the stands, transect length varied from 100 to 275 m. All transects were laid parallel to the contour lines, and the first point for a transect was selected randomly. At each point, the species of, and distance to the nearest seedling (0.5–1.4 m in height), sapling (>1.4 m in height, <5 cm DBH) and live tree (>5 cm DBH) were measured in each of the four quarters. The diameter (DBH) of each tree was also measured. To identify tree age, each live tree was also

cored to the pith with an increment borer 30 cm above the soil surface. The elevation, location, aspect, pitch, slope position, and slope configuration for each site were recorded. The last four variables were used to calculate the topographic relative moisture index (TRMI; Parker, 1982), a measure of relative site moisture availability based on topographic characteristics that ranges from 0 to 60 (mesic to xeric).

Tree ages were determined by sanding each core to high-polish and then cross-dating the annual rings using standard dendrochronological techniques (Stokes and Smiley, 1968). The year of the inner most ring was then used as the tree age. Annual growth rings could not be consistently identified in the oak species so they were not included in the age–structure analysis. Tree ages were successfully determined for 78% of the conifer cores ($n = 667$). Ages for trees with incomplete cores (22%) were estimated using least squares regression equations of age on DBH. A regression equation was developed for each species at each site using the age data for complete cores. All the regression equations were highly significant ($P < 0.001$).

The structure and composition of recently dead trees ($> 5\text{cm DBH}$) on each site were also determined using the point-centered quarter method. Recently dead trees included any standing stems and downed trees in Maser et al. (1979) decay class 1, 2, or 3. At each point, the distance, species, and DBH of the nearest dead tree in each quadrant were recorded. Each dead tree was inspected to record any evidence of bark beetle activity such as pitch tubes and beetle galleries. Topographic influences on tree mortality were then inferred by comparing the density (trees ha^{-1}) and percentage of dead trees by slope aspect using a Kruskal–Wallis H -test. We chose to use non-parametric statistical tests because the time–frequency distribution of dead trees was not normally distributed (Zar, 1999). All statistical analyses were performed using SPSS software (SPSS Inc., 2001).

2.2. Dates of tree death

The year a tree died was determined by identifying the date of the last year of annual growth in partial wood cross-sections removed from each dead tree using a chainsaw. If the outermost growth rings were visibly eroded due to weathering, insect galleries or

decay, the next nearest dead tree in each quarter was selected for sampling. The wood samples were sanded to high polish and the annual growth rings were cross-dated using standard dendrochronological techniques (Stokes and Smiley, 1968). The date of the last annual growth ring for each sample was used as the year of tree death. The accuracy of the death-date estimate using this method may be influenced by erosion of the outermost ring(s) on a wood sample or by the lack of production of annual growth rings prior to the year of death (Villalba and Veblen, 1998). To account for possible differences in the accuracy of tree-death dates among samples, we classified each sample into one of three categories based on the condition of the wood sample: 3 = visible evidence of ring erosion; 2 = no visible evidence of ring erosion (bark not always present); and 1 = no ring erosion (bark attached). Thus, reported death dates represent the earliest possible death date; actual death dates could be later.

The influence of topography (north versus south aspect) on the temporal patterns of tree death dates was determined by comparing the time–frequency distribution of tree-death dates for all north- and south-facing sites, and for each north- and south-facing slope pair, using a Kolmogorov–Smirnov two-sample test. This test allowed us to compare the goodness of fit, or shape, of the frequency distributions of pairs of samples (Gotelli and Ellison, 2004). We also made identical comparisons by species to determine if the time–frequency distribution of tree-death dates varied by species according to slope aspect.

To determine if tree death was preconditioned, or influenced by prior years' growth, we determined if reduced radial growth was associated with the year of tree death. Preconditioning was defined as a succession of 2 or more years of radial growth less than the width of the previous two rings. For each sample, we recorded if there was evidence of preconditioning and then counted the number of narrow growth rings preceding death.

2.3. Drought and tree mortality

The relationship between drought and tree mortality was determined by comparing tree death dates with two climatic variables: the Palmer Drought

Severity Index (PDSI) and April snowpack depth. PDSI is a composite climatic index that includes immediate (same month) and lagged (previous month) precipitation and temperature effects on drought (Alley, 1984). Negative PDSI conditions represent drought while the opposite conditions prevail when PDSI is positive. We used PDSI values calculated for California Climate Division 5, which includes Yosemite (NCDC, 2003). Prolonged drought is often necessary to induce elevated rates of tree mortality, so we calculated contemporaneous (same year) and previous years' averages (2, 3, 4 and 5 years) for annual and seasonal PDSI. The seasonal PDSI variables included averages for the spring (March–May), summer (June–August), and winter (December–February) periods.

In the Sierra Nevada, April snowpack depth is a strong predictor of annual water availability at the beginning of the growing season (Dettinger and Cayan, 1995). We used average April snowpack depth of two snow survey courses in Yosemite, Gin Flat Outlook, 2134 m, and Perego Meadows, 2134 m (CDWR, 2003), as a proxy for April snowpack depths in our study area. We also calculated contemporaneous and previous years' averages (2, 3, 4 and 5) for the snowpack variable.

The association between tree-death dates and climate was identified in two ways. First, we calculated Pearson product–moment correlations (Zar, 1999) of the tree death time series with the time series for each climate variable. Second, we compared the number of trees that died during periods with above normal, normal, or below normal PDSI and April snowpack depth. The three climate groups were identified by calculating Z-scores for each variable based on the 1931–2002 record of climate. This standardization procedure involves transforming variables that have different units to make them comparable (Gotelli and Ellison, 2004). Z-scores ± 0.43 were then used as cut-offs for the three groups (Taylor, 1990). The number of trees dying in each of the three climatic periods was then compared using a Kruskal–Wallis *H*-test. The correlation analysis and paired comparisons between the frequency of tree death dates and climate were conducted only for the period spanned by the tree death date record (1975–2001). The longer climate record (1932–2002) was used exclusively to calculate historical trends and averages.

Errors in estimating tree-death dates due to ring erosion might influence associations between tree-death date frequency and climate. The actual date a tree died may have occurred later than the identified date. To address possible misinterpretations in the climate tree-death date association we also determined the association between climate, single, and 2-year averages of death date frequency for the current and the following year.

3. Results

3.1. Forest structure and composition

The structure and composition of forests varied by slope aspect. Ponderosa pine and incense cedar were the dominant species in all diameter classes on south-facing slopes, while sugar pine and canyon live oak were concentrated in the forest understory (Table 1; Fig. 1). On the other hand, white fir shared co-dominance with a wide range of species including incense cedar, ponderosa pine, sugar pine, and Douglas-fir in the large and intermediate diameter classes on north-facing slopes. Black oak was confined to small and intermediate size diameter classes, while incense cedar and white fir were the most abundant species in the small diameter classes. Douglas-fir was restricted to north-facing slopes and was abundant only on the most mesic site (SFM2).

