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Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California

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Anthropogenic and natural disturbances have been implicated in recent mortality episodes in montane forests. While the role of natural disturbance in patterning forest ecosystems has been widely explored in recent decades, the agency of human influence is less well understood. In this paper, stand structure analysis is used to characterize patterns of mortality in a montane mixed conifer forest in southern California subject to multiple influences, both anthropogenic and natural, including fire suppression, air pollution, drought, competition, and insect infestation. While it is difficult to separate the contribution of any one of these factors to tree death, because there have been cumulative and synchronous disturbances, successional trends can be identified. Anthropogenic influences appear to abet the effects of natural disturbance in enhancing the shift from early successional pines to species that tolerate stresses such as drought, fire suppression, or competition that result from increased stand density, or a combination of such stresses.

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Des perturbations d'origine humaine et naturelle ont été invoquées pour expliquer les récents épisodes de mortalité dans les forêts subalpines. Quoique le rôle des perturbations naturelles dans le façonnement des écosystèmes forestiers ait été beaucoup étudié au cours des dernières décennies, l'influence de l'activité humaine est moins bien comprise. Dans cette étude, l'analyse de la structure du peuplement est utilisée pour caractériser le comportement de la mortalité dans une forêt subalpine composée d'un mélange de conifères dans le sud de la Californie et sujette à de multiples pressions tant naturelles que d'origine humaine incluant : la suppression des feux, la pollution de l'air, la sécheresse, la compétition et les infestations d'insectes. Même s'il est difficile d'identifier dans quelle mesure chacun de ces facteurs contribue à la mort des arbres, étant donné qu'il y a eu des perturbations cumulatives et synchrones, on peut identifier des tendances successionnelles. L'influence de l'homme semble encourager les effets des perturbations naturelles en favorisant le remplacement des pins de début de succession par des espèces tolérantes aux stress tels les sécheresses, la suppression des feux ou la compétition qui résulte d'une densité accrue du peuplement, ou à une combinaison de ces stress.

[Traduit par la rédaction]

Introduction

Human influences on forest landscapes can alter natural disturbance regimes or initiate novel disturbances in ways that are poorly understood. Such influences are often not direct or isolated, but cumulative and interactive (Urban et al. 1987). The role of natural disturbances, such as fires or windstorms, in patterning forests has been widely explored (e.g., Watt 1947; Sprugel and Bormann 1981; Veblen and Ashton 1978; Bormann and Likens 1979). Together with such factors as species performance and site availability, natural disturbances shape the composition and structure of forest communities (Pickett et al. 1987; Veblen et al. 1991). But anthropogenic disturbances often have subtle and long-term influence, and are thus difficult to assess in the presence of other, natural events.

The demographics of tree mortality offer an opportunity to explore the agency of human influence in patterning forest landscapes. Both anthropogenic and natural disturbances have been implicated in recent episodes of forest mortality (Franklin et al. 1987; Innes 1992), or in a gradual general deterioration, which may end in tree death, a process that has been termed forest decline by Manion (1981). Manion (1981) proposes the notion that a series of serial or synchronous factors may be involved in causing a decline, some of which weaken the tree while others may simply deal the final blow. He terms these multiple, cumulative stresses as predisposing, inciting, and contributing factors, any of which can be natural or anthropogenic. Muller-Dombois (1988) proposes the term "dieback" for mortality of whole stands or patches of forest, as opposed to the death of scattered individual trees, and argues that multiple, synchronous events may be more common in causing such dieback than single catastrophic disturbances.

In recent years, pine species in mixed conifer communities on the western slopes of California mountain ranges have experienced widespread mortality from bark beetle outbreaks (*Dendroctonus* spp.) in weakened individuals following a prolonged, severe drought. These forests are one of California's most extensive forest type, covering about 14% of the state's area (Barbour 1988), and represent a valuable timber and recreational resource. By 1991, mortality in pine-dominated forests in the Sierra Nevada was estimated to have reached at least 15 times normal levels (J. Neisses, April 4, 1991 testimony, U.S. Senate Committee on Natural Resources and Wildlife). Human influence in these forests has been profound for more than a century. Fire suppression, for example, has caused increased forest density as well as compositional shifts to species that are fire sensitive (e.g., Kilgore 1973; Kilgore and Taylor 1979). In the absence of fire, species that do not readily survive even light fires have increased in density. In recent decades, ozone pollution from urban air plumes has seriously damaged some forest trees (Barbour 1988).

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This study explores patterns of forest dieback in the forests of the San Jacinto Mountains of southern California, and patterns of synchronous disturbances responsible for the mortality. In a sense, the forest originated with a stand-originating human disturbance, logging. Much of this forest was cut in 1875–1876 (McAdams 1955), initiating the development at the site of a relatively even-aged stand dominated by early successional forest trees. As the cohort grew, fire-suppression policies were instituted, largely eliminating the frequent, low-intensity fires common in the presettlement era. The San Jacinto Mountains, bounding the eastern margin of the Los Angeles metropolitan basin, are located in the path of the urban smog plume, where upslope winds may have allowed the accumulation in the midelevation forests from the 1950s onward. Similar forests on neighboring ranges, particularly the San Bernardinos, display chronic pollution damage. Episodic natural factors, a serious 5-year drought and a concurrent beetle outbreak, thus visited a forest in which anthropogenic disturbances were already chronic.

The analysis of stand age structure, or the relative abundance of trees of different ages, can provide insights into the role of human and natural disturbances in the origins of a forest stand, its development over time, and potential future trends (Veblen 1986). I employ the use of stand structure analysis in this study to: (*i*) describe the composition and structure of a forest community characterized by significant levels of insect-caused mortality, (*ii*) document the differential impact of combined disturbances on the component species, and (*iii*) describe regenerational potential and predict near-term compositional shifts in the forest. In a more general sense, I propose to explore the role of anthropogenic influences on tree mortality from natural disturbances in a mixed conifer montane forest in southern California.

Species' response to disturbance

The response of individual species to disturbances will depend on the strategies employed by the species in coping with its environment, including such factors as a species' vulnerability to various stresses, its pattern of reproduction, and its tolerance of competition (Sousa 1980). To understand the recent dieback and the differential mortality of tree species at the site, it is helpful to review our knowledge of the adaptive response of the component tree species to a variety of disturbances, some historical and some novel.

