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The role of anthropogenic influences in a mixed-conifer forest mortality episode

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Abstract. Anthropogenic influences on recent tree mortality in mid-montane mixed conifer forests of southern California, USA, and northern Baja California, Mexico, were investigated. The *Pinus jeffreyi-Abies concolor* phase of the mixed-conifer montane community was sampled at three sites, characterized by: (1) low levels of air pollution and long-term fire suppression (Holcomb Valley in the San Bernardino Mountains, California); (2) chronic, severe air pollution and long-term fire suppression (Barton Flats in the San Bernardino Mountains, California); and (3) little air pollution and no fire suppression (La Corona Arriba in the Sierra San Pedro Martir in Baja California, Mexico). Similar percentages of dead standing trees, around 14 %, were found at both San Bernardino sites, but a comparatively low level, 4 %, was found in the Mexican forest. Anthropogenic effects, in particular fire suppression, may play an important role in enhancing the impact of natural stresses on the dynamics of mixed conifer forests.

Keywords: *Abies concolor*; Air pollution; Disturbance; Drought; Fire suppression; Forest decline; *Pinus jeffreyi*; Tree mortality.

Introduction

The complex interaction of human and natural stress and disturbance factors in many forest communities has made the determination of the causal factors of mortality difficult to assign. A wide variety of factors may be involved, including air pollution, acid rain, pests, pathogens, and climate fluctuations such as drought (e.g. Innes 1992). Often overlooked is the fact that the response of forests to disturbances and stresses may depend in part on their successional and demographic status. For example, the importance of cohort senescence in creating vulnerability to forest mortality has been documented in Hawaiian *Metrosideros polymorpha* (ōhi'a) forests in Hawaii (Mueller-Dombois 1986; Akashi & Mueller-Dombois 1995) and balsam-fir forests in the northeastern USA (Sprugel & Bormann 1981).

Mixed conifer forests in southern California, USA have changed markedly in structure and composition in this century (Vankat & Major 1978; Kilgore & Taylor 1979). Most recently, starting in the mid-1980s, widespread mortality occurred (Barbour 1988). There are multiple stresses in these forests, including a recent severe drought, outbreaks of western pine bark beetle (*Dendroctonus* spp.) (Savage 1994), and chronic exposure to air pollution (Miller et al. 1991). Higher forest density resulting from suppression of fire by humans in this century has also increased competitive stress (Kilgore & Taylor 1979). The effects of multiple disturbances and stresses can be damped or enhanced by their interaction. The intensity of beetle attack, for example, is enhanced by drought (Burns & Honkala 1990), exposure to photo-oxidants (Stark et al. 1968), and fire exclusion (Kilgore 1973).

The objective of this work is to compare stand structures and levels of tree death in the *Pinus jeffreyi* (Jeffrey pine)/*Abies concolor* var. *concolor* (white fir) phase of three mixed conifer forests that differ in pollution exposure and fire history. Two sites are in the San Bernardino Mountains of southern California; the third is in the Sierra San Pedro Martir in Baja California, Mexico. Both southern California sites have experienced fire suppression for ca. 90 yr. One site experiences severe air pollution and the other two relatively little. The Mexican site is in a remote area with little air pollution and no history of fire suppression. As the last landscape-scale mixed conifer forest in North America with an unmanaged fire regime, it offers a unique opportunity to assess the influence of fire suppression (Minnich et al. 1995). The null hypothesis of the research is that similar levels of mortality have occurred at the three sites. I compare traits of stand structure such as density, basal area and age structure to investigate whether variation in stand structure is associated with varying levels of mortality.

Environment and disturbance in mixed conifer forests

The southern California and Mexican sites are located in the mountain ranges that stretch across the international border from California into Baja Mexico. Both ranges have a mediterranean climate, with droughty summers and rainy winters (Minnich 1985; Reyes et al. 1990). Mean annual precipitation in the western San Bernardinos is around 80 cm/yr, and in the Sierra San Pedro Martir around 60 cm/yr (Minnich 1985). Minnich et al. (1995) document the floristic and ecological similarity of mixed conifer communities in the region, and suggest that disparities in structure have been created by fire management in southern California.

A complex of disturbances of varying frequencies and intensities play a role in these forests, including two natural disturbances, drought and beetle attack, and two anthropogenic stresses, air pollution and fire suppression. Variation in environmental factors can alter the susceptibility of tree species to drought stress. In particular, increased competition due to higher stand density results in enhanced water stress during a drought, making trees more vulnerable to mortality factors (Gerecke 1990).