There were similarities in forest age structure across all sites. Older trees (>100 years) were sparse and occurred in a wide range of age-classes from 100 to 300 years old, while young (<100 years) trees were very abundant (Fig. 2). However, there were differences by slope aspect, in the dominant species in older and younger age-classes. On south-facing slopes, the oldest trees were mainly ponderosa pine, while incense cedar was much more abundant in the younger age classes. On north-facing slopes, the oldest trees were ponderosa pine and incense cedar, and young trees were mainly incense cedar and white fir; there were virtually no young pine.

The density, size and species composition of dead trees also varied by slope aspect. The average density (\pm standard error) of dead trees on north-facing slopes (955.3 ± 93.7 trees ha^{-1}) was higher than on south-facing slopes (412.1 ± 69.1 trees ha^{-1}) as was the

Table 1
Site and stand characteristics for mixed conifer forests sampled on south- and north-facing slopes in Yosemite National Park

Site	South-facing				North-facing											
	AC1	AC2	SFM1	Average	AC3	SFM2	SFM3	Average								
Site characteristics																
Elevation (m)	1608	1660	1490	1586	1610	1410	1519	1513								
Slope (°)	14	22	20	19	12	16	9	12								
Aspect (°)	225	180	210	205	1	2	18	7								
TRMI	21	12	29	21	45	51	45	47								
Site	AC1		AC2		SFM1		Average		AC3		SFM2		SM3		Average	
	BA	Den.	BA	Den.	BA	Den.	BA	Den.	BA	Den.	BA	Den.	BA	Den.	BA	Den.
Forest structure and composition																
Abco	0.0	0.0	0.4	7.0	0.2	11.0	0.2	6.0	31.0	319.0	9.0	168.0	31.0	453.0	23.7	313.3
Cade	33.0	293.0	38.0	307.0	25.0	781.0	32.0	460.3	48.0	129.0	38.0	295.0	14.0	204.0	33.3	209.3
Pila	2.0	50.0	0.1	21.0	0.5	74.0	0.9	48.3	6.0	16.0	4.0	40.0	24.0	38.0	11.3	31.3
Pipo	13.0	149.0	51.0	439.0	39.0	253.0	34.3	280.3	6.0	8.0	6.0	7.0	12.0	51.0	8.0	22.0
Psme	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.0	201.0	0.3	6.0	8.8	69.0
Quch	0.3	32.0	1.0	56.0	2.0	53.0	1.1	47.0	0.0	0.0	0.1	7.0	0.0	0.0	0.0	2.3
Quke	1.0	18.0	0.1	7.0	15.0	95.0	5.4	40.0	3.0	12.0	12.0	87.0	2.0	13.0	5.7	37.3
Total	49.3	542.0	90.6	837.0	81.7	1267.0	73.9	882.0	94.0	484.0	95.1	805.0	83.3	765.0	90.8	684.7

TRMI is the Topographic Relative Moisture Index (Parker, 1982), which ranges from 0 (xeric) to 60 (mesic). Basal area (BA; m² ha⁻¹) and density (Den.; ha⁻¹) are for trees ≥5.0 cm DBH. Species acronyms are: Abco: *Abies concolor* (white fir); Cade: *Calocedrus decurrens* (incense cedar); Pila: *Pinus lambertiana* (sugar pine); Pipo: *Pinus ponderosa* (ponderosa pine); Psme: *Pseudotsuga menziesii* (Douglas-fir); Quch: *Quercus chrysolepis* (canyon live oak); Quke: *Quercus kelloggii* (black oak).

proportion of dead trees in the forest ($58.2 \pm 5.9\%$ in north-facing and $31.9 \pm 12.5\%$) ($P < 0.05$, Kruskal–Wallis H -test) (Table 2). Ponderosa pine and white fir were the most frequent dead species on south- and north-facing slopes, respectively. On all sites, for all species, dead trees were more frequent in small and intermediate (5–45 cm DBH) than large (>45 cm DBH) size classes ($P < 0.001$; Kruskal–Wallis H -test), except for ponderosa pine ($P > 0.05$, Kruskal–Wallis H -test) (Fig. 3). These data indicate that dead pine were all sizes whereas dead white fir were mainly small in diameter.

Evidence of bark beetle activity on dead trees was pervasive. Sixty-two percent of ponderosa pine, and 67% of white fir, had either beetle galleries or pitch tubes. Furthermore, 16% of the incense cedar was visibly infected by cedar rust.

3.2. Tree death date record

The date of death was successfully determined for 60% of the dead tree samples ($n = 706$), and dating was most successful for ponderosa pine (73%, $n = 280$) followed by white fir (60%, $n = 259$) and

Table 2
Density (ha⁻¹) of live and dead trees (>5 cm DBH) and proportion of dead trees in mixed conifer forests on south- and north-facing slopes in Yosemite National Park

Site	South-facing				North-facing			
	AC1	AC2	SFM1	Average	AC3	SFM2	SFM3	Average
Live	542.0	837.0	1265.6	881.3	484.0	805.0	766.3	685.0
Dead	490.9	361.5	383.9	412.1	1087.2	774.1	1004.6	955.3
Total	1032.3	1198.5	1649.5	1293.4	1571.5	1578.1	1770.9	1640.2
Proportion dead (%)	47.6	30.2	23.3	31.9	69.2	49.1	56.7	58.2

See Table 1 for the environmental and stand characteristics for each site.