Fire suppression

Frequent, light fires were common in these summer-dry forests of flammable species before European settlement, as they were in other such forests of the West (Kilgore 1973; Vankat and Major 1978). McBride and Lavin (1976) suggest a natural fire frequency of every 10–30 years in similar mixed conifer forests of the nearby San Bernardino Mountains.

These patchy presettlement fires burned rapidly on the surface, favoring species morphologically adapted to survive fire or those with strong regenerative strategies. Adult ponderosa pine (*Pinus ponderosa* Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), with their thick bark and high crowns, survive such surface fires handily. Morphological traits of other pines make them more susceptible (Laacke 1990). (*Pinus coulteri* D. Don) self-prunes poorly, while the thinner, denser bark of sugar pine (*Pinus lambertiana* Dougl.) insulates cambium poorly against heat damage (Wagener 1961). Incense cedar (*Calocedrus decurrans* (Torr.) Florin.) and white fir (*Abies concolor* (Gord. & Glend.) Lindl.), in small diameter classes, and with branches reaching the ground, are fire susceptible, and probably were rare in stands where fires were frequent. Adult incense cedar are protected by thick bark, but younger trees are readily killed (Burns and Honkala 1990). Marked increases in density of incense cedar and white fir in Sierran mixed conifer forests have resulted from fire suppression (e.g., Biswell et al. 1966; Vankat and Major 1978; Rundel et al. 1977). Although aboveground stems of California black oak (*Quercus kelloggii* Newb.) and canyon live oak (*Quercus chrysolepis* Liebm.) suffer fire mortality, these species can be common in fire-prone communities because of their ability to resprout profusely and establish seedlings on mineral soil (Abrams 1992).

The species at this site, then, respond differentially to fire suppression. In general, in the absence of fire, fire-sensitive species will tend to regenerate successfully at the expense of fire-tolerant species. In addition, stand density will increase, making the stand more vulnerable to a destructive crown fire (Vankat and Major 1978; Kilgore and Taylor 1979). The study site has experienced no fires since the timber harvest in 1875–1876. In its early stages of development, the fuel load of the post-timbering stand did not support fire, and suppression policies of this century have thus far excluded fire on the site.

Air pollution

The San Jacinto Mountains are at the eastern edge of the metropolitan Los Angeles basin, where the air pollution plume accumulates against the mountains, and is drawn into the forests by upslope flows and marine layer intrusions (Edinger et al. 1972). In general, concentrations are often exacerbated by summer temperature inversions, and mid-elevation damage may be most severe (Edinger et al. 1972). The most important potential damaging agent is ozone, first identified as the cause of injury to pines in the early 1950s (Miller et al. 1963).

Many of the species present in mixed conifer forests have been shown to be sensitive to ozone (Miller et al. 1983). Chronic exposure of evergreen foliage to damaging levels of air pollution results in premature needle loss, reduced growth, and greater susceptibility to drought and disease (Williams 1983). Pollution appears to weaken trees without being a direct cause of death. Ponderosa and Jeffrey pine, the first species to exhibit pollution damage, continue to suffer the most extensive damage. Experimental evidence indicates that the order of decreasing sensitivity of other conifers to ozone is white fir, incense cedar, and sugar pine (Miller et al. 1991). Sugar pine appears to be the least affected conifer in this forest type (Williams 1983). Oaks are less susceptible to damage by photooxidants than pines, and several authors suggest a shift toward oak in pollution-stressed pine forests following fire owing to the dual oak strategy of resprouting and reseeding (McBride 1978; Miller et al. 1980).

Chronic exposure to photooxidants has weakened tree vigor of many species in the region (Miller et al. 1991). While mean ozone levels declined in the 1980s, air pollution is still a serious ambient stress in affected midelevation forests in southern California (Miller et al. 1991). The air pollution level at the study site was not quantified, and thus its role in stressing the trees is not certain. However, the conditions for pollution stress are good, and in fact damage to conifer foliage is visible throughout the forest at this elevation.

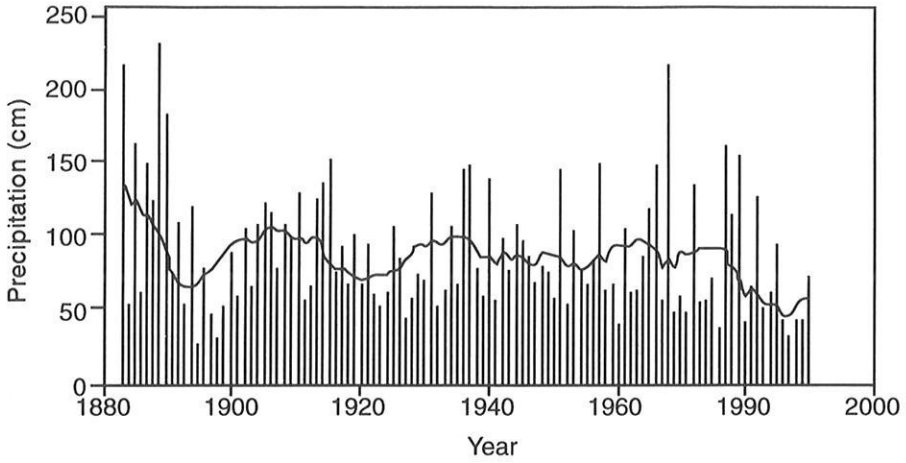


FIG. 1. Precipitation record, with 10-year running mean, 1883–1990, at Big Bear Dam, San Bernardino Mountains. (From Miller et al. 1991).

Drought

Adverse climate conditions have been implicated in many cases of forest dieback (Innes 1992). Southern California mixed conifer forests recently experienced a serious and prolonged drought. A precipitation record over the last century at a station in the neighboring San Bernardino Mountains suggests that a decline beginning in the late 1970s has now reached a low unequaled in the instrumental record (Fig. 1). Severity of the drought continued to deepen up to the year of the study. Moisture storage at relatively deep soil levels is considerably depleted in such a prolonged drought.

Severe annual summer droughts are typical of this habitat, however, and the species in this community are all physiologically adapted to drought stress. Both ponderosa and Jeffrey pine are moderately, and Coulter pine, extremely drought tolerant. Sugar pine prefers more mesic microhabitats, and is less drought tolerant than other pines. Incense cedar, although preferring to germinate in mesic, shady sites, is relatively drought tolerant as an adult (Burns and Honkala 1990). Black and canyon live oak also have drought adaptations, including deep roots, xeromorphic leaves, and low water-potential threshold for stomatal closure (Abrams 1992).