The vulnerability of trees to insect attack is highly dependent on community status and environmental conditions (Schowalter 1985). Periodic droughts have been implicated in predisposing pine trees to attack by *Dendroctonus* beetle species *(D. brevicomis, D. ponderosa*, and *D. jeffreyi*) (Burns & Honkala 1990). Likewise, chronic exposure to oxidant pollution has been linked to attack of pine species by *Dendroctonus* insects in the San Bernardinos (Stark et al. 1968). Mortality episodes in pine forests in the past have resulted from drought combined with chronic exposure to ozone (Dale 1991) and with beetle attack (Burns & Honkala 1990). Prior to fire suppression, the intensity of insect outbreaks in mixed conifer forests was reduced by light fires that burned susceptible and dead trees in which insects bred (Kilgore 1973). Stand structure in such forests results from the interaction of insect attack with the structural legacy of past disturbances, producing spatial heterogeneity (Schowalter 1985).

Patchy, low-intensity fire was a frequent natural disturbance in unmanaged summer-dry mixed conifer forest and created an open park-like structure (Vankat & Major 1978; Kilgore & Taylor 1979). In the Sierra San Pedro Martir, this fire regime still prevails (Minnich et al. 1995). In southern California, however, fire suppression began soon after the turn of the century, initiating increased stand density, composition changes, and a shift toward younger age classes (Vankat 1977; Kilgore & Taylor 1979; Minnich et al. 1995). Fire sensitive species such as white fir became more abundant at the expense of fire-tolerant species such as pines (Rundel et al. 1977). Importance values for white fir have almost quadrupled in California, while those of ponderosa pine have declined by half over the last century (Rundel et al. 1977).

Photo-oxidants have been implicated in forest damage in southern California for four decades (Innes 1992). While air pollution seldom results directly in adult tree death, adverse effects of ozone on physiological functioning of trees has been widely documented (Coyne & Bingham 1981). Chronic exposure to photo-oxidants does not appear to result directly in the death of adult trees, but in increased susceptibility to disease (Williams 1983) and drought, by amplification of whole-tree stress (McLaughlin & Downing 1995). Experimental evidence indicates that *P. jeffryi* is considerably more susceptible to foliar damage from ozone than *A. concolor* (Miller et al. 1991).

Site characteristics

Holcomb Valley and Barton Flats

The San Bernardino Mountains are an 80 km east-west trending range that bounds the Los Angeles basin on the north and east at about 116° W, 34° N (Fig. 1). Substrates are primarily granitic of Mesozoic age (Foster 1980). Holcomb Valley (HV) and Barton Flats (BF) have been accessible to Euroamerican uses for two centuries. Grazing by cattle and sheep began after 1860, but had virtually ceased by 1900 (Minnich 1988). Although logging occurred in parts of the range, the higher, more rugged areas, such as HV and BF, largely escaped (Minnich 1988).

Fire suppression was instituted after 1905 in the San Bernardino Mountains by the U.S. Forest Service. Fire mean return interval, estimated from tree-ring scars in *P. jeffreyi* pine trees, more than doubled after fire suppression, from 12 yr for a period prior to 1905 to 29 yr after 1905 (McBride & Laven 1976). Descriptions of the forest at the turn of the century emphasized an open, park-like structure associated with frequent light fires (Minnich 1988). Mixed conifer forests at HV and BF now display traits characteristic of fire suppression, high-density stands with increased abundance of fire-sensitive understory species. While lengthening fire return intervals may lead to increased severity of fires (Kilgore 1973), the high density and abundance of young trees at HV and BF suggest that there have been no fires at these sites in this century.

Ozone damage to pines was first described in the San Bernardino Mountains in the early 1950s (Miller et al. 1991). Concentrations have declined from high levels in the mid-1960s, but remain locally severe. Pollutants from the urban plume are drawn into mid-elevation forests by upslope flows and marine layer intrusions. Quite different air pollution conditions prevail in parts of the range where rugged terrain creates locally protected valleys. Levels of ozone concentration are relatively

Fig. 1. Map of the southern California/northern Baja region showing the locations of study sites: Holcomb Valley (HV) and Barton Flats (BF) in the San Bernardino Mountains, and La Corona Arriba (LCA) in the Sierra San Pedro Martir in Baja California, Mexico.

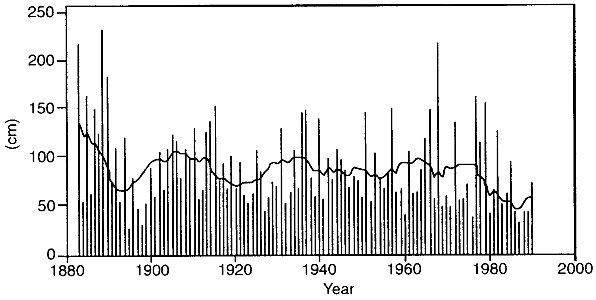

Fig. 2. Precipitation record, with a 10-yr running mean, at Big Bear Dam, San Bernardino Mountains (from Miller et al. 1991).