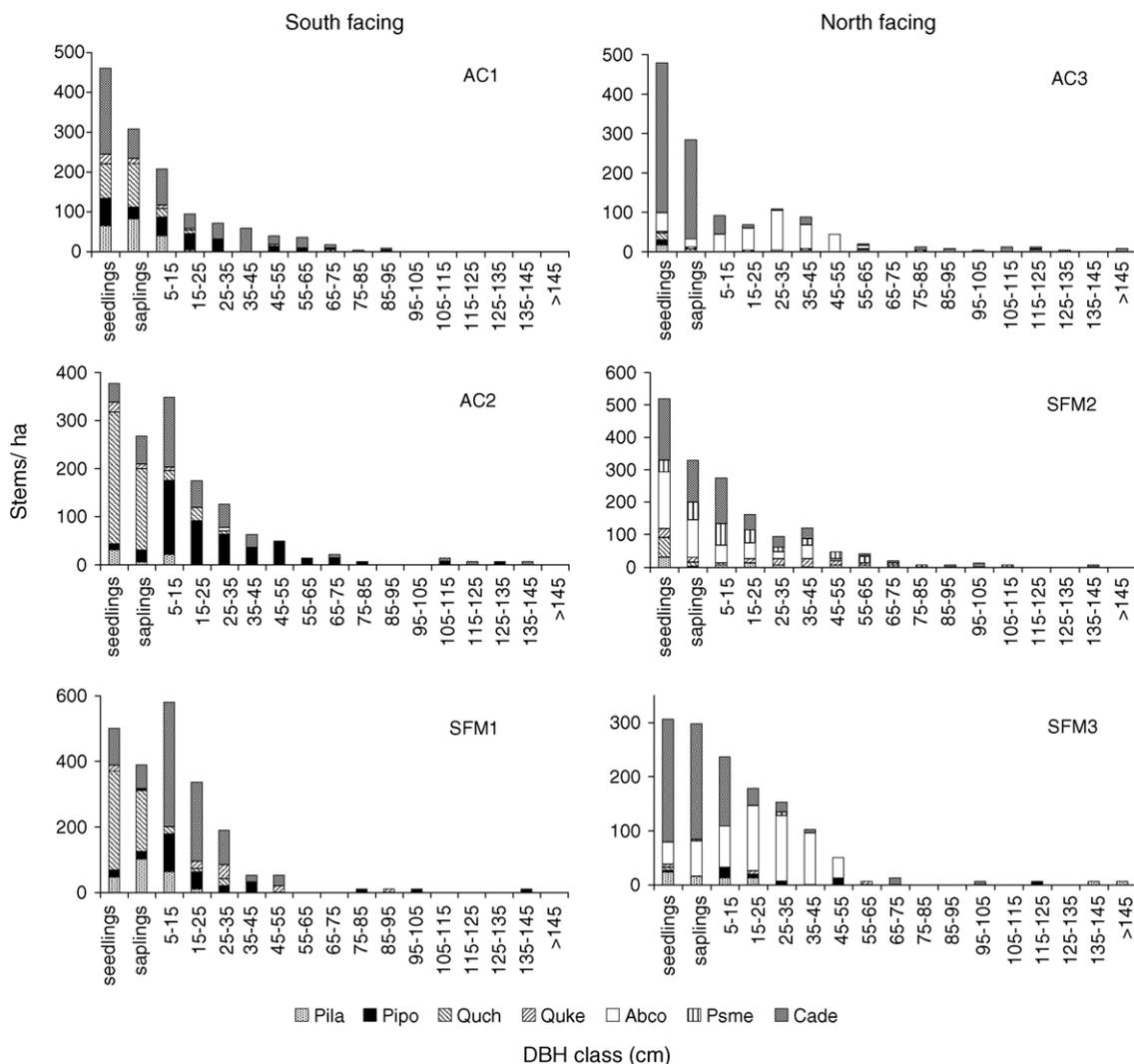


Fig. 1. Size-class distribution of live trees on south- and north-facing slopes in mixed conifer forests in Yosemite National Park. See Table 1 for species acronyms and environmental conditions on each site.

incense cedar (45%, $n = 14$). More death dates were successfully identified on south-(mean = 66%, range 60–74%) than north (mean = 53%, range = 34–67%)-facing slopes. Complacent or highly suppressed tree ring series were the main reasons death dates could not be determined by cross-dating. Only 17% ($n = 75$) of the dated samples had evidence of ring erosion. The earliest identified date of tree death was 1975 and the latest was 2001, 1 year before data collection. Only trees with known death dates were included in further analysis.

3.3. Temporal patterns of tree death

Tree death was episodic and concentrated over an 8-year period between 1986 and 1992. Sixty percent of the trees died between 1988 and 1991, and another 30% died in 1990, the year with the highest tree mortality (Fig. 4).

Temporal patterns of tree death were not influenced by slope aspect. North- and south-facing slopes had similar ($P > 0.05$, Kolmogorov–Smirnov two-sample test) death-date frequency distributions for 12 of 15

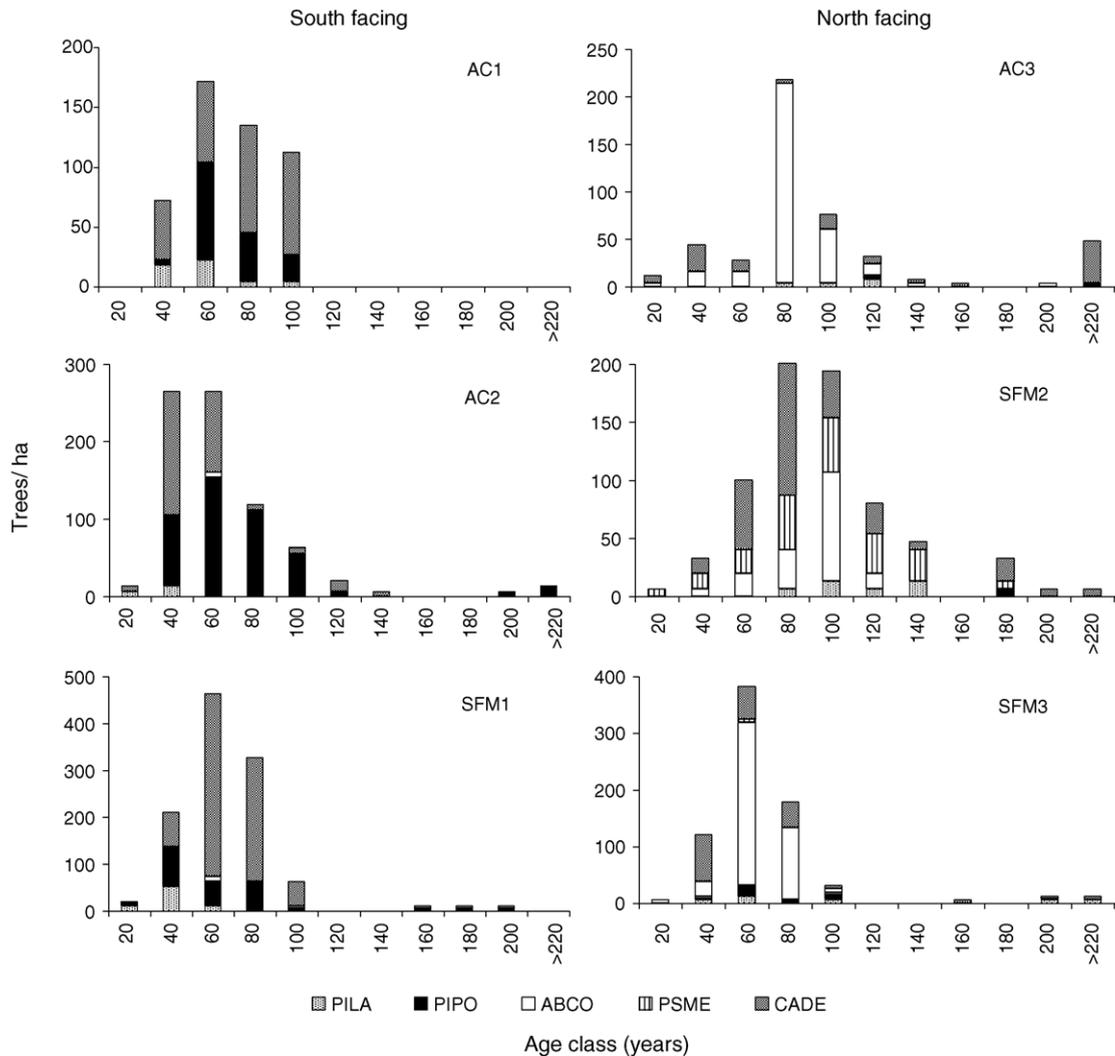


Fig. 2. Age-class distribution of live trees on south- and north-facing slopes in mixed conifer forests in Yosemite National Park. Open bars are tree ages from cores with a pith and filled bars are tree ages estimated using regression equations for cores without a pith. See Table 1 for species acronyms and environmental conditions on each site. Note that only every other age class is labeled and that the scale of the vertical axis is different for each graph.

paired comparisons while site AC1 had a different death-date frequency distribution ($P < 0.05$, Kolmogorov–Smirnov two-sample test) than three of the other sites. Furthermore, temporal patterns of tree death dates did not vary by species ($P > 0.05$, Kolmogorov–Smirnov two-sample test).