The members of the community are thus reasonably resistant to moderate drought. Other environmental factors at a site, however, may enhance the vulnerability of the trees to drought stress. Increased competition due to increased stand density, for example, will reduce available soil moisture even without a drought. Chronic air pollution is reported to increase the sensitivity of symptomatic pines to drought stress by reducing reserves needed to survive a prolonged drought (Innes 1992).

Beetle attack

Bark beetle infestation is often contingent on forest stand condition. Conifer trees severely affected by drought in California are usually killed by bark beetles (Innes 1992). *Dendroctonus* species (including *Dendroctonus brevicomis* LeConte, *Dendroctonus ponderosa* Hopkins, and *Dendroctonus jeffreyi* Hopkins) are more likely to attack ponderosa, Jeffrey, Coulter, and sugar pine during and after a drought (Burns and Honkala 1990). While mainly older trees ordinarily succumb to bark beetle attack, younger second-growth forest mortality is often linked to drought conditions (Struble 1965) and an attendant insect attack. Severe droughts of the past have resulted in widespread mortality episodes in pine forests, such as extensive losses in the Pacific Northwest forests in the 1930s (Burns and Honkala 1990). Trees further weakened by ozone damage are even more susceptible to insect mortality. Severe levels of mortality in Coulter pine and moderate levels of mortality in ponderosa, Jeffrey, and sugar pine from beetle attack have been reported in the mountains of southern California affected by air pollution (Dale 1991). By contrast, white fir, incense cedar, and oaks suffer less from lethal insect pests.

Fire historically played an important role in reducing the threat of insect infestation in these forests, by thinning stands and removing high risk trees in which insects could breed (Kilgore 1973). Fire-suppression policies have thus increased the potential for insect attack in western forests. Dense stands are stressed by competition and hence more vulnerable to *Dendroctonus* attack (Weaver 1964).

Study area

Tree mortality was studied in a mixed conifer forest in the San Jacinto Mountains, 150 km east of Los Angeles, at 33°50′N, 116°45′W. This small mountain range is oriented southeast to northwest and forms the northernmost portion of the peninsular range system of Southern California. The research was conducted in Hall Canyon Research Natural Area, a 293-ha National Forest reserve managed by the University of California at about 1650 m in elevation.

The regional climate is a Mediterranean type, with mild wet winters and hot dry summers. Precipitation falls primarily in the winter as snow and rain, but unstable tropical air masses also bring infrequent summer thunderstorms during July and August. The highest peak in the range, San Jacinto Peak, averages 90 cm of precipitation annually. Soil development in the range is weak, with limited horizonation and depth to bedrock often less than 1 m on slopes, but up to 2.5 m deep in the valley bottom (Hanawalt and Whittaker 1976). Soils are derived from granitic parent material, and permeability to precipitation is relatively high (Hamilton 1983).

The mixed conifer forest of the area is characterized by a diverse mix of pines and oaks in a transition area with overlapping elements of Mexican, Sierran, and Rocky Mountain floras (Hamilton 1983). Pines dominate the forest type. Ponderosa pine, tolerant of both drought and fire, dominates most of the lower montane mid-elevations. Jeffrey pine, also drought tolerant but more cold tolerant than ponderosa, is found at higher midmontane elevations (Barbour 1988). These two pines are morphologically and ecologically similar, and often overlap in a narrow band, where they

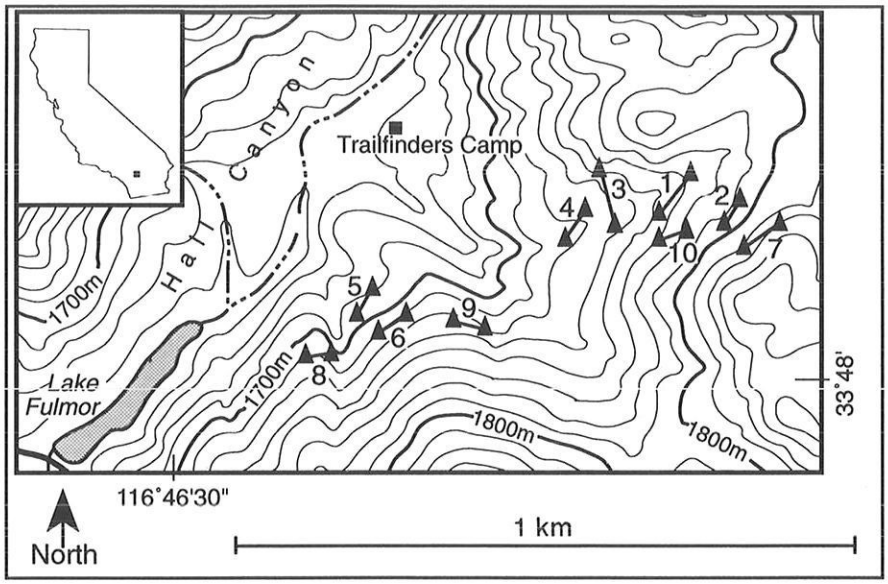


FIG. 2. Map of study area. Numbers designate paired sample plots.

commonly display a low rate of hybridization (Haller 1962). In the San Jacintos, the two pines appear to hybridize where they share dominance (Thorne 1977), as they do at the study site.

Patches of Coulter pine penetrate into the study site from the lower, drier zone, where fire-prone pine–oak associations of Coulter pine and canyon live oak, or dense chaparral communities of *Arctostaphylos*, *Cercocarpus*, and *Adenostoma* are found (Hanawalt and Whittaker 1976). Sugar pine, a white pine and often the tallest tree in the association, is more shade tolerant but less drought tolerant than the yellow pines, and occupies slightly more mesic microhabitats at the site. The most mesic, shaded sites support white fir at the lower edge of its distribution in the mixed conifer type. Incense cedar is a minor associate, also found in mesic sites, particularly shallow ravines. Fir, incense cedar, and sugar pine are seral species in this community, establishing in the shade of other trees.

Two oaks are important subdominants in the mixed conifer forest, winter deciduous black oak and evergreen canyon live oak. Both display a wide variety of growth forms, tending to shrubbiness where fire is frequent and soils are xeric and poor, or arborescent in more favorable circumstances. These oaks are common associates of ponderosa pine over large areas of California, often serving as a nurse tree to pine and incense cedar seedlings (Burns and Honkala 1990), and dominating in places where conifers have been removed by crown fires or logging (Thorne 1977).