high at the BF site, and damage to the foliage of mixed conifer species at this site has been documented (Miller et al. 1986). Its location in the broad valley of the Santa Ana River valley allows ozone penetration far into the mountains by funneling upcanyon air flow. HV, 15 km to the east, however, is cut off from the flow of urban air by intervening ridge crests around 2500 m. Miller et al. (1986) used daily pollution measurements from a May-October period over 5 yr at HV and BF to generate ozone concentration data. The estimated average maximum ozone pollution level at HV was 0.05 ppm, barely above the maximum baseline rural mean for North America of 0.048 ppm, while estimated average maximum at BF was 0.07 ppm, nearly 50 % higher than the rural baseline mean (Lefohn et al. 1992).

A persistent and severe drought began in the southern California region around 1985 and lasted until the early 1990s. An instrumental record of precipitation over the last century at Big Bear Dam in the San Bernardinos suggests that the decline reached a low unequaled in the instrumental record (Fig. 2); 1989 and 1990 were exceptionally dry years. A water deficit calculation (Mather 1978) using temperature and precipitation at Lake Arrowhead, 25 km to the west and at 1500 m elevation, indicates the depth of the drought of the late 1980s relative to the short term record (Fig. 3). Patches of dead trees, infested with *Dendroctonus* beetles, are visible throughout the forest.

La Corona Arriba

The Sierra San Pedro Martir is a gently sloped plateau with steep escarpments on the east and west sides, located at ca. 115° W, 31° N, 350 km south of the San Bernardinos. Substrates, as in the San Bernardino Mountains, are primarily granitic, with scattered alluvials (Gastil et al. 1975). Grazing by cattle and sheep in montane meadows began in the 18th century and continues today at moderate levels.

In contrast to Californian mountains, wildfires are allowed to burn, and the forest displays the open structure associated with unmanaged fires. A fire history at LCA reconstructed from tree-ring scars in *P. jeffreyi* trees by Burk (unpubl.), gives a fire return interval of 13.5 yr (sd ± 10.6 yr), unchanged over the past 200 yr and similar to return intervals in the San Bernardinos before fire suppression. The current unmanaged regime of frequent fire seems to be consistent with that described for forests of southern California before fire suppression (Minnich et al. 1995). Frequency of ignition and variation in topography result in low-intensity, patchy fires.

There is little evidence of air pollution at LCA. The site is located in the middle of a narrow peninsula, with large water bodies on either side. The nearest urban area, Ensenada, is 150 km to the northwest. While there are no local instrumental data on air pollution, air quality appears to be relatively pristine.

Instrumental climate records in the range are brief, but there is evidence that the San Pedro Martir also experienced the recent regional drought over the same period as southern California. A water deficit, calculated from temperature (Miranda et al. 1991) and precipitation (Reyes Coca et al. 1990) data at the nearby

Santa Cruz station (9 km away, 900 m elevation) from 1970 to 1990 indicates a steady decline in available water the latter half of the 1980s (Fig. 3). During 1989-1990, precipitation was less than half of normal, and the 1989/1990 pair of tree rings appear strikingly narrow as do those in southern Californian trees. There is no visible evidence of recent insect outbreak in the conifer forests of the San Pedro Martir.

Methods

Pinus jeffryi-Abies concolor stands were sampled in 1994 at the three sites located between 2200 and 2500 m a.s.l. and similar in slope, aspect, and canopy dominance. At each site, tree ages and sizes were sampled on eight systematically placed 200-m transects. An initial pair of transects, separated by 60 m, was randomly located on the contour of the slope in a relatively homogenous *P. jeffrey-A. concolor* stand. Three more pairs of transects were established at 300 m intervals apart on the slope and parallel to the first pair. All eight transects lay on gentle to moderate slopes facing NNE.

Forest composition and condition were estimated using the point-centered quarter method (Cottam & Curtis 1956). At points 20 m apart, I recorded the species and condition (live or dead standing) of the nearest adult tree ($\geq$ 1.4 m in height and $\geq$ 4 cm DBH), seedling (<1.4 m in height), or sapling (> 1.4 m in height, < 4 cm DBH) within 15 m in each quarter, and its distance from the point. For each live and dead standing adult tree, dbh was recorded to the nearest centimeter. A small number of beetle-killed trees had been removed at BF to lower fire risk. For these stumps, basal circumference (bc) was measured and dbh estimated using linear regression equations relating bc to dbh.

Live adult trees were cored for age determination at ca. 30 cm above the ground. Cores were sanded smooth and annual rings counted under a microscope to estimate age at coring height (Stokes & Smiley 1968). Ages of dead trees and trees with rot or where the center was not reached could not be determined directly. Their ages were reconstructed, or estimated, using linear regression equations relating age to DBH. Population structures, for both directly aged and reconstructed ages of trees of the two species, were represented in 20-yr age classes to accommodate error due to variation in growth to 30 cm and regression estimation of age.

Density, cover expressed as basal area, and age structure of the sampled forest were characterized. Age class histograms of the distribution of live and dead adult trees were constructed to illustrate differences in composition, abundance, and mortality by site. Density and basal area of all trees and relative density and basal area of each species were calculated using distance from the transect point. In closed canopy forests, where there can be a regenerational response to mortality, lumping together live and dead trees for density calculations might present a problem. In the southern California forests, however, tree death is recent, and in the San Pedro Martir, stands are so open that the death of a tree makes little difference in terms of regenerational opportunity. A correction factor was employed to compensate for the presence of empty quadrats, those with no tree within 15 m, which would otherwise overestimate density (Warde & Petranka 1981).

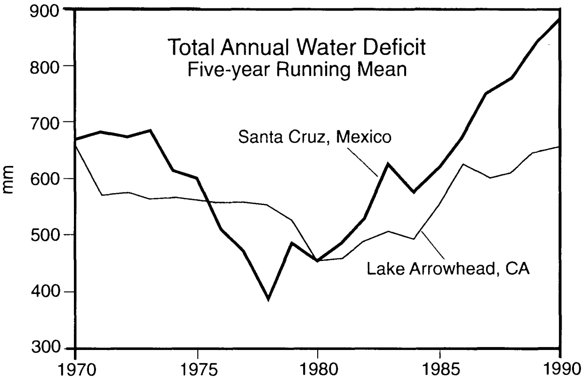

Fig. 3. Total annual water budget deficit 1970 to 1990, calculated from temperature and precipitation data from stations at Lake Arrowhead, California and Santa Cruz, Mexico.

An undetermined number of pine trees in the lower transects at BF may have been ponderosa pine or hybrids of *Pinus jeffreyi* with *P. ponderosa*. These two morphologically and ecologically similar pines often overlap in a narrow band, where they display a low rate of hybridization (Haller 1962). Ponderosa pine and trees with intermediate traits at this site were grouped with *Pinus jeffreyi* for analysis.

Results

1029 trees of six species were sampled at the three sites, predominantly *Pinus jeffreyi* and *Abies concolor*, with small numbers of *P. lambertiana*, *Juniperus occidentalis*, *P. monophylla* and *Calocedrus decurrans* (Table 1). *Pinus jeffreyi* and *Abies concolor* accounted for 94 % of the adult trees, and the following analysis presents data only on these two species. Roughly similar proportions of living *P. jeffreyi* and *A. concolor* trees comprise the populations (HV: 58% PJ, 42%AC; BF: 49% PJ, 51% AC; LCA: 46% PJ, 54% AC).

Table 1. Adult tree density and basal area values for the sampled stands on a per ha basis. Live = standing live; † = standing dead; %† = percentage standing dead of total. HV = Holcomb Valley, BF = Barton Flats, LCA = La Corona Arriba. P.j. = *Pinus jeffreyi*; A.b. = *Abies concolor* var. *concolor*; J.o. = *Juniperus occidentalis*; P.m. = *Pinus monophylla*; C.d. = *Calocedrus decurrans*; P.l. = *Pinus lambertiana*.

		Density (/ha)				Basal Area (m^2/ha)			
Stand	Spec.	Total	Live	†	%†	Total	Live	†	%†
HV	P.j	158	142	16	10	29.52	24.08	5.44	18
	A.c.	127	103	24	19	14.95	7.26	7.69	51
	J.o.	8	8	0	-	0.15	0.15	0	-
	P.m.	13	12	1	8	1.42	0.23	1.19	84
	Total	306	265	41	13	46.04	31.72	14.32	31
BF	P.j.	190	161	29	15	33.42	29.80	3.62	11
	A.c.	191	168	23	12	9.77	7.31	2.46	25
	C.d.	7	7	0	-	0.03	0.03	0	-
	P. m.	7	0	7	100	0.02	0	0.02	100
	Total	395	336	59	15	43.24	37.14	6.10	14
LCA	P.j.	70	64	6	9	12.34	10.60	1.74	14
	A.c.	80	77	3	4	11.01	10.11	0.90	8
	P.l	12	12	0	-	5.51	5.51	0	-
	Total	162	153	9	6	28.86	26.22	2.64	9

Mortality

Stand structure analysis of the *P. jeffrey*/*A. concolor* phase of these forests reveals that numbers of dead standing trees were dramatically higher at both of the San Bernardino sites than at the Sierra San Pedro Martir site. The percent of dead standing *P. jeffrey* and *A. concolor* was 14.3 % at HV and 14.7 % at BF, in contrast to 4.3 % at LCA (Table 2). A difference of proportions test indicates that the proportion of dead standing trees at HV was not significantly different from that at BF, but significantly greater at both sites from that at LCA ($p < 0.05$). There were no marked trends in numbers of dead standing trees by species (Table 2). Dead trees were found across the range of age classes at all sites (Fig. 4), suggesting that demographic structure of each species has not been much altered. Among adult trees, more white fir than *P. jeffrey*were dead at HV, whereas more *P. jeffrey* than *A. concolor* were dead at BF and LCA (Table 2).

At HV and BF, the dead trees appeared to have died within the past few years. Small limbs and twigs remained on virtually all dead trees, and dead needles clinging to branches were common. In a study of mixed conifer forest mortality in 1991 in similar forests in the nearby San Jacinto Range, 87 dead standing trees were crossdated (Savage 1994). All of these trees died over a period of 8 yr from 1984 to 1991; 50 % died in 1989 and 1990. By contrast, dead trees at LCA appeared to have been dead for a longer time. Only large limbs remained on dead standing trees, trunks were barkless, and needles were absent.

Table 2. Actual numbers and percentages of live and dead standing *Pinus jeffreyi* and *Abies concolor* adults in the sampled stands. HV = Holcomb Valley, BF = Barton Flats, LCA = La Corona Arriba.

Stand	Species	Live Adults	Dead Adults	% Dead	% Dead P.j. + A.c.
HV	*Pinus jeffreyi*	121	14	10	
	Abies concolor	88	21	19	14.3
BF	*Pinus jeffreyi*	76	15	17	
	Abies concolor	81	12	13	14.7
LCA	*Pinus jeffreyi*	71	5	7	
	Abies concolor	85	2	2	4.3

Age structure

A total of 526 Jeffrey pine and white fir were cored for age determination. Of these, 390 or 74 %, were successfully aged. The relative youth of the majority of trees, and the presence of distinct, narrow rings at all sites (1857, 1900, 1934, 1951, 1961, 1989 and 1990) made visual cross-dating feasible. Ages of dead and unaged live adult trees were estimated using linear regression equations; the best relationship for each of the species from the San Bernardinos was used to reconstruct tree ages from HV and BF, where there was a significantly positive relationship between age and size in both cases:

P. jeffrey ($n = 52$): $\ln a = 2.27 + 0.68 \ln d$
($p < 0.001$, $r^2 = 0.85$) and
A. concolor ($n = 73$): $\ln a = 3.6 + 0.02\, d$
($p < 0.001$, $r^2 = 0.51$), where a = age and d = DBH (cm).
At LCA, the regression equations were
P. jeffrey ($n = 33$): $\ln a = 1.38 + 0.86 \ln d$
($p < 0.001$, $r^2 = 0.74$) and
A. concolor ($n = 38$): $\ln a = 3.18 + 0.04\, d$
($p < 0.001$, $r^2 = 0.62$).

Jeffrey pines were in general much older than white fir. Mean age of *P. jeffrey* exceeded that of *A. concolor* by 33 % at HV, by 63 % at BF, and by 26 % at LCA (Table 3). A two-tailed *t*-test for differences of means indicated mean ages of *P. jeffrey* were not significantly different in any comparison of sites, whereas mean ages of *A. concolor* were significantly different in every comparison of sites ($p < 0.05$). Among aged trees, the oldest Jeffrey pines were about twice as old as the oldest white fir. The oldest Jeffrey pines at both HV and BF were near 300 yr, while the oldest white fir at HV was near 150 yr, and at BF, near 100 yr. The oldest aged Jeffrey pine at LCA was 448 yr compared to the oldest aged white fir at 285 yr. However, there were a number

Table 3. Age and DBH characteristics of adult live *Pinus jeffreyi* (P.j.) and *Abies concolor* (A.c.) trees in sampled stands, for which ages were determined from ring count. % aged = percentage of all adults of each species for which approximate age was determined. HV = Holcomb Valley, BF = Barton Flats, LCA = La Corona Arriba.

Stand	Species	Age (yrs)			% aged	DBH (cm)		
		n	mean	range		n	mean	range
HV	P.j.	95	89	29 - 289	79	122	37	5 - 120
	A.c.	76	67	26 - 155	86	87	24	4 - 104
BF	P.j.	55	96	18 - 285	72	77	38	4 - 127
	A.c.	71	59	22 - 96	88	80	20	5 - 57
LCA	P.j.	42	108	17 - 448	59	71	56	6 - 117
	A.c.	51	86	15 - 285	60	85	44	4 - 143

of white fir at LCA, not aged, that far exceeded the size of the Jeffrey pines (Table 3).

Populations of both species at all three sites are for the most part uneven-aged (Fig. 4). The population age curve for *A. concolor* in the San Bernardino Mountains, however, reflects a major recent expansion, with most trees establishing in the last 100 yr. At HV, and to a lesser extent at BF, *P. jeffreyi* also shows a shift toward younger age classes. In the Sierra San Pedro Martir, both species have trees in many age classes, but many young white fir in the 30-50-yr age class as well as in old age classes (Fig. 4).

Numbers of seedlings and saplings of both species at the sites appear adequate to maintain current stand structure, with totals for both species varying between 64 at HV to 156 at BF. At both these San Bernardino sites, *A. concolor* seedlings outnumbered those of *P. jeffreyi* with 55% at HV and 74% at BP. At LCA, *P. jeffreyi* seedlings predominated with 72%. Saplings were more abundant at BF (50) than at either HV (26) or LCA (28), although the species were about equally abundant at all sites. The numbers and size of saplings suggest that they contribute to competitive effects in the stands, notably at BF, where adult numbers were lower than at the other sites.

Interpretation of the composition and abundance of seedling populations must be very tentative, as the fate of seedlings is often uncertain and anomalous conditions may temporarily distort the structure of young age classes. It is not clear why white fir seedlings, a more drought-sensitive species, have fared so well during this period. Also, although the stand at LCA displays an adult structure that is compatible with a natural fire regime, the presence of these young trees suggests either very patchy recent fire or no fire within the time frame of seedlings and saplings. Long-term monitoring of these sites will reveal the effects of the drought and patchiness of fire on regeneration.

Size, cover and density

Jeffrey pines were in general much larger than white firs at all three sites. Mean DBH of live *Pinus jeffreyi* exceeded that of live *Abies concolor* by 54% at HV, by 90 % at BF, and by 27 % at LCA (Table 3). At LCA, however, trees of both species were significantly larger than in the San Bernardinos; Jeffrey pines were about half again as large, and white fir about twice as large as in the San Bernardinos (Table 3). A two-tailed differences of mean *t*-test ($p < 0.05$) indicates that white fir diameter at LCA was significantly different from values at HV and BF, but not significantly different at HV and BF. *P. jeffreyi* mean diameter values were not significantly different in any site comparisons ($p < 0.05$).

Basal area was greater at the San Bernardino sites for live and dead *P. jeffreyi* and *A. concolor* combined than at the Sierra San Pedro Martir site. Basal area of live and dead trees combined was similar at the San Bernardino sites at 46 m^2/ha (HV) and 43 m^2/ha (BF) (Table 1), compared with 29 m^2/ha total basal area for these species in the San Pedro Martir (LCA) (Table 1).

Recent reduction in basal area in the San Bernardinos can be attributed to the death of trees in many age classes, including many large old Jeffrey pines and young adult white firs. *P. jeffreyi* dominated basal area at these sites whether considering both live and dead standing trees or only surviving trees. *A. concolor* basal area was significantly more reduced relative to that of *P. jeffreyi* at the San Bernardino sites (Table 1). BF, with more young trees than HV, had a lower proportion of loss of white fir basal area than HV (Table 1).

At LCA, on the other hand, dead standing trees accounted for the smallest proportion of basal area relative to the San Bernardino sites. At LCA, basal area of live *P. jeffreyi* just equaled that of live *A. concolor*, and dead standing trees accounted for 14% of total *P. jeffreyi* and 8 % of total *A. concolor* basal area (Table 1). Dead standing basal area of *P. jeffreyi* and *A. concolor* combined accounted for 31 % at HV, 14 % at BF, and 8 % of total basal area at LCA.

Adult tree densities were lowest at LCA (162/ha), nearly double at HV (306/ha), and even higher at BF (395/ha) (Table 1). In general, the higher density of the southern California sites can be accounted for by trees which established in this century (Fig. 4). At LCA, *A. concolor* also shows a small regeneration pulse in the 30-50 yr age class (Fig. 4), possibly reflecting a fire-free period in these years in the sample area at this site.

Did more mortality occur in those cohorts that established after fire suppression, which produced higher overall densities? The percentage of adult *P. jeffreyi* with ages from10 - 90 yr, as a percentage of all *P. jeffreyi* adults, was 51 % at HV, 44 % at BF and 32 % at

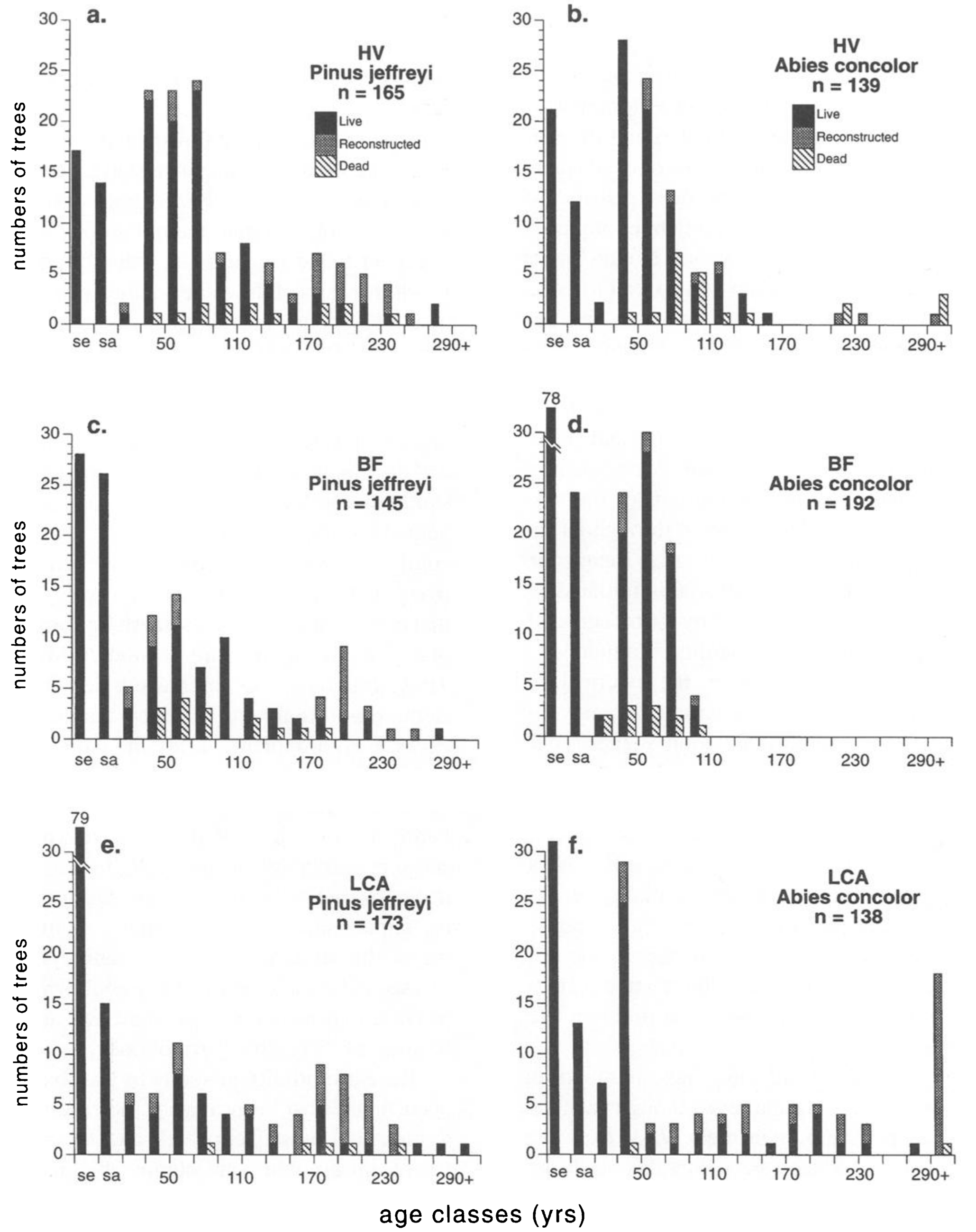

Fig. 4. Age distributions of *Pinus jeffreyi* and *Abies concolor* seedlings, saplings, and adult trees in the sampled stands (raw data), in 20-yr age classes at sites HV: Holcomb Valley (**a**, **b**); BF: Barton Flats; (**c**, **d**) and LCA: La Corona Arriba (**e**, **f**). Percentage of trees successfully aged is given in Table 3. Reconstructed live and dead trees that could not be aged were estimated from linear regression equations relating age to DBH. Se = seedling, sa = sapling.

LCA. *P. jeffreyi* in age classes 10-90 yr accounted for 29 % at HV, 67 % at BF and 20 % at LCA of mortality of all adult *P. jeffreyi*. Only at BF did more mortality occur in young adult *P. jeffreyi* than in the population as a whole. The percentage of adult *A. concolor* 10 - 90 yr, as a percentage of all *A. concolor* adults, was 66 % at HV, 84 % at BF and 41 % at LCA, while *A. concolor* in age classes 10-90 yr accounted for 43 % at HV, 83 % at BF and 50 % at LCA of mortality of all adult *A. concolor*. For young *A. concolor* adults, mortality was lower than the population as a whole at HV, similar at BF, and slightly higher at LCA (note the low sample size at LCA). Except for *P. jeffreyi* at BF, then, older trees suffered as much mortality as young adults at all sites.

Discussion

Dead standing *Pinus jeffreyi* and *Abies concolor* in the mixed conifer forest in southern California were over three times as numerous as in similar forests in Baja California. The lowest percentages of dead standing trees were found at the site with lowest density and basal area values. Even when surviving trees alone are considered, density and basal area values remain higher in southern California forests than in Mexican forests.

An increase in the density of forests in the San Bernardino Mountains has been widely documented as the result of a surface fire return interval considerably lengthened by fire suppression (e.g. Vankat 1977; Barbour 1988; Minnich et al. 1995). A rapid and pervasive trend toward increased abundance of fire sensitive species such as white fir under conditions of fire suppression has also been widely reported throughout the western U.S. (e.g.Vankat 1977; Swetnam & Betancourt 1990; Savage 1994). Successional trends initiated by fire protection have been accelerated by the recent death of large, old pines in the San Bernardino Mountains.

At the San Pedro Martir site, where the historical fire regime still prevails, no such successional trends are evident and an uneven-aged population suggests balanced regeneration. One feature of the LCA site that remains unexplained is the large number of old white fir trees, more than expected under a regime of frequent fire. An explanation might be sought in site differences, for example a smaller or more patchy spatial pattern of burning that allows white fir trees to reach a fire resistant size. The presence of old *A. concolor* in the San Pedro Martir, especially in light of the relative paucity of trees in many adult age classes, is a problem that deserves further attention.

At the two southern California sites, numbers of dead standing trees were similar, even though each has very different air pollution intensities. While exposure to air pollution may reduce tree vigor, this study revealed no more mortality in polluted versus unpolluted forests. This suggests that stresses associated with increased density created by fire suppression may be more important than those related to exposure to air pollution in predisposing trees to mortality.

The conclusions of this study are constrained by the limited data set and by the limitation to one site of each set of stresses. The hypothesis that structural changes in mixed conifer forests are primarily due to fire suppression policies needs testing at multiple sites and/or by long term monitoring of mortality in forests, particularly in those uncommon communities with natural disturbance regimes. In addition, the abundance of dead standing trees have been used here as a static measure of mortality, and therefore is only a rough approximation, as the time of death of trees is unknown. A conclusive comparison of mortality rates can only be made using permanent plots to monitor the dynamics of these forests.

The mixed conifer forest of the Sierra San Pedro Martir represents a disjunct stand, and comparisons with stands in the San Bernardino Mountains must be tentative. For example, the more open structure of the Mexican forest might be explained in part by greater moisture stress of the more southerly location. Minnich et al. (1995), however, argue that modern forests in the Sierra San Pedro Martir are not more open than those in northern parts of the region because of a more arid environment. They suggest that precipitation patterns and amounts are well within southern California values, and document mixed conifer forests as dense as those in southern California where local topography has prevented burning. Minnich et al. (1995) resampled mixed conifer stands quantitatively described in 1929-1935 from the California Vegetation Type Map, and found that pre-fire suppression southern California forests displayed the open structure of modern Mexican forests. They conclude that increased density in the San Bernardino Mountains has been caused, not by differences in environment, but by the reduction of fire frequency. Minnich also observed uniformly low numbers of dead standing trees in the forests of the Sierra San Pedro Martir. 61 % of the 1-ha sites analyzed using aerial photography taken in 1991 had no dead standing trees; the rest had a mean of one dead standing tree per ha (unpublished data). This analysis supports the finding of this study that recent mortality is light in these forests and argues against the possibility that the sampled site may have missed evidence of insect infestation because of its patchy distribution.

Recent mortality in southern California forests has been thought to be primarily the result of the recent drought and subsequent beetle attack. If the severity of the recent drought were comparable at the three sites considered in this study, then one interpretation of the mortality data is that the more open structure of the forest in Baja Mexico, maintained by frequent surface fires, may have resulted in lower stress to trees during the recent drought. A striking difference in the southern California sites is the increase in density and basal area in mixed conifer forests in this century. Both adult density and basal area values at the southern California sites are generally double those at the Mexican site, suggesting that the size of trees may be as important as density in indicating competitive conditions for soil moisture. Moreover, density and basal area values at HV and BF have changed considerably in this century, and competition for soil moisture then, may have changed considerably as well. At LCA, there is some increase in young adult white fir, but overall, the populations are more stable in this century. A reconstruction of annual climate values generated from a tree-ring chronology currently being developed will allow a better assessment of the relative strength of competitive conditions for moisture in the San Pedro Martir during the recent drought.

Muller-Dombois (1986) observed that aging cohorts become increasingly vulnerable to stresses. In the southern California mixed conifer stands, it may be that fire suppression in this century has created a forest with greater susceptibility to drought, beetle attack, and other natural stresses. The enhanced potential for stand destroying fires in increasingly dense forests of the western USA is already a concern for forest managers. If it is the case that fire exclusion also enhances susceptibility to natural disturbances such as drought, there are additional reasons to consider management choices, such as prescribed fire, that create more open stands.

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