Preconditioning, or reduced annual radial growth before a tree died, was only observed in 33% of the samples. Reduced radial growth (mean = 2.25 years,

range = 1–4 years) before the date of death was observed most frequently in ponderosa pine (26%), followed by white fir (11%) and incense cedar (10%).

3.4. Drought and tree mortality

Both dry and wet periods occurred in the 70-year climatic record (Fig. 5). The overall pattern of wet and

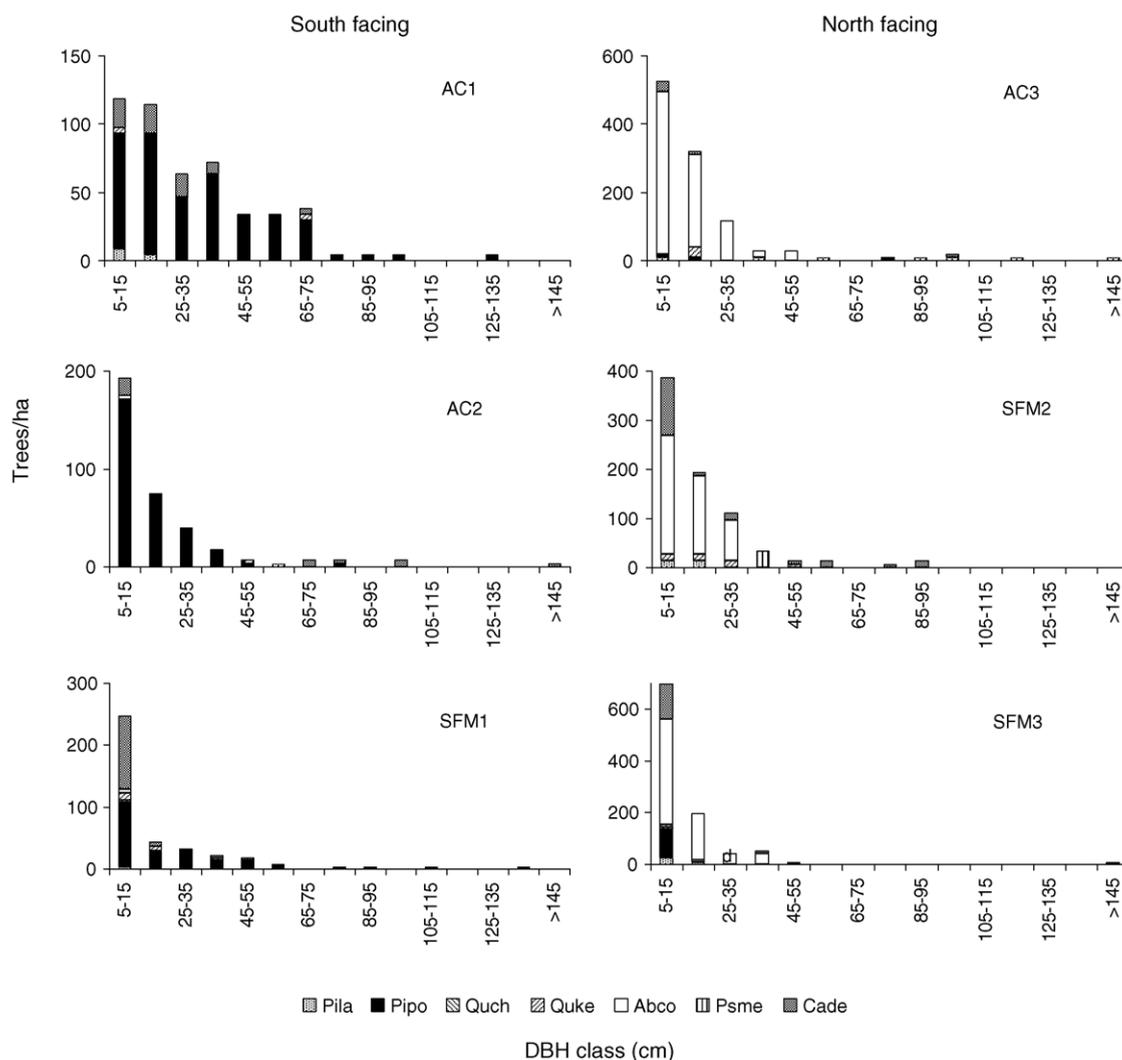


Fig. 3. Size-class distribution of dead trees on south- and north-facing slopes in mixed conifer forests in Yosemite National Park. See Table 1 for species acronyms and environmental conditions on each site.

dry years, as expressed by PDSI and April snowpack depths, suggests that short (1–3 years) periods of either above or below normal moisture conditions are typically followed by short periods of the opposite condition. However, between 1987 and 1992 there was an extended drought and PDSI was below normal for each of these 5 years and so was April snowpack depth, except in 1991 (Fig. 5a and b).

Temporal variation in the frequency of tree deaths was associated with drought (Table 3). Tree death-date frequency by year for multi-year averages (i.e., 2–5

years) was negatively correlated ($P < 0.05$) with annual and seasonal PDSI and April snowpack depth, and the correlations were stronger for April snowpack depth than for PDSI. Correlations were not significant ($P > 0.05$) for single-year average values. Similarly, more trees died in years that had below normal annual and seasonal PDSI and snowpack depths ($P < 0.05$, Kruskal–Wallis H -test) (Table 4). Again, the frequency of tree death was associated with below normal moisture conditions over periods of 2–5 years, but not for single-years.