Forest composition prior to timbering is suggested by historical accounts of the timber operations, which emphasize the abundance of the desirable timber tree sugar pine but also mention yellow pines, oak, and cedar. The logged trees were described as among the largest trees cut in southern California at this time, with some estimated at 75 m tall (McAdams 1955).

Methods

Sample plots were located in a relatively homogeneous forest stand on a northwestern slope in a sample area with an elevational range of 135 m and a lateral distance of 900 m. In summer 1992, tree ages and sizes were sampled by species in 10 pairs of 900-m^2 plots (Fig. 2). Each pair consisted of a subjectively chosen patch of trees that had suffered extensive mortality of adult trees, and a nearby healthy patch of similar composition and age. Most mortality appeared to be very recent, with most trees still retaining dead needles and bark. Plots in which many or most adults were dead standing I termed severe-mortality plots; those which had few or no dead adults I termed light-mortality plots. The goal was to compare stands with similar species composition and age structure to investigate differential patterns of mortality. The light-mortality plots were taken to represent the premortality sample of the forest and the severe mortality plots, a postmortality sample. A two-sampled t-test was performed between mean abundances of both live and dead adult trees, by species, in light- and severe-mortality plots to verify similarity of composition before the mortality episode.

Species and diameter at breast height (DBH) to the nearest 0.5 cm were recorded for all live and dead adult trees (>1.4 m in height and ≥5 cm DBH) in each of the 20 plots. Seedlings, defined as stems ≤1.4 m, and saplings, >1.4 m in height but <5 cm DBH, were counted and identified by species.

All trees in each plot were cored for age determination at ca. 30 cm above the ground. Cores were sanded smooth, examined under a stereomicroscope, and annual rings counted to estimate age at coring height (Swetnam et al. 1985). The relative youth of the majority of trees, and presence of distinct marker rings (1934, 1950, 1951, and 1961), made visual cross-dating possible for virtually all cores. Dead trees were cored and aged, and date of death determined by visual cross-dating. This verified that the vast majority had died within 2 or 3 years of coring, and none more than 5 years before coring. Rings of some adult trees, such as those with scars or rot, or where the center was not reached, could not be counted. Ages of these trees were estimated using linear regression equations generated for each species based on the relationship of successfully aged trees to DBH. Population structure of the component species was represented in age-classes of 20 years. Broad age-classes were used to accommodate error due to variation in growth to coring height and in regression estimates of ages.

Since harvesting of seedlings to estimate growth to coring height was not allowed in the reserve, only age to coring height, not actual tree age, is reported in histograms. Estimated dates of tree establishment are discussed as a range of years and are necessarily general. As most trees established in a favorably open site after logging, only 10 years were added to ring counts as an estimate of establishment dates for discussions of the timing of stand development.

Several analyses were used to characterize the changes in forest structure that resulted from the recent mortality episode. Density and cover, expressed as basal area, as well as relative densities, by species, in light- and severe-mortality plots were calculated. In addition, age-class histograms of the distribution of live and dead adult trees were created for each species, to illustrate the dif-

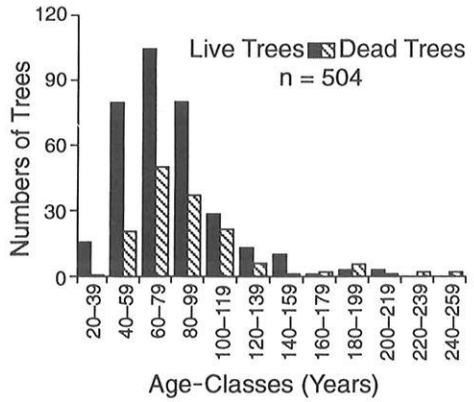


FIG. 3. Frequency of trees of all species sampled in 20 plots. Numbers of trees with inner-most ring dates of trees falling in each 20-year age-class, plus seedlings (<1.4 m) and saplings (≥1.4 m in height but <5 cm DBH). n, total number of adult trees.

ference in composition and abundance between light and severe mortality stand structure. Annual rings of canyon live oak were not legible in the majority of cores; the distribution of this species is presented in a size-class histogram. A Kolmogorov–Smirnov (K–S) two-sample test was used to test the hypothesis that the distribution of living adult trees of each species in light-mortality plots was similar to that in severe-mortality plots (Sokal and Rohlf 1981), that is, that the mortality episode had not significantly changed the forest structure.

The vertical structure of the forest, expressed by a measure of the potential successor to canopy trees, was used to predict possible future composition of the forest. The species of each potential successor, defined as the species of the largest seedling or sapling within 2 m of a live adult tree, and the species of its canopy tree, was recorded. This relatively small perimeter was used because of forest density; beyond a 2-m perimeter, a seedling or sapling was often another canopy tree's successor. Transition probabilities of a Markovian tree by tree replacement model were used to predict the next generation of canopy trees (Horn 1975). Because of the strong likelihood of near-term natural disturbance such as fire or continued beetle mortality, prediction of the state of the forest beyond the next generation did not seem to be warranted.

Results

Stand structure analysis of this forest reveals the rapid development of a post-logging forest stand (Fig. 3). An analysis of the pattern of establishment of each species shows an initial development of a cohort of pioneer pine species, followed by gradual establishment of shade-tolerant species. A total of 504 adult trees of eight species were sampled in 20 plots. The paired plots were 53.1 ± 45.7 m (mean ± SD) apart. Slope of the light-mortality plots was 18.9 ± 6.7° and of the severe-mortality plots, 18.1 ± 6.1°. Results of the two-sample t-test of species abundances, using both live and dead trees, indicate that each species had similar abundances in light- and severe-mortality plots ($P < 0.001$), confirming the similarity of premortality to postmortality structure.

Of the sampled adult trees, 381 or 74% were successfully aged. Ages of the remaining 123 live and dead adult trees were estimated using linear relationship of age to size separately for each species (Table 1). The relationship ranged from fair to good. Generally speaking, age predictions were better for those species for which more ages were estimated,

TABLE 1. Regression equations for estimating tree age in years [a] from diameter at breast height in cm [d]

Species	n*	Regression equation	P	r
Ponderosa pine	25	$a = 62.3 + 0.668d$	<0.001	0.65
Jeffrey pine	22	$a = 41.8 + 2.01d$	<0.001	0.87
Coulter pine	34	$a = 43.8 + 1.44d$	<0.001	0.81
Sugar pine	4	$a = 55.2 + 0.805d$	<0.001	0.51
White fir	4	$a = 41.5 + 0.957d$	<0.100	0.37
Incense cedar	12	$a = 43.4 + 1.06d$	<0.001	0.55
Black oak	22	$a = 44.3 + 1.73d$	<0.100	0.52

*Number of trees of each species for which age was reconstructed. Total n = 123.

with ages of only four trees each predicted by the two fair correlations. There was a significantly positive relationship between age and size in all cases.

Pines constitute the majority of dead trees at the site (Table 2). Forty-two percent of all ponderosa pine, 50% of all Jeffrey pine, and 49% of all Coulter pine in the sample were dead, compared with 13% of sugar pine, 4% of white fir, and no incense cedar or oak individuals. Comparisons of light- and severe-mortality plots suggest that the species in the mixed conifer forest have responded differently to the recent stresses of drought and insect infestation. Of adult trees in the light-mortality plots, 93% were living. Of the 7% dead, most were ponderosa pine (63%) and Coulter pine (19%). By contrast, in the severe-mortality plots, 50% of the adults were dead, of which over 99% were pines. Eighty-one percent of ponderosa pine, 82% of Jeffrey pine, 65% of Coulter pine, and 28% of sugar pine in the severe-mortality plots were dead. This means a shift in each species' abundance within the stand, resulting in a dramatic decline of pine species (Table 2). (Coulter pine abundance did not decline dramatically, despite high mortality rates, owing to slightly higher abundance in severe-mortality plots before the mortality episode.) Whereas pines constitute 70% of the remaining live trees in the light-mortality plots, they constitute only 42% in the severe-mortality plots.

Live tree density was differentially reduced by the mortality episode. In the severe-mortality plots, there was about a one-half reduction of live ponderosa, Jeffrey, and Coulter pines; a small decline in sugar pine; but virtually no change in the density of other four species (Table 3). The difference in cover, expressed as basal area, between light- and severe-mortality plots was substantial owing to the death of many large old ponderosa and Jeffrey pines. Basal area for all species in the light-mortality plots was 112.31 $m^2 \cdot ha^{-1}$, compared with a basal area in the severe-mortality plots of 62.97 $m^2 \cdot ha^{-1}$, a reduction of 44% (Table 4).

The age structure histograms illustrate the mortality patterns and trace stand development originating after logging, a little more than a century ago. Ponderosa pine had a robust regenerational response to the timber cut. Advance regeneration may have accounted in part for the immediacy of the response, and establishment continued to rise for several decades until the density of the stand appears to have slowed further establishment (Fig. 4a). Light-mortality plots have large numbers of trees in the oldest age classes, while severe-mortality plots have similarly large numbers with 100% mortality in the same age-classes. Many forest stands in regenerational equilibrium display a negative exponential distribution of trees in age-class histograms, with high numbers of seedlings and saplings and decreasing numbers

TABLE 2. Percentage of live and dead trees, by species, in light and severe mortality plots

Species	Light-mortality plots		Severe-mortality plots	
	Live trees	Dead trees	Live trees	Dead trees
Ponderosa pine	88	12	19	81
Jeffrey pine	96	4	18	82
Coulter pine	90	10	35	65
Sugar pine	94	6	72	28
White fir	100	0	92	8
Incense cedar	100	0	100	0
Black oak	100	0	100	0
Canyon live oak	100	0	100	0

TABLE 3. Density characteristics of live and dead trees by species, in light and severe mortality plots (adult trees/ha)

	Light-mortality plots		Severe-mortality plots		% difference in live trees
	Live trees	Dead trees	Live trees	Dead trees	
Ponderosa pine	178	25	30	128	−28
Jeffrey pine	58	3	15	63	−74
Coulter pine	70	8	63	118	−10
Sugar pine	83	5	33	13	−60
White fir	33	0	30	3	−9
Incense cedar	68	0	88	0	29
Black oak	38	0	60	0	58
Canyon live oak	30	0	18	0	−40

TABLE 4. Cover characteristics of sampled stands by species, expressed as basal area (m^2/ha)

Species	Light-mortality plots				Severe-mortality plots			
	Live trees	Dead trees	Total	% decline	Live trees	Dead trees	Total	% decline
Ponderosa pine	18.72	1.38	20.10	7	0.40	23.56	23.96	98
Jeffrey pine	7.47	0.11	7.58	1	—	18.79	18.79	100
Coulter pine	6.22	0.25	6.47	4	1.29	15.18	16.47	92
Sugar pine	8.43	0.13	8.56	2	1.18	0.95	2.13	45
White fir	0.12	—	0.12	0	0.20	0.04	0.24	17
Incense cedar	8.21	—	8.21	0	4.99	—	4.99	0
Black oak	1.89	—	1.89	0	2.54	—	2.54	0
Canyon live oak	0.86	—	0.86	0	0.45	—	0.45	0
Total	51.92	1.87	53.79		11.05	58.52	69.57	

of older trees. Compared with this distribution, ponderosa pine currently has a marked paucity of seedlings and saplings.

Jeffrey pine participated only slightly in the post-logging regeneration pulse (Fig. 4*b*). Its distribution is characterized by trees in many age-classes, including the oldest individuals of any species in the stand, trees that survived the timber cut. The older Jeffrey pine were hard hit in the recent dieback, and few live Jeffrey pine now remain in the forest. Again, there is a dearth of seedlings and saplings. Coulter pine participated in this regeneration pulse over a slightly longer period of time, with establishment peaking several decades after logging (Fig. 4*c*). About half of this cohort died, leaving a somewhat younger group. The seedling and sapling classes, while larger than that of the other yellow pines, are probably not sufficient to maintain the species' canopy share.

The remaining five species were virtually untouched by the mortality episode. Sugar pine is more shade tolerant than pioneer pines, and age distributions indicate only a slight regeneration response upon stand initiation a century ago (Fig. 5*a*). One sign of its regenerational success is the relatively large number of seedlings that survive into sapling status. There are few dead sugar pine of any age, and seedling and saplings appear to continue to contribute to a shift in canopy composition. Incense cedar began to enter the stand with the pioneers, but increased as the stand developed (Fig. 5*b*). It currently shows somewhat diminished regeneration. White fir began to establish several decades later and now has relatively high numbers in young age-classes (Fig. 5*c*). All three of these species are shade tolerant and prefer mesic microhabitats, and were fostered by the cohort of pioneering pines.