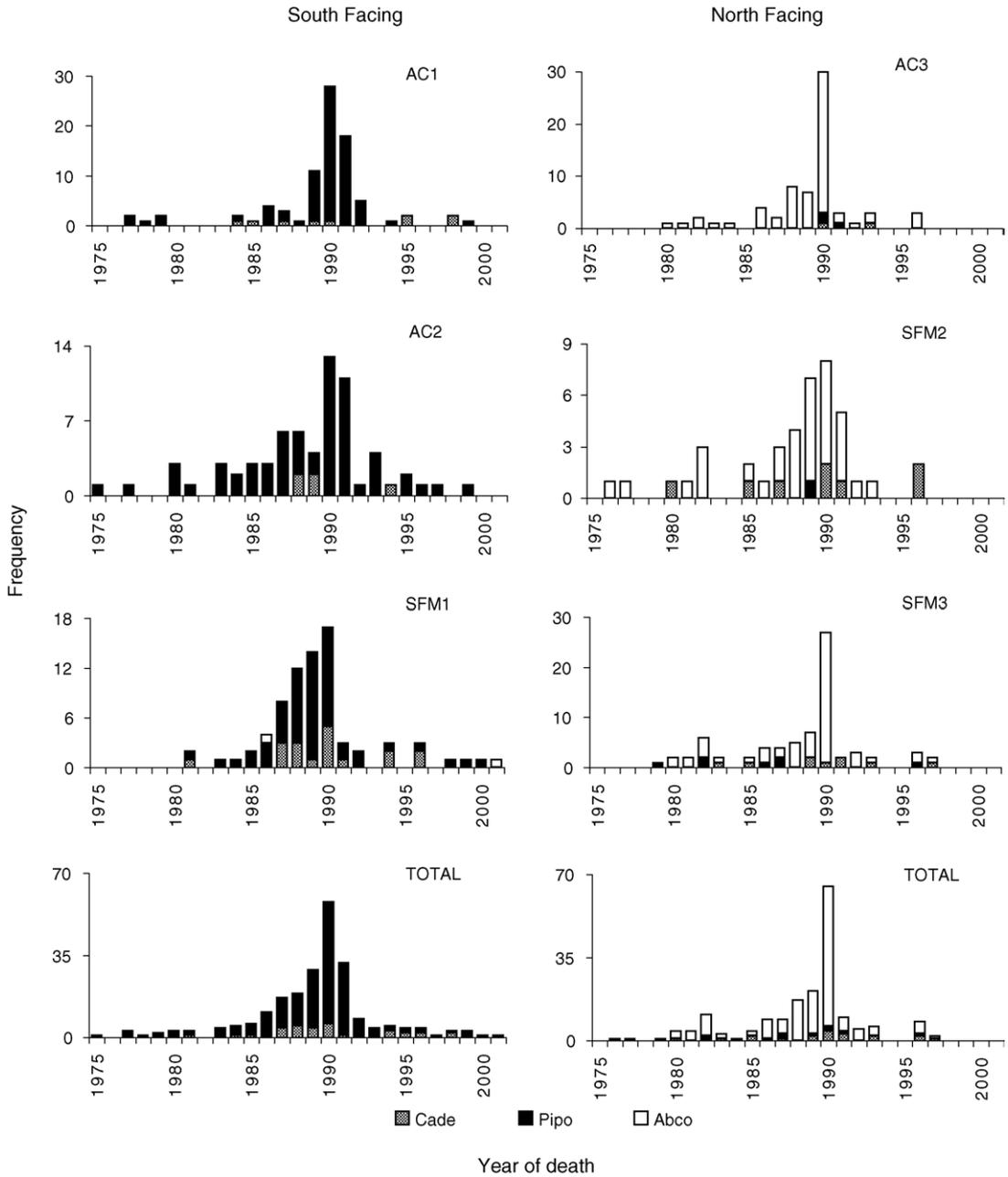


Fig. 4. Frequency of death dates on south- and north-facing slopes in mixed conifer forests in Yosemite National Park. See Table 1 for species acronyms and environmental conditions on each site.

The associations between annual and seasonal PDSI and April snowpack depth, and the frequency of tree deaths by year, were also significant ($P < 0.05$) if the frequency of tree deaths was averaged for a

two-year period. Possible errors in the determination of the date of tree death due to missing rings do not account for the climate-tree mortality associations.

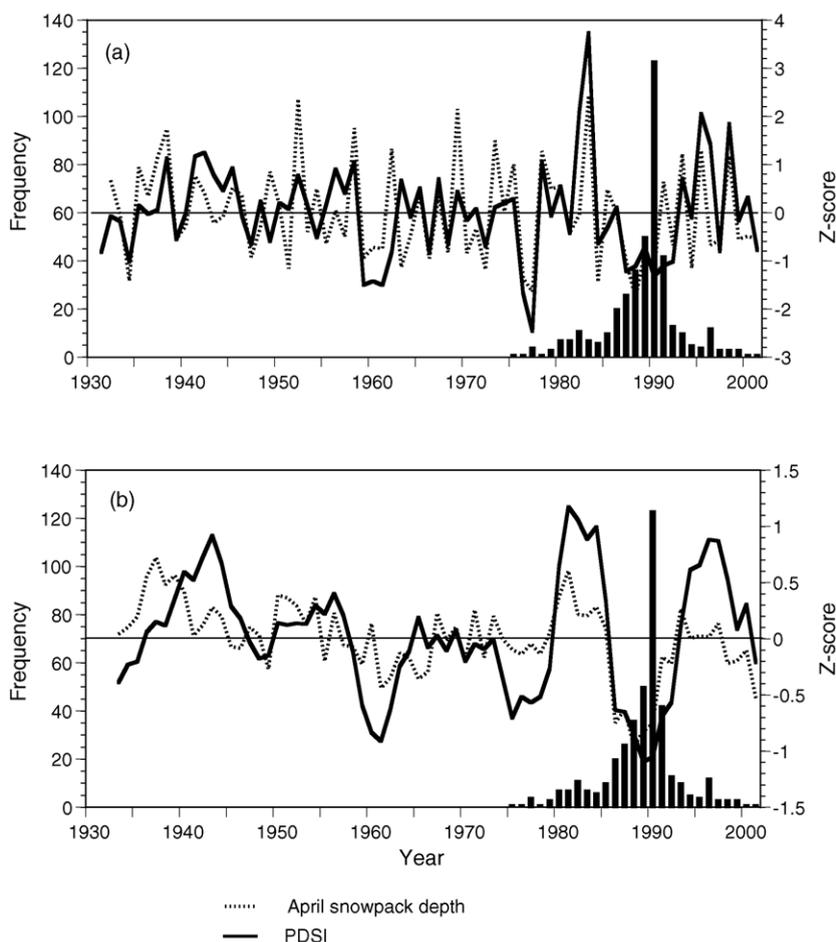


Fig. 5. Frequency of tree death dates for all sites in mixed conifer forests in Yosemite National Park and Z-scores for (a) annual and (b) 5 year running mean of Palmer Drought Severity Index (PDSI) (California Climate Division 5) and April snowpack depth in Yosemite National Park.

4. Discussion

The structure and composition of the forests we sampled in Yosemite varied with topography in a manner similar to mixed conifer forests elsewhere in the Sierra Nevada (Vankat and Major, 1978), and further north towards the Oregon border in the southern Cascades (Beaty and Taylor, 2001), and the Klamath Mountains (Taylor and Skinner, 1998, 2003). Drought tolerant ponderosa pine, sugar pine and canyon live oak were dominant on xeric south-facing sites, while Douglas-fir and white fir were more abundant on mesic north-facing slopes.

The size and age structure of the old-growth stands we studied are also similar to those described for other old-growth mixed conifer stands under the influence of nearly a century of fire exclusion (Parsons and DeBenedetti, 1979; Savage, 1997; Taylor, 2000; Taylor and Skinner, 2003). Historically low and moderate severity surface fires killed mainly seedlings, saplings, and small-diameter trees. Thick-barked, large diameter trees such as large pines (*Pinus* spp.) and Douglas-fir are more fire-resistant than species of fir (*Abies* spp.) (Agee, 1993). The presence of large diameter white fir, which is relatively fire-sensitive, in all stands suggests that the burns were

Table 3

Association between climatic conditions and number of tree deaths each year for six mixed conifer stands sampled on south- and north-facing slopes (combined) in Yosemite National Park

Climate variable	Time period	Pearson correlation coefficient (<i>r</i>)	
		Tree death current year	Tree death 2 year average
PDSI	Annual, pre. 3 years	−0.42*	−0.43*
	Annual, pre. 4 years	−0.42*	−0.40*
	Spring, pre. 2 years	−0.41*	−0.45*
	Spring, pre. 3 years	−0.49*	−0.50**
	Spring, pre. 4 years	−0.48*	−0.45*
	Spring, pre. 5 years	−0.39*	−0.37
	Summer, pre. 2 years	−0.36	−0.40*
	Summer, pre. 3 years	−0.42*	−0.46*
	Summer, pre. 4 years	−0.43*	−0.44*
	Summer, pre. 5 years	−0.40*	−0.41*
	Winter, pre. 2 years	−0.37	−0.39*
	Winter, pre. 3 years	−0.41*	−0.40*
	Winter, pre. 4 years	−0.39*	−0.33
	Snowpack	Pre. 2 years	−0.45*
Pre. 3 years		−0.63**	−0.67**
Pre. 4 years		−0.70**	−0.69**
Pre. 5 years		−0.64**	−0.60**

r is the Pearson product–moment correlation ($n = 27$) of current year and smoothed 2-year (current year and the previous year) averages of annual tree death date frequency with contemporaneous and previous (pre.) years' averages (2, 3, 4 and 5 years) for annual and seasonal Palmer Drought Severity Index (PDSI) and April snowpack depth. Only periods with significant correlations are reported.

* $P < 0.05$.

** $P < 0.01$.

light and patchy enough to allow white fir to grow to a fire-resistant size (Agee, 1993). Thus, frequent fire promoted development of an open forest consisting of mainly large diameter fire-resistant trees that varied widely in age (Parsons and DeBenedetti, 1979; Savage, 1997; Taylor, 2000). Due to a lack of surface fires, large populations of young (<100 years old) fire-intolerant white fir and incense cedar are now established beneath an overstory of older pines and incense cedar. Consequently, the stands are experiencing a shift in proportional abundance from mixed forests dominated by pine and incense cedar to forests dominated by incense cedar and white fir. We did not develop a fire history for each of our sites, but the frequency and extent of fires prior to the fire suppression period has been quantified in mixed conifer forests in other areas of

Table 4

Tree death date frequency during periods of below normal, normal, and above normal climatic conditions in six mixed conifer forest stands on south- and north-facing slopes (combined) in Yosemite National Park

Climate variable	Mean number of trees		
	Below normal	Normal	Above normal
Tree death, current year			
PDSI			
Annual, pre. 3 years*	27.4	3	6.5
Spring, pre. 3 years**	32.5	3.3	5.9
Spring, pre. 4 years*	25.8	4.5	4
Summer, pre. 2 years*	29.6	4.3	6
April snowpack depth			
Pre. 4 years*	28.7	7.3	7.2
Pre. 5 years**	22.4	9.8	9.3
Tree death, 2 year average			
PDSI			
Annual, pre. 3 years*	54.1	2.1	3.6
Spring, pre. 3 years*	63.4	7.8	12.5
Spring, pre. 4 years*	50.4	21.8	11.5
Summer, pre. 2 years*	59.4	8.3	11.9
April snowpack depth			
Pre. 4 years**	54.5	17	15.3
Pre. 5 years**	42.3	23.5	19.8

Current year and smoothed 2-year (current year and the year before) averages of annual tree death date frequency were compared (Kruskal Wallis *H*-test) with contemporaneous and previous (pre.) years' averages (2, 3, 4 and 5 years) for annual and seasonal Palmer Drought Severity Index (PDSI) and April snowpack depth. Only periods with significant differences are reported

* $P < 0.05$.

** $P < 0.01$.

Yosemite (Caprio and Swetnam, 1995). In these Yosemite mixed conifer stands, low and moderate severity surface fires burned every 5–12 years, on average, and fire was virtually eliminated from them after 1890. The onset of widespread tree establishment in our stands corresponds with the cessation of fire and the beginning of the fire suppression period.

Fire exclusion in Yosemite mixed conifer forests has caused stand density to increase dramatically and this may have predisposed the forest to high mortality from drought. A comparison of our forests with those that have not experienced fire suppression management in the San Pedro de Mártir Mountains in northern Baja California, Mexico illustrate this point. The average density of live trees in Yosemite mixed conifer

forests is 783 trees ha⁻¹ (range = 484–1267 trees ha⁻¹), five- to 10-fold greater than the density (range = 82–174 trees ha⁻¹) in mixed conifer forests in Baja California (Savage, 1997; Minnich et al., 2000). Similarly, the average basal area of 82.4 m² ha⁻¹ (range = 49.3–95.1 m² ha⁻¹) in our stands is two to three-fold greater than the basal area (26.2–46.0 m² ha⁻¹) of Baja California forests (Savage, 1997; Minnich et al., 2000). The density (trees ha⁻¹) of standing dead trees, which is an index of recent tree mortality, was also much higher in Yosemite. On average, Yosemite forests have >100-fold more dead trees (mean = 730 trees ha⁻¹) than Baja California forests (3–23 trees ha⁻¹) (Savage, 1997; Maloney and Rizzo, 2002; Stephens, 2004).

Recent tree mortality in old-growth mixed conifer stands in Yosemite was synchronized by a sustained period of drought when PDSI and April snowpack depth were below normal. In the Mediterranean climate of the Sierra Nevada, precipitation input to the ecosystem occurs mainly in winter. Consequently, April snowpack depth and spring and early summer temperatures are critical determinants of annual site water availability and the length and intensity of summer drought (Stephenson, 1990; Dettinger and Cayan, 1995). Our results indicate that co-occurring periods of high spring and summer temperatures and low annual and seasonal precipitation triggered high tree mortality. However, mortality was not simply associated with dry years. Statistically significant associations between low moisture and high tree mortality were only found for multi-year periods. This indicates that although any annual drought may be severe, elevated tree mortality is mainly associated with dry conditions over extended periods.