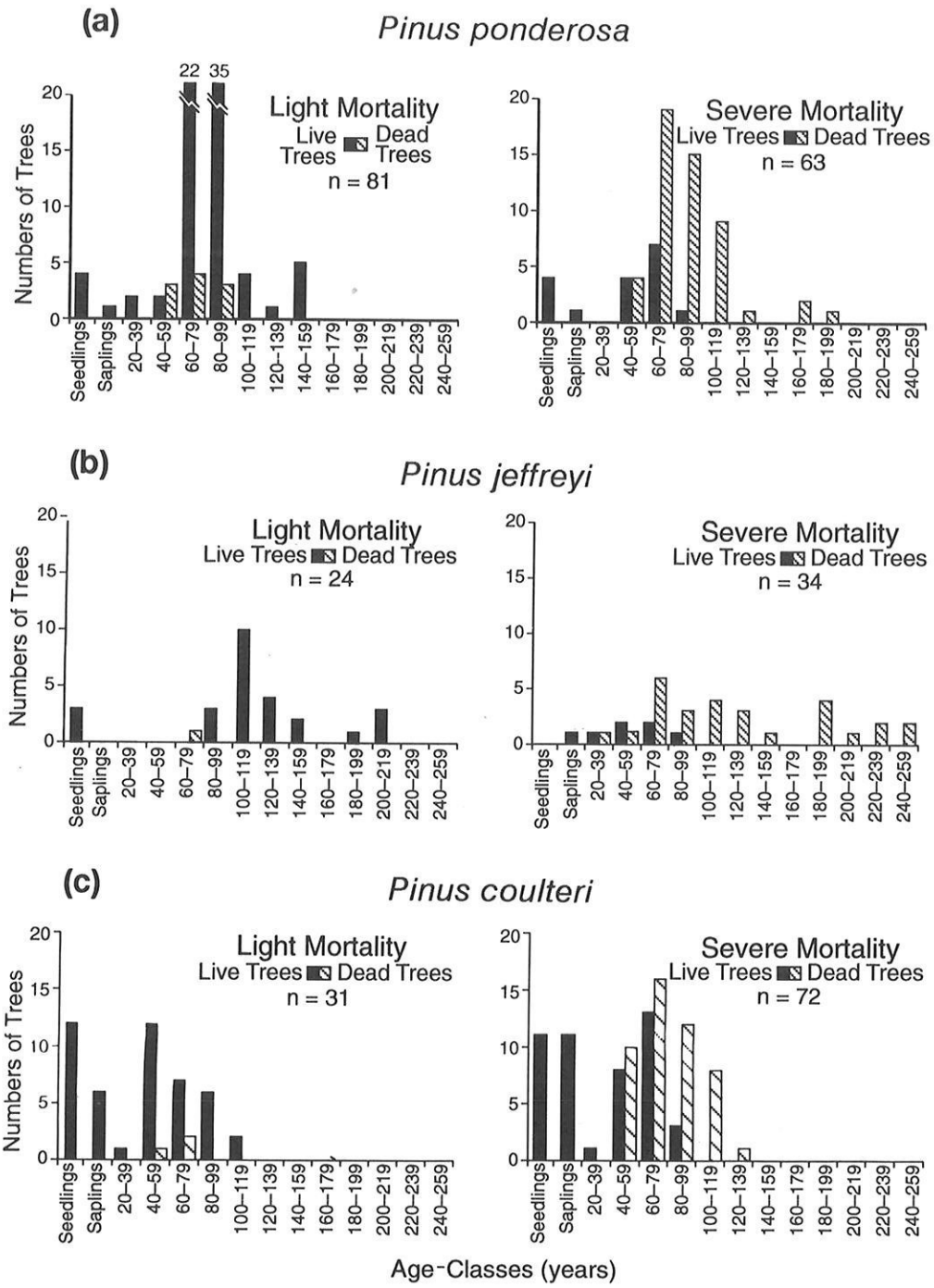


FIG. 4. (*a*) Frequency of *Pinus ponderosa* in 20-year age-classes, plus seedlings and saplings. (*b*) Frequency of *Pinus jeffreyi* in 20-year age-classes, plus seedlings and saplings. (*c*) Frequency of *Pinus coulteri* in 20-year age-classes, plus seedlings and saplings. Tree ages at coring height.

Black oak maintains a low but steady presence in the forest from around 130 years ago (Fig. 6). As a shrubby, multi-stemmed tree, it would have survived the logging episode. Its exceptionally large numbers of seedlings may not be an indication of a greatly increased share of the canopy in the future. Seedling abundance of black oak are often extremely high in relation to adult presence in the forest, but require full sun for continued growth (Rundel et al. 1977). Few of the black oak seedlings at this site appear to graduate into sapling or older classes on a continuing basis. A size-class histogram for canyon live oak suggests a presence similar to black oak (Fig. 7), particularly with respect to high seedling numbers that may not survive to older age classes.

Of those species suffering the greatest beetle-induced mortality, ponderosa and Jeffrey pine display significantly different distributions of age-classes of live trees in the light-mortality plots as compared with live trees in the severe-mortality plots (K–S test; $P < 0.001$). The distribution of ages of live Coulter pine did not differ significantly in light- versus severe-mortality plots, despite high mortality, but this was due to greater abundance of Coulter pine in the severe-mortality plots. None of the nonhost tree species dis-

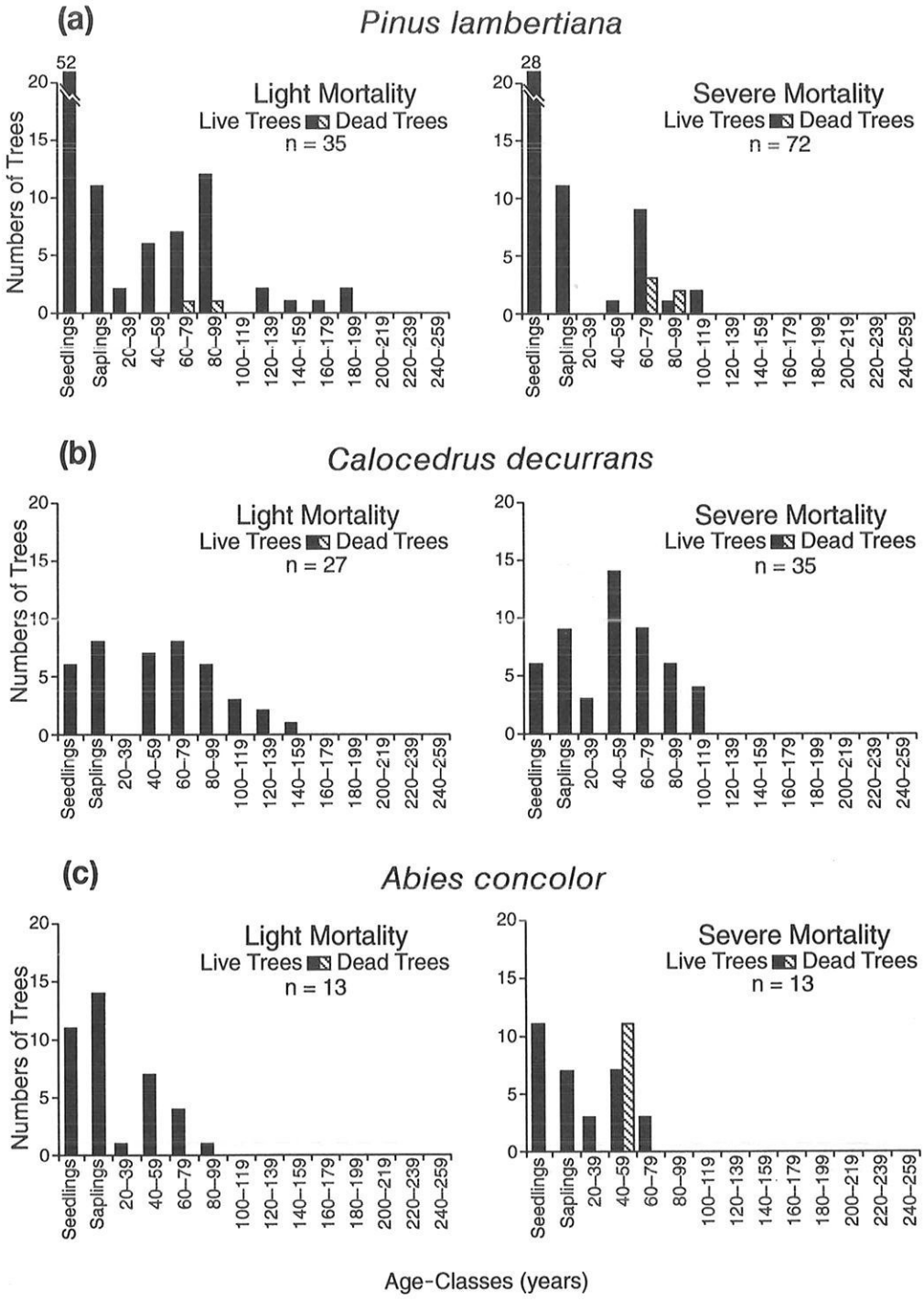


FIG. 5. (*a*) Frequency of *Pinus lambertiana* in 20-year age-classes, plus seedlings and saplings. (*b*) Frequency of *Calocedrus decurrans* in 20-year age-classes, plus seedlings and saplings. (*c*) Frequency of *Abies concolor* in 20-year age-classes, plus seedlings and saplings. Tree ages at coring height.

play significantly different age-class distributions of live trees in the light-mortality plots compared with live trees in the severe-mortality plots (K–S test; $P < 0.001$).

There were no significant differences in age distribution of dead trees of those species escaping beetle kill, sugar pine, white fir, and the oaks, in light-mortality plots (K–S test; $P < 0.001$). The K–S two-sample test did not indicate significant differences in age distributions of dead yellow pines in the two sets of plots despite high levels of mortality. Visual inspection of the histograms of these species reveals very dissimilar age-class distributions, and test failure is probably due to sample size disparity in light- versus severe-mortality plots.

The tree replacement model (Horn 1975) overpredicts the probable future share of oak of the forest canopy owing to high seedling numbers but poor recruitment into older age-classes. In the light-mortality plots, the next generation of canopy trees predicted are ponderosa pine, 1%; Jeffrey pine, <1%; Coulter pine, 3%; sugar pine, 10%; white fir, 6%; incense cedar, 3%; black oak, 29%; and canyon live oak,

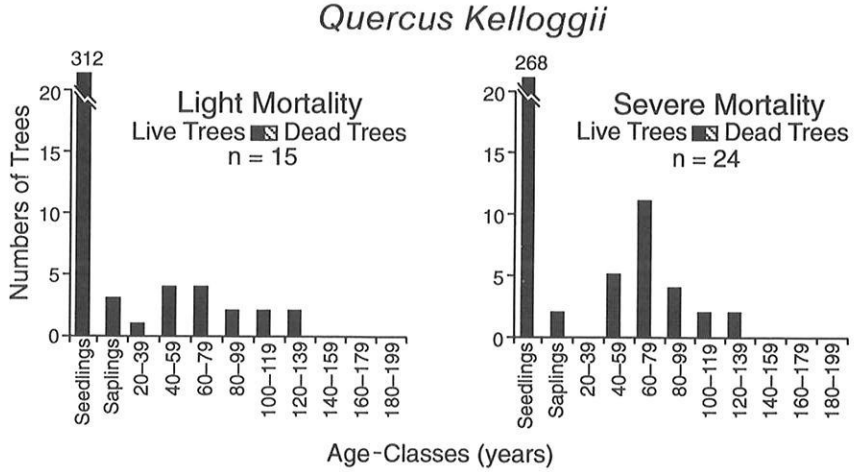


FIG. 6. Frequency of *Quercus kelloggii* in 20-year age-classes, plus seedlings and saplings. Tree ages at coring height.

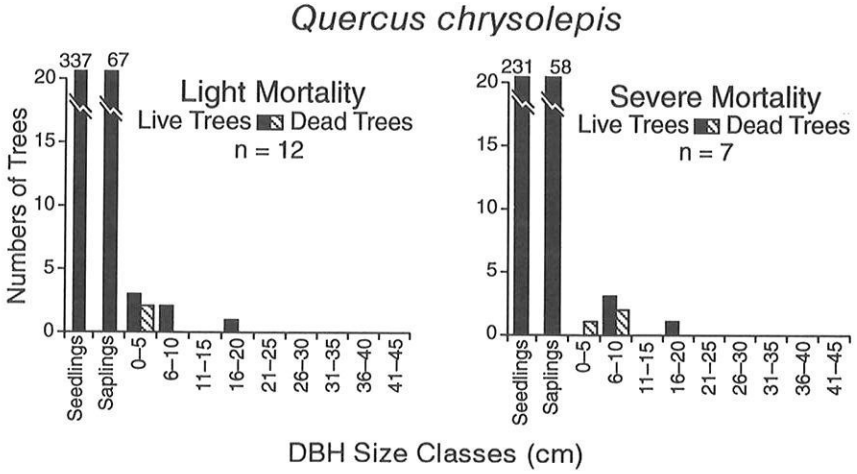


FIG. 7. Frequency of *Quercus chrysolepis* in seedling, sapling, and size classes in centimetres.

47%. The next generation in the severe-mortality plots would be ponderosa pine 4%; Coulter pine, 4%; sugar pine, 8%; white fir, 4%; incense cedar, 2%; black oak, 33%; and canyon live oak, 45%. These results suggest that regardless of patterns of overstory mortality, the forest would shift from a pine- to an oak-dominated forest. This, however, is highly unlikely. Life-history strategies of these species, especially their responses to competitive interactions and potential natural disturbance, make a realistic regenerational response more complex. The model is probably correct, however, in suggesting relatively higher percentages of shade-tolerant sugar pine and white fir than of shade intolerant ponderosa, Jeffrey, and Coulter pines.

To a large extent, prediction of the fate of the seedling cohort is uncertain because of the scale of change now occurring in the forest. An unknown percentage of seedlings probably died during the prolonged drought, masking and altering regenerational trends. Changes in seedling response after the return of normal precipitation levels is also unpredictable in the altered conditions of the forest after the mortality episode. Reduced canopy density, for example, may again favor seedlings of intolerant species to a greater extent.

Discussion

Age structure of the study area suggests the following scenario. As the cohort of pioneer species, ponderosa, Jeffrey, and Coulter pine, developed soon after timbering, canopy closure and the accumulating litter layer created an unfavorable environment for these early successional species. Shade-tolerant species, especially intense cedar and, most recently, white fir, slowly began establishing in the shady, more mesic conditions of the understory. Under the competitive conditions of the current dense stand, shade-tolerant species continue to recruit at a higher rate than the pines. The oaks display little success in recruitment into these forests, perhaps because they may not be well adapted to thrive under low light levels (McDonald 1990; Abrams 1992).

The recent mortality episode has favored late-successional species as well. Stand dominance, already changing because of increased stand density and protection from fire, is now rapidly shifting away from the pines. If there is further mortality, the structure of severe-mortality plots suggests that pines will have greatly reduced density and cover, by comparison with more shade-, pollution-, and insect-tolerant species.

There are clear signs of beetle attack on virtually all dead trees at the study site. Bark beetles, however, may simply be the coup de grace for trees stressed by pollution, drought, and competition in the density of a fire-free stand. The steep decline in ring width visually observed in the last five or six rings in many core samples clearly reflects the impact of the drought on tree resources. In addition, the paucity of

seedlings of most species may reflect high rates of mortality due to the drought. Although the pine species are relatively drought tolerant, they appear to be more susceptible to other current stresses, notably air pollution and insect attack, than the remaining species in the stand. The susceptibility of Coulter pine may be enhanced by the fact that the oldest trees are closer to the end of their relatively shorter life span than the other pines. Drought and beetle induced mortality in sugar pine has been reported from other sites, particularly in older age classes (Dale 1991), but at this site it is relatively unscathed, perhaps because of its young age structure. Likewise, white fir, incense cedar, and oak species have not suffered serious insect attack. This may be due to lower susceptibility to insects and ozone, or, in part, to a preponderance of young trees.

Tree density levels resulting from human protection from fire appears to be high enough to implicate competition as an additional burden during the drought. The density of compositionally similar mixed conifer forest in the Pedro San Martir Range near the northern border of Baja Mexico, where a fire-suppression policy has not been implemented, appears to be much lower than that of the forests of southern California ranges; here a recent intense drought has brought little bark beetle mortality in the more sparse woodland forest (R.A. Minnich, personal communication).

Several future states for this forest stand are possible. The winters of 1992 and 1993 brought a substantially increased level of precipitation. If the recent drought eases, the bark beetle infestation may taper off. Vulnerable component species may experience some additional mortality and the survivors remain with a lower canopy share. Stand composition in this case will reflect continuing favorable conditions for shade-tolerant, fire-intolerant species and low levels of recruitment. Canopy openings created by dead trees, however, with more light and soil moisture resources, would allow recovery of shade-intolerant pine species.

A more likely fate for this stand is devastation by crown fire. Not only is the forest dense, but large numbers of dead trees and quantities of needle and twig litter can now support a stand-destroying conflagration. Pines may seed in slowly after such a fire, due to poor dispersal mechanisms, irregular cone crops, long generation time to cone production, and potential competition from chaparral species (Bock and Bock 1977). Coulter pines are at a slight advantage owing to a fire-opening cone strategy. Depending on the intensity of the fire, oaks and other chaparral species would recover quickly, aided by resprouting strategies, and could dominate the site, especially by competition for soil moisture, for an indefinite period of time (Lanini and Radosevich 1982). Minnich (1988) reports succession to black oak and chaparral thickets after several stand-destroying fires in second growth mixed conifer forests in this century.

Conclusions

Muller-Dombois (1988), in revising Manion's (1981) terminology of the causes of dieback, terms the complex of deleterious factors: predisposing, precipitating, and accelerating factors. While the proximate causes of mortality in the San Jacinto forests are natural disturbances, there appears to have been an underlying demographic instability largely created by chronic anthropogenic influences. Innes (1992) reviews a large literature pointing to the role of adverse climatic conditions in triggering forest mortality, and in this forest, drought may be only the contributing or factor in tree death. As Muller-Dombois (1988) suggests, predisposing factors, here chronic fire suppression and perhaps air pollution, may predispose the forest to mortality, precipitated by a severe climate event and dealt a coup de grace by insect attack. Fire suppression and air pollution, now affecting large areas of western montane conifer forests, may well be factors predisposing them to increased mortality. Studies that isolate, by site, the influence of these disturbances could more fully explain the degree to which anthropogenic factors are responsible for patterns of mortality in this forest landscape.

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