Intense competition for water in the very dense forests in Yosemite probably increased their vulnerability to drought triggered dieback. In dense stands, increased water stress during drought increases the susceptibility of trees to mortality factors (Gerecke, 1990; Ferrell, 1996; Allen and Breshears, 1998). In northern Baja California, mixed conifer forests experienced the same 1987–1992 drought as forests in Yosemite. Yet, tree mortality was not extensive nor were there insect outbreaks as in California forests (Savage, 1997; Minnich et al., 2000; Maloney and Rizzo, 2002; Stephens, 2004). Fire suppression, by increasing tree density, appears to have predisposed

Yosemite forests to high tree mortality. Thus, fire suppression amplified the effects of the 1987–1992 drought that triggered widespread tree mortality. The attack of cambium-feeding bark beetles (*Dendroctonus* spp.) was probably the ultimate cause of tree mortality, but prolonged water stress from drought increases the susceptibility of trees to insect attack (Mattson and Haack, 1987; Ferrell et al., 1994; Ferrell, 1996). During the extended 1987–1992 drought bark beetle outbreaks were observed elsewhere in the Sierra Nevada and in the San Bernadino Mountains where they triggered widespread tree mortality in some areas (CFPC, 1970–1997; Savage, 1994; Ferrell, 1996). In the northern Sierra Nevada, 15% of the standing timber volume was killed by insect attacks during the 1987–1992 drought (Macomber and Woodcock, 1994).

Topographic characteristics such as slope aspect and slope position are known to influence soil moisture availability in mountainous terrain (Stephenson, 1990), and spatial patterns of tree mortality and topography are associated in some forest ecosystems. For example, in a Pacific Northwest Douglas-fir forest, tree mortality caused by bark beetles was higher on xeric east and south-facing slopes than on more mesic north-facing slopes (Powers et al., 1999). Similarly, in *Metrosideros* sp. forests in the Hawaiian Islands (Akashi and Mueller-Dombois, 1995) and in New Zealand (Jane and Green, 1983), patterns of tree dieback vary with slope configuration which appears to modulate tree mortality associated with cohort senescence, especially on poorly drained soils. In Southwestern USA ponderosa pine forests, drought triggered more rapid and severe tree mortality on xeric low elevation sites than at higher elevation (Allen and Breshears, 1998). In Yosemite, the temporal pattern of tree mortality was similar on south- and north-facing slopes. This suggests that topography had a limited effect on the timing of tree mortality because of the strong and coincident effects of drought and insect outbreak on mortality in the dense stands. The higher density of dead trees and the higher dead to live ratio of trees on north than south-facing slopes suggests, however, a topographic influence on the magnitude of drought-induced tree mortality. The greater mortality on north than south-facing slopes is probably related to how site quality affects stand composition and density, especially during a period of highly altered

fire regimes. Prior to fire exclusion, low to moderate severity surface fires burned frequently through mixed conifer stands in Yosemite (Caprio and Swetnam, 1995) and these fires would have been particularly effective at thinning fire sensitive white fir and incense cedar seedlings and saplings, the dominant species on north-facing slopes. With fire exclusion, forests on mesic north-facing slopes increased more in density than on xeric south-facing slopes. Thus, competition between trees on north-facing slopes was probably more intense and this led to higher mortality on north-facing slopes during the subsequent drought. This suggests that spatial patterns of drought-induced mortality may vary considerably between types of forests depending on initial site conditions and how forests respond to land use changes such as fire suppression.

Our results may have important implications for conifer forest dynamics under changing climate regimes. Climate change influenced by greenhouse gas emissions (for example, $2 \times \text{CO}_2$ scenario) is expected to increase average temperatures in California by about 2.4°C in the next 100 years, but the prevailing precipitation regime is not expected to change (Leung and Ghan, 1999; Dettinger et al., 2004). Warming is predicted to cause earlier spring snowmelt, a trend that has already been observed (Dettinger and Cayan, 1995), and this is likely to increase the length and severity of summer droughts that are experienced by Sierra Nevada forests (Knowles and Cayan, 2002; Dettinger et al., 2004). Drought-triggered mortality may become more frequent and severe (Auclair et al., 1992). This seems likely given the high forest density found in the Sierra Nevada that has resulted from fire suppression (Weatherspoon et al., 1992), and the amplifying effect of drought on tree mortality, especially on mesic sites, we identified in dense Yosemite forests. Consequently, drought associated with greenhouse gas induced climate change has the potential to cause rapid vegetation change through drought-induced forest dieback as different species replace contemporary forest dominants. Similar interactions among fire exclusion, forest density, drought, and insect outbreaks are associated with tree mortality in ponderosa pine and piñon pine-juniper (*Pinus* spp. –*Juniperus* spp.) forests in the arid southwestern USA (Allen and Breshears, 1998) and in mixed conifer forests in

southern California (Savage, 1994). Moreover, the increase in dead fuels caused by widespread tree mortality increases the risk and hazard of stand-replacing fire in forests that historically experienced mainly low and moderate severity surface fires. Thus, fire suppression may not only have caused changes in the structure and composition of forests, it may have altered the historical response of forests to climate variation. Drought induced tree mortality in Yosemite mixed conifer forests highlights the importance of the interaction between the historical legacy of fire suppression and the exogenous control of climate variation as a driver of vegetation change.

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References

- Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, p. 493.
- Akashi, Y., Mueller-Dombois, D., 1995. A landscape perspective of the Hawaiian rain forest dieback. *J. Vegetation Sci.* 6, 449–464.
- Allen, C.G., Breshears, D.D., 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc. Nat. Acad. Sci. U.S.A.* 95, 14839–14842.
- Alley, W.A., 1984. The Palmer Drought Severity Index: limitation and assumptions. *J. Clim. Appl. Meteorol.* 23, 1100–1109.
- Auclair, A.N.D., Worrest, R.C., Lachance, D., Martin, H.C., 1992. Climatic perturbation as a general mechanism of forest dieback. In: Manion, P.D., Lachance, D. (Eds.), *Forest Decline Concepts*. APS Press, St. Paul, pp. 38–58.
- Barbour, M.G., 1988. California upland forests and woodland. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, United Kingdom, pp. 131–164.

- Beatty, R.M., Taylor, A.H., 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, southern Cascades, California, USA. *J. Biogeogr.* 28, 955–966.
- California Department of Water Resources, 2003. April snow-pack depth for Gin Flat Outlook and Perego Meadows Snow Survey Courses. Available online <http://cdec.water.ca.gov> [accessed 23 May 2003].
- California Forest Pest Council, 1970–1997. Forest pest conditions in California annual reports 1970–1997. California Forest Pest Council, Sacramento, California.
- Caprio, A. C., Swetnam, T.W., 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In: Brown, J., Mutch, R.W., Spoon, C.W., Wakimoto, R.H., (Technical Coordinators), Proceedings of the Symposium on Fire in Wilderness and Park Management USDA Forest Services Intermountain Research Station, Ogden, UT, Gen. Tech. Rep. INT-GTR-320.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Dettinger, M.D., Cayan, D.R., 1995. Large scale atmospheric forcing of recent trends towards early snowmelt run-off in California. *J. Clim.* 8, 606–623.
- Dettinger, M.D., Cayan, D.R., Meyer, M.K., Jeton, A.E., 2004. Simulated hydrologic responses to climatic variations and change in the Merced, Carson and American river basins, Sierra Nevada, California, 1999–2099. *Clim. Change* 62, 283–317.
- Dolph, K.L., Mori, S.R., Oliver, W.W., 1995. Long-term response of old-growth stands to varying levels of partial cutting in the eastside pine type. *West. J. Appl. For.* 10, 101–108.
- Fensham, R.J., Holman, J.E., 1999. Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *J. Appl. Ecol.* 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, Waters Resources Center Report No. 37, pp. 1177–1192.
- Ferrell, G.T., Orosina, W.J., Demars, C.J., 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. *Can. J. For. Res.* 24, 302–305.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *Bioscience* 37, 550–556.
- Gerecke, K.L., 1990. Tannensterben und Neuartige Waldschaden Eit Beitrag aus der Sicht der Waldwachstumskunde. *Allg. Forst. Jagxstg.* 161, 81–96.
- Gotelli, N.J., Ellison, A.M., 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland.
- Hill, M., 1975. Geology of the Sierra Nevada. University of California Press, Berkeley, California.
- Huber, N.K., 1987. The geologic story of Yosemite National Park, USGS Bulletin 1595.
- Innes, J.L., 1992. Forest decline. *Progress Phys. Geogr.* 16, 1–64.
- Jane, G.T., Green, T.G.A., 1983. Episodic forest mortality in the Kaimai Ranges, North Island, New Zealand. *New Zeal. J. Bot.* 21, 21–31.
- Kilgore, B.M., Taylor, D., 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60, 129–142.
- Knowles, N., Cayan, D.R., 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. *Geophys. Res. Lett.* 29 (18) (art. no. 1891).
- Krebs, C.J., 1989. *Ecological Methodology*. Harper and Row, New York.
- Lertzman, K., Fall, J., 1998. From forest stands to landscapes: spatial scales and the roles of disturbances. In: Peterson, D.L., Parker, V.T. (Eds.), *Ecological scale: Theory and Applications*. Columbia University Press, New York, pp. 339–367.
- Leung, L.R., Ghan, S.J., 1999. Pacific Northwest climate sensitivity simulated by a regional climate model driven by a GCM Part II: $2 \times \text{CO}_2$ simulations. *J. Clim.* 12, 2031–2053.
- Macomber, S.A., Woodcock, C.E., 1994. Mapping and monitoring conifer mortality using remote sensing in the Lake Tahoe Basin. *Rem. Sens. Environ.* 50, 255–266.
- Maloney, P.E., Rizzo, D.M., 2002. Pathogens and insects in a pristine forest ecosystem: the Sierra San Pedro Martir. Baja, Mexico. *Can. J. For. Res.* 32, 448–457.
- Maser, C., Anderson, R.G., Cromack, K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington*. USDA Agriculture Handbook No. 553. Washington Office, Washington, D.C..
- Mattson, W.J., Haack, R.A., 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37, 110–118.
- Minnich, R.A., Barbour, M.G., Burk, J.H., Fernau, R.F., 1995. Sixty years of change in California conifer forests of the San Bernardino Mountains. *Conserv. Biol.* 9, 902–914.
- Minnich, R.A., Barbour, M.G., Burk, J.H., Sosa-Ramírez, J., 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja California, Mexico. *J. Biogeogr.* 27, 105–129.
- Mitchell, T.P., Blier, W., 1997. The variability in winter time precipitation in the region of California. *J. Clim.* 10, 2261–2275.
- Mueller-Dombois, D., 1987. Natural dieback in forests. *Bioscience* 37, 575–583.
- Mueller-Dombois, D., 1992. A natural dieback theory, cohort senescence as an alternative to the decline disease theory. In: Manion, P.D., Lachance, D. (Eds.), *Forest Decline Concepts*. APS Press, St. Paul, pp. 38–58.
- National Climatic Data Center, 2003. Palmer Drought Severity Index for California Climate Division No 5. Available from <http://www.ncdc.noaa.gov> [accessed 22 May 2003].
- Overpeck, J.T., Rind, D., Goldberg, R., 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343, 51–53.
- Parker, A.J., 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Phys. Geogr.* 3, 160–168.
- Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manage.* 2, 21–33.
- Powers, J.S., Sollins, P., Harmon, M.E., Jones, J.A., 1999. Plant-pest interactions in time and space: a Douglas-fir bark beetle outbreak as a case study. *Landscape Ecol.* 14, 105.

- Savage, M., 1994. Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Can. J. For. Res.* 24, 1149–1159.
- Savage, M., 1997. The role of anthropogenic influences in a mixed conifer forest mortality episode. *J. Vegetation Sci.* 8, 95–104.
- Skinner, C.N., Chang, C.R., 1996. Fire regimes, past and present. In: *Sierra Nevada Ecosystem Project: Final report to Congress*, vol. II. Assessments, Scientific Basis for Management, Options, Wildland Resources Center Report No. 37, Centers for Water, Wildland Resources, University of California, Davis, CA, pp. 1041–1069.
- Speer, J.H., Swetnam, T.W., Wockman, B.F., Youngblood, A., 2001. Changes in Pandora moth outbreak dynamics during the last 622 years. *Ecology* 82, 679–697.
- SPSS, 2001. *Procedures Guide*, Version 11.0. SPSS Inc., Chicago, IL, USA.
- Stephens, S.L., 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine mixed conifer forest in northwestern Mexico. *For. Ecol. Manage.* 199, 103–113.
- Stephenson, N.L., 1990. Climatic control of vegetation distribution: the role of water balance. *Am. Natur.* 135, 649–670.
- Stephenson, N.L., 1998. Actual evotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* 25, 855–870.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.
- Taylor, A.H., 1990. Tree invasion of meadows in Lassen Volcanic National Park. *Calif. Prof. Geogr.* 42, 457–470.
- Taylor, A.H., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California USA. *J. Biogeogr.* 27, 87–104.
- Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve in the Klamath Mountains, California, USA. *For. Ecol. Manage.* 111, 285–301.
- Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol. Appl.* 13, 704–719.
- Vankat, J.L., Major, J., 1978. Vegetation changes in Sequoia National Park, California. *J. Biogeogr.* 5, 377–402.
- Villalba, R., Veblen, T.T., 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79, 2624–2640.
- Weatherspoon, C.P., Husari, S., van Wagendonk, J.W., 1992. Fire and fuels management in relation to owl habitat in forests of the Sierra Nevada and southern California. In: Verner, J., Mckelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, G.I., Beck, T.W. (Technical Coordinators). *California spotted owl: a technical assessment of its current status*. USDA Forest Services Pacific Southwest Station, Berkeley, California, Gen. Tech. Rep. PSW-GTR-133, pp. 247–260.
- Williamson, G.B., Laurance, W.F., Oliveira, A.A., Delamônica, P., Gascon, C., Lovejoy, T.E., Pohl, L., 2000. Amazonian tree mortality during the 1997 El Niño drought. *Conserv. Biol.* 14, 154–1538.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey.