

EIGHTEEN

Southern California Conifer Forests

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**INTRODUCTION TO THE DISTRIBUTION AND SPECIES
COMPOSITION OF THE REGION'S FOREST**

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In southern California (SCA) south of latitude 35°N, a handful of coniferous tree species make up most forests and woodlands of the region, mostly at the middle and high elevations of the Transverse and Peninsular Ranges (Fig. 18.1). Scattered groves of closed-cone and mixed evergreen forests on chaparral-dominated windward coastal escarpments with high orographic rainfall give way to Sierran mixed-conifer forest along moist mountain crests and pinyon-juniper woodlands on rain-shadowed leeward slopes. Subalpine forests grow on the highest summits. Closed-cone forests also dot the coastal bluffs and the northern Channel Islands. Many of these assemblages reach their southern limits in southern California and adjoining Baja California, Mexico.

Southern California conifer forests exhibit a predictable spatial pattern that is accompanied by gradients in climate, productivity, topography, and chaparral understory. At the same time, it is difficult to explain their biogeography from static reference; that is, the momentary spatial pattern of biotic distributions and landscape variables (slope, aspect, elevation, and soils) does not provide explanation of species fitness. Furthermore, ecological research based on local field studies covering a few years precludes the generation of realistic null hypotheses (Jackson et al. 2001). Spatial pattern must be assessed from a dynamic perspective. Important insight comes from natural and anthropogenic disturbances that influence the long-term dynamics of conifer forests. The natural functioning of southern California conifer forests can also be understood from studying remote pristine forests without fire control in Baja California that lie beyond the air pollution plumes of the Los Angeles–San Diego megalopolis.

Extensive field mapping of conifer forests of SCA in the early 1930s by the Vegetation Type Mapping (VTM) Survey



FIGURE 18.1 Mixed-conifer forests are common throughout the montane zone of the Transverse and Peninsular Ranges. North-facing slopes (foreground) have closed-canopy white fir and Jeffrey pine stands, whereas south-facing slopes (background) have more open Jeffrey pine stands. San Gabriel Mountains: west Fork of Lytle Creek, north of Mt. San Antonio, San Bernardino National Forest. Photograph courtesy of Robert Thorne.

(Wieslander 1935; Griffin and Critchfield 1976) provides an historical reference for analysis of species composition and distribution change. Subsequent aerial photograph surveys (Minnich and Everett 2001) reveal local change in vegetation distribution in the twentieth century, with most boundaries shifting locally from stand-replacement fires. Large apparent differences in the range of ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*) are due to taxonomic errors made by VTM workers. The distributions given below are described by species in Minnich and Everett (2001). Distributions of forests in Baja California (BCA) are from Minnich (1987a) and Minnich and Franco-Vizcaino (1998).

Closed-Cone and Four-Needle Pinyon Forest

Closed-cone conifer forest comprises species in *Pinus* subsect. *Oocarpae*: knobcone pine (*Pinus attenuata*), bishop pine (*P. muricata*), and Monterey pine (*P. radiata*; Millar 1986), and the partially serotinous bigcone pines (*Pinus* sect. *Sabinae*): Coulter pine (*P. coulteri*) and Torrey pine (*P. torreyana*). These forests also include Arizona cypress (*C. arizonica* ssp. *arizonica* of the *C. arizonica* complex; Rehfeldt 1997), Tecate cypress (*C. forbesii*), and Guadalupe island cypress (*C. guadalupensis*). Most of these tree species form monospecific stands in chaparral, often in soils with low fertility (Vogl et al. 1988). Herb cover is most abundant in early succession after chaparral fires. Cyresses and members of *Pinus* subsect. *Oocarpae* are typically <10 to 15 m tall, and the bigcone pines 15 to 30 m tall.

Small, compact stands of Bishop pine grow within 20 km of the Pacific Coast in the Purisima Hills and the west end of

Santa Inez Mountains, mostly on diatomaceous shales or Careaga sandstones, which yield shallow acid soils with high water-holding capacity (Schoenherr 1992). Stands grow on the west and north flanks of Santa Cruz Island, but only a few trees occur on Santa Rosa Island. This type is associated with mixed coastal sage scrub and chaparral. In the Purisima Hills associated species are *Arctostaphylos crustacea*, *Cercocarpus betuloides*, *Rhamnus crocea*, *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, *Toxicodendron diversilobum*, *Artemisia californica*, *Lotus scoparius*, and *Baccharis pilularis* (Vogl et al. 1988). Pines near Pt. Conception occur within extensive stands of *Quercus agrifolia*. On Santa Cruz Island, Bishop pine grows with *Heteromeles arbutifolia*, *Arctostaphylos subcordata*, *A. tomentosa*, and *Quercus wislizenii* (Minnich 1980). In BCA, Bishop pine recurs 60 km south of Ensenada on the coastal headlands at Erendira, the southern limit of species. While Monterey pine does not occur in southern California, it is found on Guadalupe and Cedros Islands west of the BCA peninsula (Moran 1996). Associated species in Guadalupe Island include *Quercus tomentella*, *Cupressus guadalupensis*, *Ceanothus insularis*, and *Rhamnus pirifolia* (Axelrod 1980). On Cedros Island it grows with desert scrub dominated by *Viguiera lanata*, *Pachycormus discolor*, *Ambrosia chenopodifolia*, and *Salvia cedrosensis* (Oberbauer 1986).

Knobcone pine grows in the San Bernardino Mountains (SBM) between 1,000 and 1,400 m on granitic convex summits and ridges covered with chaparral dominated by *Adenostoma fasciculatum*, *Quercus wislizenii*, and *Arctostaphylos glandulosa* (Minnich 1999). Two colonies grow in the northern Santa Ana Mountains with *Adenostoma fasciculatum*, *Ceanothus crassifolius*, *C. tomentosus*, *Quercus berberidifolia*, *Cercocarpus betuloides*, *Garrya fremontii*, *Heteromeles arbutifolia*, and *Rhus ovata* (Vogl 1973). The Santa Ana Mountain populations are found on fine-grained, acidic soils associated with hydrothermally altered volcanics (Vogl et al. 1988). In BCA knobcone pine occurs locally in the coastal ranges of the Sierra Juarez (SJZ) from Ensenada to Santo Tomás (Minnich 1987a).

Tecate cypress is found at Otay Mountain, Tecate Peak, and Guatay San Diego County and at Gypsum Canyon in the northern Santa Ana Mountains. Stands in San Diego County grow on alkaline clay soils derived from gabbro basalts rich in iron and magnesium (Zedler 1981; Schoenherr 1992), with the exception of a stand at Guatay that grows on granite. The Gypsum Canyon stand grows on Paleocene sandstone. Tecate cypress is common in the coastal ranges of northern BCA as far south as San Quintín. California stands grow in dense chaparral of *Adenostoma fasciculatum*, *Arctostaphylos glandulosa*, *A. otayensis*, *Ceanothus crassifolius*, *Cercocarpus betuloides*, *Fremontodendron mexicanum*, *Garrya flavescens*, *Heteromeles arbutifolia*, *Quercus berberidifolia*, *Malosma laurina*, *Rhus ovata*, and the coastal sage scrub species *Salvia apiana*, *S. clevelandii*, and *Xylococcus bicolor* (Vogl et al. 1988). In BCA, common shrubs are *Adenostoma fasciculatum*, *Ceanothus oliganthus*, *Malosma laurina*, *Xylococcus bicolor*, *Comarostaphylis diversifolia*, and

Ornithostaphylos oppositifolia, and the drought-deciduous woody shrubs, *Fraxinus trifoliata* and *Aesculus parryi*. The closely related Guadalupe Island cypress (*Cupressus guadalupensis*) grows on Guadalupe and Cedros Islands (Rogers 2002). A single colony of Arizona cypress grows near Cuyamaca Peak at 1,400 m in mixed chaparral of *Adenostoma fasciculatum*, *Arctostaphylos glandulosa*, *Ceanothus crassifolius*, *C. greggii* var. *perplexans*, *C. leucodermis*, *Cercocarpus betuloides*, and scattered Coulter pine (Vogl et al.). Arizona cypress also occurs in chamise chaparral in the southern SJZ (Moran 1977).

Torrey pine is found on coastal bluffs in Eocene sandstone in San Diego County, and on sea bluffs of upper Miocene sandstone above Beechers Bay on Santa Rosa Island, 270 km to the northwest. It grows in a shrub layer of *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, *Rhus integrifolia*, *Malosma laurina*, *Quercus berberidifolia*, *Arctostaphylos glandulosa*, *Artemisia californica*, *Baccharis glutinosa*, and *Encelia californica*; the most abundant shrubs on Santa Rosa Island stands are *Adenostoma fasciculatum* and *Heteromeles arbutifolia*, mostly in open stands (Vogl et al. 1988; Wells and Getis 1999).

Coulter pine grows from 1,000 to 2,300 m on moist windward escarpments and upper desert watersheds of the Transverse and Peninsular Ranges, almost exclusively on granite or sandstone substrates. It occurs locally in the Sierra Madre and San Rafael, Santa Inez Mountains, and western San Gabriel Mountains (SGM). Coulter pine is widespread in SBM and the Peninsular Ranges from the San Jacinto Mountains (SJM) and Santa Ana Mountains to Mt. Laguna and Los Pinos Mountain. Stands grow on steep, convex slopes in association with dense chamise and mixed chaparral and scrubby thickets of canyon live oak (*Quercus chrysolepis*). Dominant understory species include *Adenostoma fasciculatum*, *Arctostaphylos glauca*, *A. glandulosa*, *Ceanothus leucodermis*, *Ceanothus greggii* var. *perplexans*, and *Cercocarpus betuloides*. It is restricted to bedrock exposures in drier portions of its range such as Garner Valley, Combs Peak, and Los Pinos Mountain. The nearest stand in BCA is on Sierra Blanca. Six other populations occur on bedrock exposures in the interior SJZ and the Sierra San Pedro Martir (SSPM), the southern limit of the species. Stands in the SSPM grow with *Arctostaphylos peninsularis*, *A. pringlei*, canyon live oak, and Pacific Emory oak (*Quercus peninsularis*), a close relative to Emory oak (*Q. emoryi*) of southern Arizona and northwestern Mexico.

Four-needle pinyon (*Pinus quadrifolia*), a nonserotinous conifer, is included in this group because it grows extensively in chamise and red shank chaparral, mostly between 1,300 and 1,800 m. The largest stands in SCA occur at Thomas Mountain, southern Garner Valley, and Vandeventer Flat in the southern SJM. Small stands occur 55 km south on Mt. Laguna and in McCain Valley. Four-needle pinyon forms extensive patchy cover from 1,400 to 2,700 m in the BCA peninsular ranges southward to the SSPM, mostly with chamise and red shank chaparral dominated by *Adenostoma fasciculatum*, *A. sparsifolium*, *Ceanothus greggii* var. *perplexans*,

Rhus ovata, *Quercus cornelius-mulleri*, and *Juniperus californica*. Stands above 2,200 grow in chaparral dominated by *Arctostaphylos peninsularis* and canyon live oak.

Ghost Pine and Coulter Pine Woodlands

Mountain basins and old erosion surfaces <1,200 m elevation are covered with oak woodlands that generally lack a coniferous component. However, ghost pine (digger pine) woodland (*P. sabiniana*) occurs from the San Rafael Mountains to the Liebre Mountains. Stands consist of open parks in association with valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), interior live oak (*Q. wislizenii*), understory of open cover of *Aesculus californica*, *Heteromeles arbutifolia*, *Rhamnus californica*, *Ceanothus cuneatus*, *Arctostaphylos* spp, *Cercis occidentalis*, and exotic annual grassland (Griffin 1988). Ghost pine and the oak layer are typically 15 to 30 m tall, whereas shrubs are <6 m. Coulter pine-oak woodlands grow between 1,200 and 1,500 m in the Volcan, Cuyamaca, and Palomar Mountains and SBM. Stands consist of open cover of Coulter pine, black oak (*Quercus kelloggii*), canyon oak (*Q. chrysolepis*), Engelmann oak (*Q. engelmannii*), coast live oak (*Q. agrifolia*), and scattered cover of *Ceanothus integrifolius*, *C. palmeri*, *Rhamnus californica*, *Arctostaphylos pringlei*, and *A. pungens*. European annual grassland is an important ground layer in San Diego County.

Bigcone Douglas Fir Forest

Bigcone Douglas fir (*Pseudotsuga macrocarpa*)—canyon live oak forests, the only phase of mixed evergreen forest in southern California (Sawyer, Thornburgh, and Griffin 1988), occur in fragmented compact groves in deep convex canyons, steep, mostly north-facing slopes, and cliff faces between 1,000 and 2,200 m (Fig. 18.2). This southern California endemic is most extensive on rapidly eroding precipitous slopes in association with fault-shattered substrate (Bolton and Vogl 1969; McDonald and Littrell 1976; Minnich 1999). Stands at lower elevations are small and invariably surrounded by chaparral, but may fill entire drainages at higher elevations intergrading with the mixed-conifer forest belt. In the Transverse Ranges, it extends from the Sierra Madre and San Rafael mountains to the mountains of Ventura County. Stands follow the San Andreas Fault from the San Emidio Range to the Liebre Mountains. Bigcone Douglas-fir is widespread in the precipitous SGM as well as along the southern escarpment and desert drainages west of Lake Arrowhead in SBM. In the Peninsular Ranges, it occurs on steep escarpments along the San Jacinto Fault from Bautista Canyon to Thomas Mountain and the Elsinore Fault from the Santa Ana Mountains to Palomar and Volcan mountains, the southern limit of the species. Canyon live oak woodlands consisting of a scrubby small leaved ecotype (Myatt 1975) continue south along the SJZ and SSPM of BCA.

Forest structure consists of open stands of long-lived bigcone Douglas-fir 30 to 50 m tall in association with closed



FIGURE 18.2 Mixed evergreen forests with bigcone Douglas fir are common on moist slopes at relatively low elevations, as here on Mount Palomar at 1,600 m. Photograph courtesy of M. Barbour.

midstory of canyon live oak 10 to 25 m tall, and a sparse chaparral layer of *Ceanothus oliganthus*, *C. integerrimus*, *C. leucodermis*, *Cercocarpus betuloides*, *Rhamnus californica*, and *Toxicodendron diversilobum*. There is little herbaceous cover. Bigcone Douglas-fir and canyon live oak dbh frequency distributions mostly fall in the range of 0.5 to 1.0 m (Bolton and Vogl 1969; McDonald and Littrell 1976). Other hardwood tree species include coast live oak (*Q. agrifolia*) and California Bay (*Umbellularia californica*) especially along canyons and near streams below 1,000 m. Pacific madrone (*Arbutus menziesii*) and tanbark oak (*Lithocarpus densiflorus*) are associates in this type north of Santa Barbara. Rare colonies of madrone grow near Mt. Wilson, Santa Ana Mountains, and Palomar Mountains. Reports of madrone in Baja California by Wiggins (1980) appear to be based on a mistranslation of the plant name "madrono" in eighteenth-century Spanish diaries for *Arctostaphylos* spp. (Minnich and Franco-Vizcaino 1998). A single colony of Douglas fir (*P. menziesii*) occurs in a moist canyon in the Purisima Hills, 150 km SE of the nearest stand in the Santa Lucia Range (Griffin 1964).

Mixed-Conifer Forest

The Transverse and Peninsular Ranges above the chaparral belt are covered by mixed-conifer forest 30 to 50 m tall, mostly from 1,300 to 2,800 m. Tree dominance shifts along a precipitation gradient in which ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*) dominate moist windward slopes. Jeffrey pine and white fir dominate leeward slopes (see Fig. 18.1). Western juniper (*Juniperus occidentalis*) is common on leeward slopes of SBM and sparingly in eastern SGM. Ponderosa and Jeffrey pine tend to dominate south-facing slopes and valley floors, whereas white fir and sugar pine dominate north-facing slopes (Minnich et al. 1995; Minnich 2001). In the Transverse Ranges, mixed-conifer forest is found on Pine Mountain Ridge, Mt.

Pinos, Frazier Mountain, Alamo Mountain, and the San Emigdio Mountains, with outliers in the San Rafael Mountains and on Sawmill Mountain of the Liebre Mountains. A broad forest belt extends 100 km across SGM and SBM with a small break at Cajon Pass. In the Peninsular Ranges, mixed-conifer forest is most extensive in the SJM, with small forests covering the summits of the Hot Springs, Volcan, Palomar, and Cuyamaca Mountains. Sugar pine was recently discovered on Palomar Mountain (Goforth and Minnich 2003). Ponderosa pine is limited to moist areas with deep soils, the only extensive stands occurring in western SBM and on the west slope of SJM. Monotypic Jeffrey pine forest occurs in shrub-free basins within the chaparral belt to as low as 1,200 m, including the upper Cuyama Valley, the Garner Valley, the Mt. Laguna plateau, and nearby Pine Valley. Jeffrey pine forests also cover basins along the crest of the SJZ and mid-slopes of SSPM from 1,400 to 1,800 m. The upper elevations of SSPM have extensive mixed-conifer forest dominated by Jeffrey pine, white fir, sugar pine, and scattered colonies of incense cedar in similar topographic settings to that in SCA (Minnich et al. 2000; Minnich). The endemic mountain cypress (*Cupressus montana*) occurs in white fir-sugar pine forest on upper eastern escarpment.

Canyon live oak is an important hardwood associate from 1,300 to 2,500 m on steep slopes throughout SCA, and in SSPM. Black oak is restricted to granite substrates, sandstones and alluvium from 1,300 to 2,200 m in the Tehachapi Mountains, near Mt. Pinos and the eastern SGM. It is an important forest component in the SBM, and the Peninsular Ranges from SJM to Mt. Laguna. Forests in BCA have local midstory of Pacific Emory oak. Two colonies of quaking aspen (*Populus tremuloides*) grow in Fish Creek and Gocke Valley in the eastern SBM. Thousands of groves occur >2,300 m in SSPM.

Mixed-conifer forest has open cover of evergreen sclerophyllous shrubs, as well as perennial subshrubs and herbs. Shrub cover is absent over extensive areas. Dominant shrub species below 2,100 m are *Arctostaphylos pringlei*, *A. pungens*, *Ceanothus integerrimus*, *C. palmeri*, and *Rhamnus californica*. Dominant shrubs above 2100 m are *Ceanothus cordulatus*, *Arctostaphylos patula*, and *Chrysolepis sempervirens*. Leeward forests have cover of *Cercocarpus ledifolius*, *Artemisia tridentata*, *Ceanothus greggii* var. *vestitus*, and *Chrysothamnus nauseosus*. Numerous annual and perennial herbs occur in mixed-conifer forests including *Calystegia occidentalis*, *Carex multicaulis*, *Clarkia rhomboidea*, *Collinsia childii*, *Cordylanthus rigidus*, *Eriastrum densifolium*, *Gilia splendens*, *Iris hartwegii*, *Phacelia imbricata*, *Silene lemmonii*, *Penstemon grimmellii*, *P. labrosus*, *Sarcodes sanguinea*, *Elymus elymoides*, *Castilleja martinii*, *Chaenactis santolinoides*, *Chimaphila menziesii*, *Galium johnstonii*, *Gayophytum heterozygum*, *Lotus davidsonii*, *Mimulus johnstonii*, and *Viola purpurea* (Thorne 1988). The cover of herbaceous species is seldom >5% due to summer drought.

Most mountain meadows occur in mixed-conifer forest. However, because this assemblage relies on near-surface groundwater, it also occurs in freshwater habitats at all elevations including subalpine forests, pinyon-juniper woodland,

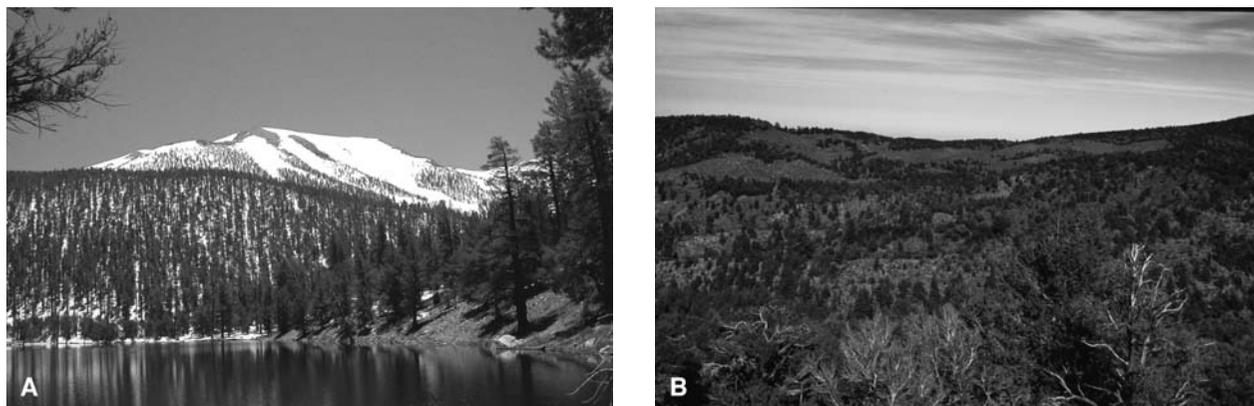


FIGURE 18.3 (A) Subalpine forests are dominated by lodgepole pine at Dry Lake in the San Bernardino Mountains, with Mt. San Gorgonio (3,500 m) in the background; photo courtesy of Victoria Minnich. (B) Pinyon-juniper woodland (*Pinus monophylla*, *Juniperus occidentalis*) at Broom Flat, eastern San Bernardino Mountains. Thirty-year old stand-replacement burn in the distance, and an 85-year old burn in the midground; photo courtesy of Richard Minnich.

and chaparral forests. Southern California meadows are floristically rich with numerous species of grasses, sedges, and rushes in the genera *Agrostis*, *Carex*, *Juncus*, *Muhlenbergia*, *Deschampsia*, and *Poa*. There are also large perennials or biennials in *Barbarea*, *Castilleja*, *Iris*, *Lilium*, *Lotus*, *Lupinus*, *Oenothera*, *Perideridia*, *Hoita*, *Senecio*, *Sisyrinchium*, *Smilacina*, *Sphenosciadium*, and *Veratrum* (Thorne 1988).

Subalpine Forest

Subalpine forests of lodgepole pine (*Pinus contorta*) and limber pine (*P. flexilis*), 20 to 30 m tall, cover the highest peaks above 2,400 to 2,700 m. Lodgepole pine is the dominant tree, but limber pine is locally abundant above 3,000 m. In SGM the largest stands extend from Throop Peak to Mt. Baden-Powell and from Mt. San Antonio to Cucamonga Peak (Fig. 18.3). In SBM subalpine forest is found on Butler Peak, Sugarloaf Mountain, and San Gorgonio Mountain. Small stands occur on the floors of Big Bear Basin and adjoining valleys, and on leeward slopes near Onyx Summit. The southernmost forests cover Mt. San Jacinto and nearby Tahquitz Peak. Outposts of limber pine grow on the dry summits of Mt. Pinos and Toro Peak, the latter being the southern limit of the species. In SSPM lodgepole pine occurs above 2,400 m near meadows and on a few summits.

The tree line occurs on Mt. San Gorgonio (3,500 m), where stems are shrubby and flagged (krummholz) due to injury from wind and ice, as well as from perennial snow burial in cornices and along leeward hollows and gullies subject to powder avalanching (Minnich 1984; Owen et al. 2003). Krummholz also occurs on Mt. San Antonio (3,050 m). Montane chaparral of *Ceanothus cordulatus*, *Arctostaphylos patula*, *Chrysolepis sempervirens*, and *Cercocarpus ledifolius* is common, especially on south-facing slopes. Herbaceous perennials and subshrubs form sparse cover and include *Antennaria rosea*, *Arabis breweri*, *Chimaphilla umbellata*, *Phyllodoce breweri*, *Sambucus racemosa* var. *microbotrys*, *Monardella*

cinerea, *Oreonana vestita*, *Penstemon caesius*, *P. grinnellii*, *Sedum niveum*, *Sibbaldia procumbens*, *Arceuthobium cyanocarpum*, *Galium parishii*, *Heuchera abramsii*, *Holodiscus microphyllus*, *Eriogonum wrightii*, *Ribes cereum*, *R. montigenum*, *Elymus elymoides*, and *Viola purpurea* (Thorne 1988).

Pinyon-Juniper Woodland

Pinyon-juniper woodland is a short tree vegetation type, with open crowns 5 to 20 m tall, and underlain with a subcanopy of shrubs. It is found on semiarid leeward slopes from 1,100 to 2,700 m, extending zonally from the arid limit of mixed-conifer forest, where pinyon-juniper stands often occur in closed forests, to the margin of the Mojave and Sonoran deserts where they form sparse woodlands. Singleleaf pinyon (*Pinus monophylla*) is the dominant tree above 1,400 m, with California juniper (*Juniperus californica*) the dominant below this level. Pinyon-dominated stands occur on the plateaus and surrounding lee slopes of the Mt. Pinos region, along the northern escarpments of the Transverse Ranges eastward to Joshua Tree National Park, and in the Santa Rosa Mountains. In San Diego County, singleleaf pinyon grows on semiarid summits detached from the spine of the Peninsular Range including Pinyon Ridge, Whale Mountain, and the eastern escarpment of Laguna Mountain. From 1,800 to 2,200 m, singleleaf pinyon frequently occurs in monotypic forests, although western juniper is an important associate above 2,100 m in SBM. Utah Juniper (*J. osteosperma*) grows locally with single-leaf pinyon on calcite and dolomite marbles in northeastern SBM, as well as on alluvial fans below carbonate bedrock outcrops in the eastern SGM. California juniper woodland forms a zonal belt on alluvial fans entering the Mojave Desert along the Tehachapi and Transverse Ranges. It forms a narrow elevational belt on the eastern escarpment of the Peninsular Ranges.

The composition of the shrub layer varies with altitude and has important differences between the Transverse and

Peninsular Ranges. Pinyon forests above 2,200 m have an understory dominated by *Cercocarpus ledifolius*, canyon live oak, and local cover of *Ceanothus cordulatus*, *Arctostaphylos patula*, *Ceanothus greggii* var. *vestitus*, and *Fremontodendron californicum*. From 1,800 to 2,200 m, the shrub understory is dominated by *Artemisia tridentata*, *Chrysothamnus nauseosus*, *Purshia tridentata* var. *glandulosa*, and *Amelanchier utahensis*. Canyon live oak is locally abundant on north-facing slopes and canyons. From 1,400 to 1,800 m, pinyon-juniper woodlands grow with desert chaparral, as well as drought-deciduous subshrubs and leaf-succulents of the Mojave Desert (Wangler and Minnich 1996; Minnich 2003). Desert chaparral dominants in the Transverse Ranges include *Quercus cornelius-mulleri*, *Quercus turbinella*, *Cercocarpus betuloides*, *Ceanothus greggii* var. *vestitus*, *Fremontodendron californicum*, *Arctostaphylos glauca*, *A. glandulosa*, *A. parryana*, *Rhamnus californica*, and *Prunus ilicifolia*. Drought-deciduous shrubs and leaf succulents including *Ericameria cooperi*, *Lycium cooperi*, *L. andersonii*, *Ephedra viridis*, *E. nevadensis*, *Salazaria mexicana*, *Prunus fasciculata*, *Eriogonum fasciculatum*, Joshua tree (*Yucca brevifolia*), and *Y. schidigera*. In the Peninsular Ranges, the understory is dominated by desert chaparral elements (*Quercus cornelius-mulleri*, *Rhus ovata*, *Cercocarpus betuloides*, *Rhamnus crocea*, *Prunus ilicifolia*, and *Nolina parryi*).

In the Transverse Ranges below 1,400 m, California juniper woodlands intergrade with creosote bush scrub. *Yucca brevifolia* is an important associate in a 10- to 20-km-wide belt from the Antelope Valley to Hesperia. In the Peninsular Ranges, California juniper woodlands form scattered cover in a distinct Sonoran Desert shrub assemblage of *Prunus fremontii*, *P. fasciculata*, *Simmondsia chinensis*, *Yucca schidigera*, and *Nolina parryi*. Small populations of California juniper grow in semiarid coastal drainages in southern California, including the Cuyama River, upper Soledad Canyon, alluvial fans of the Transverse Ranges and locally on west slope of the Peninsular Ranges in association with coastal sage scrub and chaparral. Populations in the Riverside-Perris Plain grow in exotic annual grassland and forb fields. Pinyon-juniper woodlands continue south along eastern escarpments of SJZ, SSPM, and disjunctly to the summit of the Sierra Asemblea in the Central Desert of Baja California (Critchfield and Little 1966). California juniper is an important component of the chaparral in the interior basins of northern BCA from Valle Ojos Negros to the southern SSPM (Minnich and Franco-Vizcaíno 1998).

Historical Descriptions

Conifer forests have been described or mapped since European settlement because trees were valued for lumber and fuelwood (Minnich 1988; Minnich and Franco-Vizcaíno 1998). Historical sources include the diaries of Spanish explorations, reports of the Pacific Railroad Survey, and writings of early explorers and botanists (e.g., Brewer, Watson, and Gray 1876–1880). Surveys of newly established National Forests and National Parks by foresters and

botanists resulted in rapidly increasing knowledge of California tree distributions by the turn of the twentieth century (e.g., Sudworth 1908). The first vegetation maps of SCA published between 1886 and 1908 by Kinney and Grinnell and in the Forest Reserve Reports were impressionistic or based on life zone theory (Minnich 1988). Although forest distributions were realistically portrayed, boundary criteria were not explicitly defined for systematic comparison with modern vegetation. The first systematic maps are those by the California Vegetation Type (VTM) survey of 1929–1934 (Colwell 1988).

The diaries of the Spanish Portola and Anza expeditions (1769–1776), the earliest writings of land explorations in California, were mandated by the Viceroy at Mexico City to determine whether local resources met the standards necessary to establish missions including fuelwood, timber, and pasture (Meigs 1935; Engstrand 1981). These documents give systematic daily records of the vegetation in the Portola, Anza, Garces, and Arrillaga expeditions along the coast from northern BCA to San Francisco Bay. Descriptions by Franciscan and Dominican missionaries show that tree distributions in the late eighteenth century are consistent with modern distributions (Bolton 1927, 1930, 1933; Brown 2001; Minnich and Franco-Vizcaíno 1998). For example, Arrillaga's second expedition through the SJZ in 1796 describes the Jeffrey pine forests in basins and chaparral on mountain slopes, a pattern seen throughout the range (Minnich and Franco-Vizcaíno). In the SSPM Longinos-Martínez (1792) saw tall pine forests (Jeffrey pine) fringing the three primary meadows and mixed-conifer forest at Vallecitos. His first encounter with pine forest ca. 8 km west of La Grulla meadow matches the modern limit.

There are few accounts of conifer forest in southern California because the expeditions mostly followed the coastal plains. Garcés's description in the western SBM in 1776 was the most detailed account in the region and provided a local baseline for comparison with future surveys (Minnich 1988). He stated that the forest on the north slope of the range stopped at the crest, as seen today, and that the southern front had few trees (*poca arbolada*) in apparent reference to the islands of bigcone Douglas-fir growing in the canyons. This forest boundary was later described by Bigelow of the Pacific Railroad Survey (1857), and shown on maps of logging claims (1857–1890) and on vegetation maps by Leiberg (1900) and the VTM map of the San Bernardino Quadrangle, surveyed in 1929–1930. Other striking observations by Spanish explorers include pine forest "on the heights" of Mt. Laguna where trees now silhouette the crest of the range (Arrillaga, October 25, 1792), pines on the crest of two sierras above Anza Valley (Thomas Mountain, Coahuilla Mountain, Garces, March 16, 1774), pines with pine nuts near Anza in reference to *Pinus quadrifolia* at Vandeventer Flat (Font, December 26, 1774), as well as "pines" (bigcone Douglas fir) at Newhall Pass (Crespi August 7, 1769) and in canyons north of the Santa Clara River near Sespí Creek

(Crespi August 10–12, 1769). Constanso (August 19, 1769), Font (February 26, 1776), Fages and Crespi (August 17, 1769), Font (1774) described Coulter pine forests in the mountains above Santa Barbara. Vizcaino described “pine groves” there in 1602. West of Pt. Conception, Crespi (August 25, 1776) writes of pine trees in apparent reference to bishop pines near Canyon de Gato. Perhaps the most impressive account is Crespi’s (September 11, AK Brown, field draft) account of a “pinewood” at Cambria (Monterey pine, bishop pine). He accurately describes the modern distribution, that is, . . . “two hundred paces from the shore and kept with the expedition about a league,” ca. 4 km. He also described the second grove now seen at Pico Creek, ca. 5 km north.

The current era of global change research has made a tempting environment for hypotheses of vegetation change. Aerial photographs since the 1930s reveal that ecosystems have been slower to change than some imagine. Pursuant to the scientific method, the analysis of the historical record suggests that it is best to state “no change” as the null hypothesis and design a study to reject that hypothesis.

There was little interest in the mountains during the Hispanic era (Cleland 1964). The Franciscan mission period (1769–1833), and later Mexican secularization (1833–1849) saw the development of cattle grazing for hides and tallow. Grazing focused around the missions along the coast where Franciscan missionaries quickly recognized the advantage of year-round pasture, precluding the need to drive animals into the mountains. The accounts of the Anza Expeditions in the San Jacinto basin and expeditions of the Zalvidea in 1805 and Munoz in 1806 in the Central Valley described these regions as “barrens” during the summer dry season (Bolton 1930; Cook 1960; Wester 1981). In the 1840s, a few ranchos were established in large interior basins, such as Santa Ysabel, Henshaw Basin, and the San Bernardino Valley (Pryde 1975; Beattie and Beattie 1951).

A small amount of timber, most likely bigcone Douglas-fir and ponderosa pine, was extracted from canyons along the coastal slope of SGM and SBM, Palomar Mountain, and the Cuyamaca Mountains (Phillips 1976; Minnich 1988). Most cutting took place during the secularization period. Harvested trees were ripsawed and logs hauled in ox-drawn carts.

During the late nineteenth century, California forests underwent a cycle of intense exploitation of resources (Lockmann 1981; Pyne 1982). The Gold Rush in 1849 drew large numbers of Anglo-Americans to the mines of northern California and later to agriculture after the mines were exhausted. Although forests in the Sierra Nevada experienced widespread cutting, forests in SCA generally escaped significant removal of timber due to their isolation. Extraction was also discouraged by competition with timber imported by ship from northern California and the Pacific Northwest. The land-use history of the southern California mountains after California statehood is summarized from Pryde (1976), Johanneck (1975), Minnich (1988), Robinson (1989, 1991), and Robinson and Risher (1993). Major land-

use activities, described below, were timber harvest, mining, and grazing.

Timber harvest took place in accessible forests of the western SBM, Idyllwild in SJM, and locally on Mt. Palomar and Cuyamaca Mountains. The primitive lumbering technology required 30 to 50 years to remove old-growth timber from these regions (Johanneck 1975; Minnich 1988; Robinson 1989). During the 1850s and 1860s harvest was limited to ripsaw cutting or by running saws on unreliable waterpower. Timber harvest increased when the steam sawmill was introduced about 1870. Extraction was modest because the mills required constant repair and cutting was limited to the dry season. Wood was hauled off the mountains in carts drawn by oxen and donkeys. Trees with dbhs >0.5 m were extracted. The old-growth stems were gradually thinned, with surviving canopy consisting of ever-younger cohorts.

The Brookings logging operation resulted in a forest clear cut near Running Springs in SBM because even the smallest stems were harvested to make boxes (Minnich 1988). Most forests were too remote for harvest. Commercial logging ended by 1910 with the establishment of National Forests in reaction from public pressure to protect forests for recreation and watershed (Lockmann 1981). Foresters advocated the “sponge” hypothesis of George Perkins Marsh. It asserts that stream flow was kept at higher levels if mature vegetation were maintained on watersheds, the advocates citing increased storm runoff after fires. Evapotranspiration was not understood. There is little evidence that closed-cone conifers, bigcone pines, and bigcone Douglas fir were ever harvested in the late nineteenth century, as these trees produced poor timber, and were made inaccessible by rugged terrain and impenetrable chaparral. From 1940 to 1978 there was minor commercial harvest in the SBM and SJM totaling 362 million board feet. A small amount of timber was extracted from the Mt. Pinos region and the mountains of San Diego County, but harvesting rates were insufficient to maintain viable sawmills (Stephenson and Calcarone 1999).

The effects of lumbering during the Hispanic and American periods were greatly exaggerated by early foresters who examined the newly formed Forest Reserves established ca. 1900. As summarized in Lockmann (1981), it was deduced that chaparral on the southern escarpment of the Transverse Ranges had replaced conifer forests due to cutting, fire, and logging. However, this succession model was based on first impressions of forest changes from harvesting in northern California. Indeed, historical evidences suggest that the long-standing hypothesis that lower elevation patches of ponderosa pine in the Gold Rush zone on the west slope of the Sierra Nevada are relicts of former extensive forests is without foundation (Bloom and Bahre 2003). These writers were also caught up in a political climate where nonrigorous ecological claims were made to justify the establishment of the National Forest system (Lockmann 1981; cf. Grove and Rackham 2001).

Gold discoveries in the late nineteenth century resulted in only limited use of conifer forest for timber or fuelwood.

Nearly all mining enterprises were failures, and even the successes were short-lived (Robinson 1989, 1991; Robinson and Risher 1993). The largest strikes were in the East Fork of the San Gabriel River (1854–1862), Holcomb Valley (1857 to 1870s), Baldwin Mine (1874–1878) and Rose Mine (1897–1906) in the SBM, and Julian (1870–1876) in San Diego County. Other minor strikes include the Holcume placer and Big Horn Mine in the eastern SGM. Wood extraction for smelting and stamping, domestic use in mining camps, or for mine timbers, was limited because most strikes were placers. Stamp mills played out within a few years. Photographs show mature mixed-conifer and pinyon-juniper forest in the vicinity of all the mines. The Stonewall Mine, the largest in San Diego County, illustrates the limited use of wood during the period. This 20-stamp mill consumed 12 cords of wood per day for milling, jisting, and pumping, mostly “oak and pine” (Preston 1890). This is equivalent to about one large-diameter tree per day. If the mill were to survive 3 years, wood consumption may have been ca. 1,000 trees, that is, a few hectares of forest.

The demand for meat during the Gold Rush and the growth of agriculture in the Central Valley resulted in the rapid expansion of open-range sheep and cattle grazing in California (Cleland 1964). In SCA, ranchers recognized that livestock could not be sustained in summer on the barren plains of the interior valleys and began driving animals to mountain pastures in the 1850s and 1860s. Grazing focused on the meadows, although sheep were more broadly pastured through the mountains (Robinson 1989, 1991; Robinson and Risher 1993). The best grazing lands were the meadows at Big Bear, Big Pine Flat, and the upper Santa Ana River Canyon in SBM; and Garner Valley in SJM (Minnich 1988). Livestock grazing in San Diego County centered at Mt. Cuyamaca, Mt. Laguna, Julian, and Mt. Palomar. The SGM were generally too rugged for grazing (Robinson 1991). There is little documentation of grazing in the Mt. Pinos region, although the large meadows in Lockwood Valley must have been utilized for pasture. In the 1850s the pass at Gorman was used for cattle drives from the Los Angeles plains to the gold mines east of Sacramento (Cleland 1964).

Grazing declined after the establishment of the Forest Reserves when most large meadows were drowned by reservoirs including Lake Arrowhead, Lake Gregory, Big Bear Lake, Cuyumaca Reservoir, and Lake Hemet. As public pressures mounted for recreational use of the mountains, as well as fire and watershed protection, the National Forests prohibited sheep grazing by 1900 (Lockmann 1981). Limited summer cattle grazing under lease continued until the mid-twentieth century (Stephenson and Calicarone 1999), then declined as ranchlands in the coastal plains and deserts were converted to agriculture and urbanization. Grazing continues currently in private inholdings on Mt. Palomar and the Coahuilla Indian Reservation in the Hot Springs Mountains.

Grazing has been blamed for a variety of changes in ecological processes including the removal of palatable plants,

changes in regional fire ecology, degradation of riparian habitat, the spread of alien plants, and interference with the recruitment of shrubs and trees (Bahre 1991). However, its effects during the nineteenth century were never rigorously assessed. Most writings from the period were highly politicized (e.g., Lockmann 1981; Allen-Diaz et al. 1999). For example, T.P. Lukens—an early naturalist and confidant of John Muir—concluded that the openness of forests was due to livestock that reduced conifer recruitment, but the effects of livestock were not differentiated from the effects of understory fires (Minnich 1988). Leiberg (1899, 1900) wrote that grazing had little effect in the forests owing to the scarcity of herbaceous cover caused by dry summers. In SSPM, where cattle grazing is still practiced in open range, enclosure experiments in forests showed that cattle have no significant impact on herbaceous cover and conifer recruitment (Minnich et al. 1997), but cattle reduced biomass in meadows of mostly herbaceous perennials *Aster occidentalis*, *Eleocharis pauciflora*, *Trifolium wigginsii*, *Potentilla wheeleri*, and several species of *Juncus* and *Carex*. However, the standing biomass fluctuated more with interannual precipitation variability than with grazing pressure.

Bishop pine on Santa Cruz Island have been degraded or extirpated by severe grazing of feral sheep and pigs that have numbered far beyond carrying capacities in the absence of natural predators since the mid-nineteenth century (Brumbaugh 1980; Minnich 1980). Severe grazing precluded fire-stimulated cohort cycles, leaving open savannas of large trees. Stands in protective fences form dense thickets due to continuous recruitment. The National Park Service successfully removed feral sheep from Santa Cruz Island by the early 1990s, but the postgrazing response of pines has not been documented. Grazing of feral goats has also created open parks of Monterey pine on Guadalupe Island (Rogers 2006). The number of Monterey pines surviving on the island has decreased to about 220 trees. Severe grazing has precluded fire in Torrey pine forests of Santa Rosa Island since the mid-nineteenth century (Wells and Getis 1999).

Water Relations and Microclimate

The zonal replacement of chaparral by coniferous forests with increasing elevation is related to climatic gradients in which increasing precipitation upslope is phased with decreasing temperature and potential evapotranspiration (PET). However, the primary hurdle all conifers must face is that the season of growth and plant water demand is also the dry season. During winter a water surplus spans all elevations, but the surplus extends even later into spring and early summer with altitude (Royce and Barbour 2001a, 2001b; Franco-Vizcaino et al. 2002). Winter precipitation exceeds soil field capacities and produces rock mantle saturation at all elevations except in the driest years, especially on shallow soils (Pronos, Merrill, and Dahlsten 1999). Available water in the soil layer is virtually depleted by the end

of September (Arkeley 1981), but water is still obtained from fractured bedrock (Hubbert et al. 2001a, 2001b; Witty et al. 2003). The depletion of soil water largely determines the completion of the annual growth flush.

There is large local variation in the zonation of mixed-conifer forest with mean annual precipitation. Because AET is isoclinal with temperature and elevation, a positive P-PET balance descends to lower altitudes in higher precipitation zones (Franco-Vizcaíno, Escoto-Rodriguez, and Minnich 2002). In SBM mixed-conifer forest-chaparral ecotone occurs as low as 1,400 m with an average annual precipitation (AAP) of 100 cm, to 2,400 m with an AAP of 40 cm (Minnich 1999). The zonation of soil water availability in the growing season is enhanced by winter snowpacks. Although the soil moisture recharge in rain-dominated climates at lower elevations is linked to the seasonal distribution of storms, at higher elevations replenishment is postponed to the melt season in spring or early summer, when most of the winter's precipitation is released in a period of weeks. Soil water is restored either directly by percolation of snowmelt water or indirectly through runoff and down-slope percolation.

Estimates of average annual frozen precipitation—based on the percentage of snowfall with elevation ratioed to average annual precipitation (Minnich 1986)—are <30 cm in closed-cone forests, four-needle pinyon forests, ghost pine woodlands, Jeffrey pine forests in low basins, and bigcone Douglas fir forests; 15 to 60 cm in mixed-conifer forest; and 60 to 100 cm in subalpine forests. Rain-shadowed pinyon-juniper woodlands above ca. 2,000 m receive as much frozen precipitation (15–30 cm) as low-elevation mixed-conifer forests.

Water relations at the mixed-conifer forest—chaparral ecotone may involve a feedback between snow accumulation and canopy interception. The interception of snow by contiguous chaparral, closed-cone, and mixed evergreen forests is subject to rapid melt from sunlight and air mixing, whereas snow persists longer in a shrub-free, shady floor of mixed-conifer forests (Miller 1981). During winter, the lower limit of snow cover frequently coincides at the mixed-conifer forest-chaparral ecotone. The importance of interception is perhaps manifested in the greater persistence of snow in chaparral burns compared to adjoining mature stands. Observations of snow disappearance shows that the snowpack on north-facing slopes normally melts by April at 2,200 m, May at 2,500 m, and June at 3,000 m (Minnich 1984). In subalpine forests, the early summer phasing of snowmelt and the onset of summer thundershowers may preclude soil drying most years, except in winters with high negative precipitation departures.

The gradient in available soil water in southern California versus northern California is not as large as the precipitation gradient because of increases in the ratio of runoff to ET with increasing latitude (Franco-Vizcaíno, Escoto-Rodriguez, and Minnich 2002). In northern California, a large portion of annual precipitation is lost in overland flow to the Pacific. In water-deficit watersheds of SCA and northern BCA, most

water is consumed by transpiration of vegetation with the relationship between P and ET increasingly stronger as water deficit increases, that is, the amount of recharge and ET is proportional to the amount of biomass as expressed in canopy leaf area. Franco-Vizcaíno, Escoto-Rodriguez, and Minnich found that 70% of P is lost as ET at the soil surface, 15% is lost as ET from the subsurface, 15% is lost as streamflow. In a comparison of streamflow studies in California watersheds south of the 35th parallel versus all available ET studies for extreme deficit watersheds, Franco-Vizcaíno, Escoto-Rodriguez, and Minnich found that ET in SSPM of Baja California is comparable to that of sites having similar precipitation and vegetation in neighboring SCA.

Forests on Mt. Palomar, 40 km east of the Pacific Coast (elevation 1,300–1,600 m, AAP, 70–90 cm) are uniquely dominated by white fir and incense cedar, rather than by pine species, in association with abundant arboreal cover of canyon live oak, black oak, coast live oak, and Engelmann oak. The forest composition may be related to the local climate of mild winters and summers. In the southern Sierra Nevada, Royce and Barbour (2001a, 2001b) show that shoot and foliar growth in pines begins at colder temperatures than species in *Abies*. Hence, pines have longer growing seasons before soil moisture is rapidly depleted by summer drought. Warmer winters near the coast provide extended growing seasons for white fir, and pine establishment is discouraged by shade produced by abundant cover of oaks. Mt. Palomar forests resemble those in the Santa Lucia Mountains dominated by incense cedar and Bristlecone fir (*Abies bracteata*) in woodlands of canyon live oak, coast live oak, valley oak, and black oak.

Fog and cold temperatures of the marine layer in summer play an important role in coastal forests. With low AAP, trees appear to survive in a setting of low ET rates and fog drip. The Douglas fir stand in the Purisima Hills apparently survives in cool summers and the high water table of the watercourse. Bishop pine near Point Conception and the northern Channel Islands grows between 200 and 400 m, within the range of coastal low clouds in summer. The concentration of stands on exposed ridge tops and western exposures maximize foliar fog drip condensation in strong northwesterly winds of the coastal marine layer. To the south, strong northwesterly winds remain outside the southern California bight, but move onshore in northern BCA where drip may account for the abundance of closed-cone pine and cypress forests from Ensenada to San Quintín. Fog condensation is vital to Monterey Pine forests at the north ends of Guadalupe and Cedros Islands, fully exposed to northwesterly winds of the marine layer and where AAP is only 12 to 20 cm (Rogers 2002). Vogl (1973) showed that fog drip of 10 cm per month in late spring occurs in knob-cone pine colonies at 1,000 m in the Santa Ana Mountains. However, supplemental soil moisture from drip is phased with wet soils from winter storms. In summer, the climate is warm and dry because stands lie above the marine layer (normally <600 m; DeMarrias, Holzworth, and Hosler 1965).

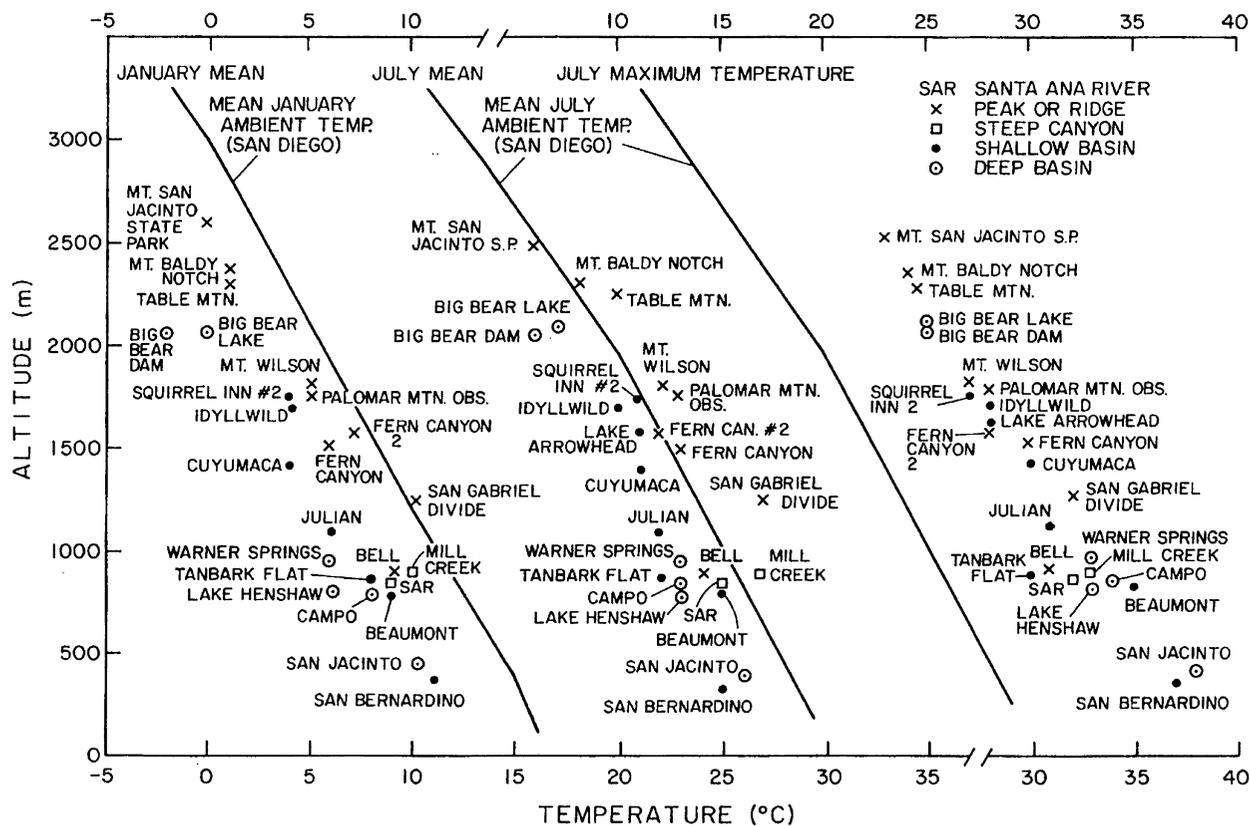


FIGURE 18.4 Mean temperature at selected mountain weather stations compared to mean ambient lapse rates. Stations in basins and canyons subject night radiation inversions (e.g., Big Bear Lake Henshaw), have larger negative mean temperatures to ambient than stations on peaks and ridges exposed to mixing by the ambient atmosphere (e.g., San Gabriel Divide, Fern Canyon). July maximum temperatures are ca. 5°C warmer than ambient temperatures at all stations due to solar superheating of surface air layers.

Coastal low clouds seldom reach interior Coulter and knobcone pine stands. Biondi, Cayan, and Berger (1997) found that summer fog is not a significant predictor of the growth of Torrey pine in San Diego County.

In SCA, night ground inversions are an important component of the climate of forests growing in valley floors because clear skies, light winds, and low relative humidity occur ca. 250 days per year. Minimum temperatures may be as much as 5°C to 15°C lower in basins than on surrounding slopes (Fig. 18.4). Cold basins often exhibit inverted vegetation zonation. At Big Bear in the SBM, there is local cover of lodgepole pine and *Chrysolepis sempervirens*, ca. 500 m below their zonal distributions. Canyon live oak and black oak are absent from the lower 100 m of the basin. Garner Valley in SJM (1,400 m) supports extensive Jeffrey pine forest, whereas chaparral climbs to 2,000 to 2,300 m in surrounding watersheds (Minnich 2001). Ground inversions may also explain the presence of Jeffrey pine at Pine Valley, San Diego County (elev. 1,200 m), Lockwood Valley near Mt. Pinos (1,300 m), and Jeffrey pine forests of SJZ. Other factors may contribute to the presence of low-elevation forests including soil water drainage and reduced night respiration cost (increasing net photosynthesis).

The occurrence of endemic floras on locally treeless pebble plains in the northeastern SBM may be related frost heaving

tied in cold basins (Neel 2000). Pebble plains are treeless areas on deep clay deposits with abundant carbonate mixed with quartzite pebbles that support assemblages of small cushion-forming plants, tiny annuals, grasses, and succulents (Stephenson and Calocarone 1999; Neel). Most sites occur on leeward slopes lacking insulating winter snow cover. Diurnal freeze thaw cycles enhanced by abundant soil carbonate clay fractions push carbonate pebbles to the surface, apparently preventing the invasion of adjoining pinyon-juniper woodlands, whose canopy would ameliorate heaving (Wangler and Minnich 1996; Chambers 2001). Pebble plains contain several local endemic species including *Arenaria ursina*, *Castilleja cinerea*, and *Eriogonum kennedyi* var. *austromontanum* (Neel).

Fire, Forest Dynamics, and Biogeography

In southern California, the Mediterranean climate of winter rain and dry summers results in inefficient decomposition, fuel buildup, and high fire hazard (Stohlgren 1988; Hart, Firestone, and Paul 1992). Recurrent fire is a primary mediating process in the structure, species composition, and distribution of southern California conifer forests. In effect, plant assemblages represent integrations between long-term successions and growth that lead to biomass (fuel) accumulation and "instantaneous" combustion events that remove biomass.

Southern California conifers are nonsprouters if entirely defoliated by fire and have divergent rates of mortality due to differences in life traits and fuel abundance in subcanopy vegetation (Table 18.1; Minnich 2001). Only bigcone Douglas-fir resprouts, but severe burns fatally injure this species. The non-sprouting trait of conifers makes them subject to intense selection pressures produced by gradients in climate and corresponding properties of fire regimes (productivity, fuel buildup rates, intervals, size, intensities, removal of biomass), depending on their life traits for recruitment, growth, and maturation, as shown for many coniferous ecosystems in the western United States (Romme and Knight 1982; Veblen, Hadley, and Reid 1991; Christensen 1993). To hold onto a site, conifers colonize burns by seedling establishment and grow to reproductive maturity within the interval between stand-replacing fires.

Landscape scale fire models on long-term forest dynamics of southern California conifer forests are undergoing continuing refinement. Studies frequently take a retrospective approach using fire scar dendrochronology (FSD) and fragmentary historical records because suppression has moved ecosystems away from presuppression states. Other studies use spatially explicit data from aerial photographs to reconstruct fire histories and vegetation dynamics. This approach assumes that the long-term characteristics of forest dynamics on the landscape can be evaluated from a large sample of fires and successions (Shugart 1984; Turner, Gardner, and O'Neill 1989). A third approach is to study Baja California, which is unfettered by fire suppression to this day, and offers a baseline landscape for comparison with fire regimes in southern California.

This survey first reviews the properties of fire regimes, then follows with summaries of three fire-regime models, and concludes with the role of fire in mixed-conifer forest assemblages.

Conifer Forest Fire Regimes

RETURN INTERVALS

How often forests burn depends on rates of growth and fuel buildup. Forests with high primary productivity on moist windward slopes burn more frequently than forests with low primary productivity on rain-shadowed leeward slopes, or on high summits where growth is limited by short growing seasons. Fire perimeter maps for the SJZ and SSPM show that fire rotation periods along an east-west gradient ranges increases from 50 to 70 years in the chaparral and mixed-conifer forest on coastal slopes to >200 years in pinyon-juniper woodlands on leeward slopes (Minnich and Chou 1997; Minnich et al. 2000). In SCA the rate of burning in chaparral and related conifer forest assemblages has been stable, ca. one to three times during the twentieth century (Wells et al. 2004). Only 20% to 30% of pinyon-juniper woodlands have burned since 1910 (Wangler and Minnich 1996). The rate of burning in mixed-conifer forests has declined due to suppression (Wells et al.).

SIZE AND DURATION

Firescapes exhibit profound spatial pattern that is self-regulated as expressed in nonrandom patch emplacement in response to time-dependent cumulative fuel buildup. Long-term fire risk thresholds (strong time dependence) produce a negative feedback between fire size and frequency (Minnich and Chou 1997; Minnich et al. 2000). Fires preferentially burn old stands, whereas younger stands with limited fuel and high fuel moisture constrain the spread of fire. In SCA, the reduction in landscape fire frequency by suppression coarsens stand mosaics and the size of flammable patches (Minnich 1983; Minnich and Chou 1997; Minnich et al.). In BCA, most burning is accomplished by fires in the order of 500 to 5,000 ha in chaparral and mixed-conifer forest, and in the order of 100 to 2,000 ha in pinyon-juniper woodland. Southern California chaparral fires scale in the order of 5,000 to 50,000 ha, and >100,000 ha in the October 2003 siege. Fire-size distributions in pinyon-juniper woodlands under suppression in SCA are comparable to that of the Sierra Juarez in BCA, the largest burns less than 3,000 ha (Wangler and Minnich 1996; Minnich and Chou 1997). There have been too few fires to establish reliable fire size statistics in mixed-conifer forest. In other regions with suppression, the 1987 Stanislaus complex and 2003 Johnsondale fire in the Sierra Nevada, and 2003 Rodeo-Chadeski burn in northeastern Arizona fires have scaled in the order of 100,000 ha.

Presuppression fire sizes in SCA are unknown, but written accounts indicate that vegetation mosaics were patchier and fires smaller than at present (Minnich 1987b, 1988). For example, in the San Jacinto Forest Reserve, Leiberg (1899, 1900) stated that fires that occurred in the previous decade were "scattered throughout the reserve in small tracts." Early settlers living near SGM appreciated the self-limiting property of wildfires, stating that fires were ". . . not very extensive due to the fact that they ran into old burns and checked themselves." William Mulholland observed in 1908 that "If a portion of a watershed burns off each year, then there is always a large majority of the [water]shed with a new green growth that will defy any fire. . . . It is better to have fire every year which burns . . . a small area, than to go several years . . . and have a big one denuding the whole watershed at once."

Late-nineteenth-century newspapers describe mountain fires persisting for months until the autumn rains (Minnich 1987b, 1988). Depending on weather and fuel conditions, flames spread actively for days, with long intervening periods where flames persisted in logs, and other coarse fuels. New flame fronts later establish from these sources. Fires of 1 to 2 months have been recently observed in the SJZ and SSPM (Minnich et al. 2000). At present, fires seldom persist more than a week in SCA because secondary recurrences are prevented by fire crews. Shifting fire behavior in long-duration fires produce large variability in intensities and complex patterns of forest damage.

TABLE 18.1
Summary of Life Traits and Presuppression Fire Regime Properties of Southern California Conifer Forests

Forest Type	Productivity	Chaparral		Canyon oak Biomass Shrub Tree	Fire Interval (freq/ 100 yr)	Fire Mort. Rate	Re-Spr.	Cone ² Serot.	Stem ³ Estab.	Cond. ⁴ Seedl. Estab.	Tree Stature = 10 m (yr)	Reprod. Maturity (yr)	Tree ⁵ Longev. (year)	Stand Age Distrib.	Stand Den-sification
		BM	BM												
Knobcone Pine/Cypress	H	H	H	-	2.0-3.0	T	-	X	P	I	15-30	10-20	FI-100	E	
Monterey/Bishop Pine	H	H	H	-	2.0-3.0	T	-	x	P/C	I/T	15-30	10-20	FI-100	E/M	
Coulter pine-chaparral	H	H	H	L	2.0-3.0	H	-	x	P	I	15-25	10-20	FI-100	E	
Torrey pine	H	M	M	-	2.0-3.0	M	-	x	P/C	I/T	15-25	10-20	40-150	E/M	
Ghost/ Coulter Woodland	H	M	M	L	2.0-3.0	M	-	x	P/C	I/T	15-25	10-20	FI-200	M	X
Four-needle pinyon pine	M-H	M-H	M-H	-	1.5-2.0	H	-	-	C	R	>50	25-50	>200	M	
Bigcone Douglas fir	H	L	L	H	2.0-3.0	L-M	X	-	C	I	30-50	50	>200	M	
Mixed-conifer/ Ponderosa-Jeffrey pine	M-H	L	L	L	2.0-3.0	L	-	-	C	I/T	30-50	50	>200	M	X
Canopy layer						M-H							<100	M	X
Polesize stems						H							<-50	M	
Saplings															
Mixed-conifer/white fir sugar pine	M-H	L	L	L	2.0-3.0	L	-	-	C	T/R	30-50	50	>200	M	X
Canopy layer						M-H							<100	M	X
Polesize stems						H							<-50	M	
Subalpine forest	L	L	L	-	<<1.0	H	-	-	P/C	I/T	>50	50	>200	E/M	-
Pinyon-juniper woodland	L	L	L	L	<<1.0	H	-	-	C	T/R	>50	>50	>200	M	-

NOTE: H = high productivity and biomass, M = medium, L = low, T = total mortality, H = high, M = medium, L = low; X = fully serotinous, x = partially serotinous; P = pulsed establishment, C = continuous; I = reproduces from seed only after disturbance, T = at any time, R = only upon vegetation maturity; FI = tree longevity defined by stand-replacing fire (number is average fire-return interval), otherwise tree longevity not related to fire regime.

WEATHER

The weather, especially relative humidity and wind velocity (advection), affects fuel moisture and rates of heat-transfer processes in flame lines that directly contribute to fire severity and conifer mortality (see review in Minnich 2006). The weather risk of individual fires involves chance timing between ignitions (a discontinuous variable of infinitely short time and spatial scale) and vegetation growth/fuel buildup (a continuous spatial and temporal variable). Hence, individual fires exhibit strong variability, even at site-specific scales, in a broad range of weather conditions. However, if fires establish at random over many fire cycles in long time scales, then by chance fires will occur most frequently in modal weather states, that is, prevailing "average" conditions rather than comparably rare than dry or wet states of the climate, as described in a normal probability distribution. In BCA, random fire occurrence is a plausible assumption because fires are not suppressed, lightning incidence occurs in predictable atmospheric states, and human fire starts occur independently.

The long-term pattern of fire spread and intensity on the landscape reflects two countering trends: (1) fire-spread rates increase with increasingly severe weather risk states, and (2) weather severity is inversely related to time. If fires occur at random in BCA, then low-intensity burning (low spread rates) will involve extensive spatial coverage because "normal" weather states dominate the fire season. By removing fuel, extensive low-intensity burns reduce the potential for high-intensity events in rare extreme weather states. Clearly, long-duration fires increase the probability that fires phase with normal weather. In SCA, efficient initial attack suppression of fire starts nonrandomly selects for the escape of fires in severe weather (high-ignition-phase energy-release states). Because the continuity of weather operates in time scales of days in association with synoptic-scale shifts in atmospheric circulation and because fires in the flaming stage seldom persist more than a few days, the weather of major fires resembles the weather risk state at the ignition. On an area-weighted basis, large fires are nonrandomly skewed to severe weather risk states compared to chance. Once fires extend past the "initial attack" phase of suppression, fire-fighting forces have little effect on them because the energy release of flame lines is orders of magnitude greater than energy of suppression. Evidence for nonrandom fire occurrence in SCA is seen in the shift from dominantly Santa Ana wind-driven fires in SCA to fires pushed by prevailing onshore flows and terrain induced slope winds in BCA (Minnich 1983; Minnich and Chou 1997).

TERRAIN AND SUBCANOPY FUELS

Since terrain is a spatially fixed variable, topographic surfaces have consistent site-specific effect on fire behavior, removal of biomass, and conifer mortality rates. In a featureless plain, tree injury and mortality depends in part on how flame lines pass through a stand. Flame line configurations tend to be

linear to elliptically shaped (e.g. Finney 1998; Fujioka 2002). Fire intensity, which is proportional to spread rates (fuel area burned per time), fluctuates around the perimeter depending on the orientation of the flame line to the wind (heat transfer by advection). Spread rates (intensities) are greatest in "head fires," where flame fronts move downwind at right angles to the wind (maximum advection). Flanking fronts spread slowly at orientations approaching the tangent of the wind (advection ceases). Fires also "back" against the wind at even lower rates and intensity in the face of the wind.

In complex terrain, steep undissected slopes orographically channel superheated flames upslope at rates and intensities that are potentially lethal to conifers. Mortality is increased by the proximate geometric position of tree canopies to surface fuels on the uphill side. Dissected escarpments have local islands of reduced flame intensities due to the interruption of flame front motion by slope discontinuities. Convex mountain crests produce less interruption than sharp ridgelines. Similarly, the steep walls of "V-shaped" canyons have reduced intensities compared to concave canyons because of abundant bedrock exposures and reduced plant cover caused by erosion. Flame intensities tend to be higher on ridges and summits compared to valleys and canyons due to greater exposure to ambient winds. Fire severity is lowest on flat surfaces because the advance of flame fronts becomes solely dependent on advection (wind) process and tree crowns have maximum distance from surface fuels.

Models

Each conifer forest assemblage is associated with a characteristic subcanopy of chaparral and oak woodlands as well as accumulation patterns of combustible biomass (Minnich 2001). Chaparral is the largest source of subcanopy fuel. The rapid establishment and growth of shrubs assures relatively short fire recurrences at time scales of decades. Flame lengths associated with "crown fire" combustion of contiguous chaparral cause high mortality to coniferous overstory at low elevations, but tend to be nonlethal in the burning of open, low-growing montane chaparral assemblages at high elevations. Midstory of arboreal oak assemblages—canyon live oak, black oak, coast live oak, Engelmann oak—are more fire-resistant than chaparral because canopies are detached from surface fuels. For example, Coulter pine growing in dense chaparral assemblages has higher rates of stand-replacement fires than bigcone Douglas fir and mixed-conifer forests growing in open shrub subcanopy (Figure 18.5). Crown fires of course cause fatal injury to all forest types.

Selection pressures by fire covary with SCA conifer forest assemblages with gradients in climate, productivity, and rates of fuel accumulation. A map of montane conifer forests of southern California is one of evershifting species composition and patterns of distribution in complex dissected terrain of the region. However, in the broadest scales, the spatial pattern of fire and forest assemblages can be

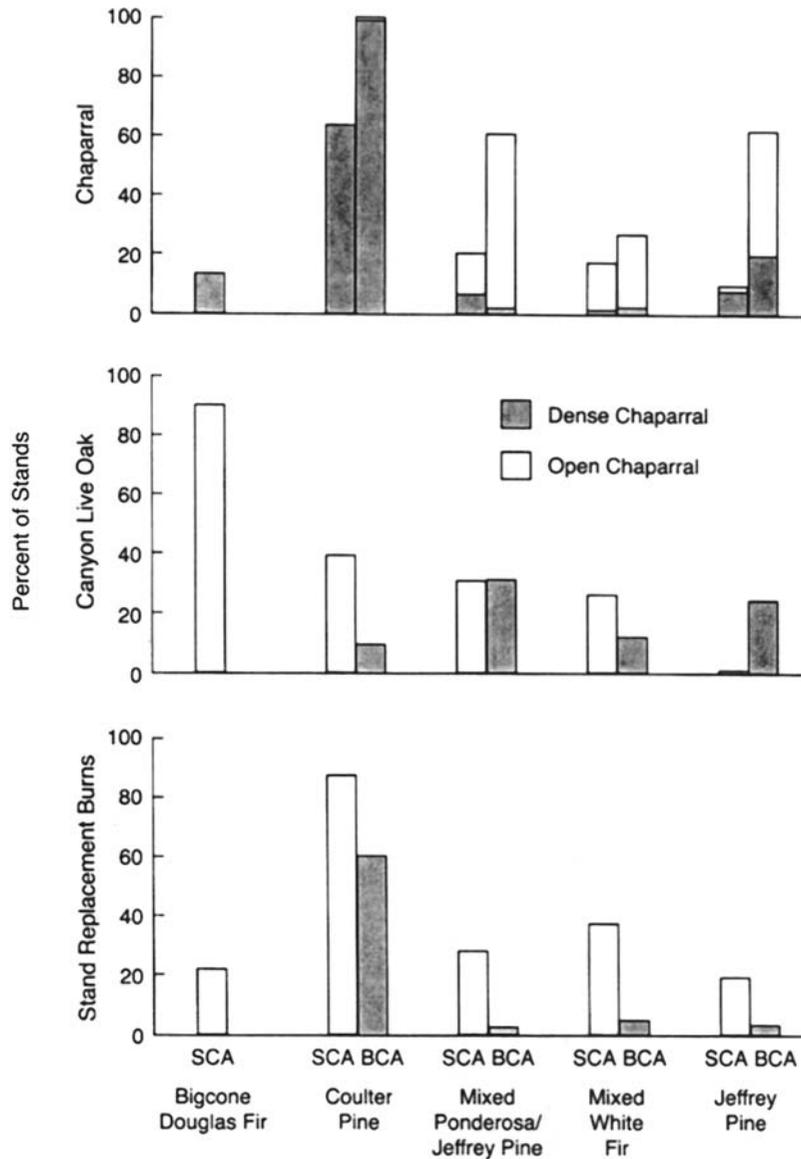


FIGURE 18.5 Conifer forest stand-replacement fire rates compared with the percentage of stands that are associated with chaparral and canyon live oak woodlands. Note that the rates are higher in forests associated with chaparral. SCA = southern California sites; BCA = Baja California. Data for SCA (Minnich 1978); data for BCA (Minnich 2001).

distilled into the following trends. With increasing elevation on mesic coastal escarpments, fires recurring at rates of two to three times per century shift from stand-replacement burns in closed-cone conifer forests growing in chaparral to litter-based understory burns in mixed-conifer forest. Surface fire regimes occur in long-lived bigcone Douglas fir forests in association with fire-resistant arboreal canyon live oak forest. Moving to the highest elevations and leeward slopes with low primary productivity, surface fire regimes of mixed-conifer forest are replaced by stand-replacement fire regimes at rates of less than once per century in thin-barked subalpine forest and pinyon-juniper woodland.

Southern California conifer forests are summarized here using shifting, standing, and patch mosaic population models after Minnich and Everett (2001). In the “shifting” model, small disjunct forests of the chaparral exhibit rapid transient fluctuations in forest structure and distribution

from large stand-replacing fires. The “standing” population model applies primarily to mixed-conifer forests that persist through recurrent understory fires with small transient spatial fluctuations. The “patch mosaic” model applies to subalpine forest and pinyon-juniper woodlands characterized by local rotation of forest gaps from stand-replacement fires. Over the past century, new selection pressures from suppression have changed forest fire regimes, especially in forests with high primary productivity.

SHIFTING FOREST MODEL—CLOSED-CONE CONIFER FOREST, FOUR-NEEDLE PINYON FOREST

The chaparral is mostly treeless except for local patches of short-lived serotinous pines and cypresses. These forests endure two to three stand-replacement burns per century in association with high chaparral fuel loads (see Table 18.1). Species of *Pinus* sect. *Oocarpae* and cypresses sustain virtually

total mortality because of their small stature, paper-thin bark, and integration of crowns with the shrub layer. The taller bigcone pines also succumb to stand-replacement fires even though trees have thick insulative bark. In SBM, 90% of Coulter pine perished in stand-replacement burns, mostly in dense chaparral on steep, undissected convex slopes (Minnich 1999). Associated canyon live oak grows as flammable shrubs because its thin, dry flaky bark does not protect arboreal stems from cambium damage, inducing resprouting of multitemmed basal rosettes (Plumb 1979). Coulter pine survives most frequently on bedrock slopes. Similarly, prescribed burn experiments in Torrey pine forest resulted in severe or fatal fire damage (Wells and Getis 1999).

Postfire succession is characterized by vigorous pulsed cohort regeneration cycles from dormant seed dispersed from fully or partially serotinous cones of fire-killed trees (see Table 18.1). Fires crack a resin seal and allow the scales to open. Beginning at ca. 10 years of age, saplings produce cones that accumulate on the bole of the tree creating an aerial seed bank. Serotiny fixes recruitment cycles to seed bed conditions of full sun and mineral soils. Cohort recruitment cycles have been documented for Coulter pine (Griffin 1976, 1982; Vale 1979; Talley and Griffin 1980; Borchert 1985; Wells 2001), knobcone pine and tecate cypress (Vogl et al. 1988), and Torrey Pine (Wells and Getis 1999). Succession can be viewed as a "race" to reach reproductive maturity before chaparral reaches flammable thresholds. Trees emerge through the chaparral layer in 10 to 15 years and are >10 m tall by 20 to 40 years. Because knobcone pine is perfectly serotinous, there is no intraburn recruitment in the species. Cones of Coulter pine and cypresses open spontaneously, but recruitment is sparse in mature stands. Apparently, recruits are shade intolerant in tree overstory and dense chaparral. In contrast, bishop pine near Lompoc and fenced exclosures on Santa Cruz Island experience continuous recruitment that lead to dense mixed-aged thickets. In these species hot or dry weather may break the resin seal of cones for seed dispersal. Mixed-aged stands also occur on bedrock slopes in BCA. The longevity of closed-cone tree species is often fixed by fire intervals, but rare stands survive multiple cycles. For example, tree cores show that Torrey pines in San Diego Country reach 168 years of age (Biondi et al. 1997).

Presuppression accounts describe stand-replacement burns and even-aged stands of Coulter and knobcone pine forests (Minnich 1988). Similarly, in BCA, knobcone pine and Tecate cypress stands are strongly even-aged, with tree growth states in phase with the age of chaparral patches mapped in Minnich and Chou (1997). Arizona cypress in the southern SJZ is also even-aged due to brushfires, but rare long-lived trees occur in the canyons protected from burning (Moran 1977). In SSPM, most Coulter pine forests sustained stand-replacement burns in association with dense *Arctostaphylos peninsularis* chaparral and canyon live oak scrub (Fig. 18.4; Minnich 2001).

There has been no research on the fire ecology of four-needle pinyon. Time-series aerial photographs of SSPM show that trees perish in chaparral burns, but stems reach mature stature in burns as recently as 50 years, suggesting rapid colonization and growth rates. It is not known at what age trees begin cone development. Rapid establishment may be related to efficient long-range dispersal and caching of seed by birds and mammals (cf. Van der Wall and Balda 1977; Van der Wall 1997). Stands in BCA have patchy distributions with tree size in phase with the age of chaparral (Minnich 2000, 2001). In SJM the largest stands occur in an 80-year-old chaparral patch.

It is unclear how fire suppression affects closed-cone conifer forests. Fire intervals under suppression in SCA broadly overlap with those in BCA (Minnich and Chou 1997). Increasing fire intensities would not increase mortality rates in a stand-replacement fire regime. Fire size may not exert selective pressure because tree establishment relies on locally dispersed dormant seed of serotinous cones. There is evidence that frequent fires can extirpate stands (Zedler, Gautier, and MacMaster 1983). To evaluate the stability of shifting populations, it may be best to document for postfire recruitment failures that can eliminate both the adult population and the seed bank, resulting in local extinctions (Vogl et al. 1988).

Closed-cone conifers may be susceptible to burning before reproductive maturation (immaturity risk). In Otay Mountain of San Diego County, Zedler (1981) suggests that short fire intervals (<20 years) reduce cone and seed production and rates of recruitment. Because seed production doubtless exceeds the frequency of mature stems, deficits in recruitment versus mature stem densities would involve high seedling and sapling mortality rates. Immaturity risk may be exacerbated in chaparral lands infested or surrounded by exotic annual grasslands capable of supporting frequent burns and more frequent ignitions (Zedler, Gautier, and MacMaster 1983). However, there is a negative feedback between fire size and frequency due to time dependence in fire occurrence in chaparral. Short fire intervals (<20 years) occur in <2% of the landscape (Minnich and Chou 1997). The reburn was encouraged by artificial reseeding of rye grass (*Lolium*). Increasing fire size may influence long-range dispersal, caching, and establishment of four-needle pinyon.

STANDING FOREST MODEL

Standing forests consist of long-lived trees that survive surface fires with thick insulative bark and tall stature. These assemblages grow in areas lacking dense chaparral cover or in dense oak forests (Minnich 2001). Over multiple fire cycles, forests exhibit "standing" spatial distributions.

Bigcone Douglas Fir Forest

A southern California endemic, this long-lived tree grows in discrete groves in canyons and shady slopes in association with solid midstory of canyon live oak, and is surrounded

by extensive chaparral (Bolton and Vogl 1969; McDonald and Littrell 1976). Chaparral fires entering bigcone Douglas fir stands shift to litter fires, the flames either scorching the canyon live oak layer or leaving the layer unburned. Taller bigcone Douglas fir are undamaged except for bole scorch from ground fires (Minnich 1999; see Table 18.1). Abundant cliff faces, erosion of organic matter, and scattered shrub understory reinforce fire resistance. After intense defoliating fires, bigcone Douglas fir survives by epicormic resprouting along the upper bole and primary branches (Gause 1966). In SBM, 25% of stands experienced in stand-replacement burns with mortality rates inversely related to slope gradient (Minnich 1999; see Fig. 18.5). Mortality does not correlate with slope aspect.

The longevity and fire resistance of bigcone Douglas fir were not appreciated in presuppression times (Minnich 1988). Early writers wrote that it sustained heavier mortality than other trees because of intense chaparral fires. They also believed that the tree was in decline because of the abundance of dead standing trees in most stands. However, its resistance to wind-fall for decades and resprouting ability were not recognized. Early foresters also asserted—without historical evidence—that fragmented forests were remnants of former continuous forests, but were apparently unaware of earlier descriptions of fragmented forests in the region. Postfire successions depend on fire severity as given in the following end-member models in a continuum of outcomes (Minnich 1999). In the low-intensity end member, mature oak midstory retains an arboreal preburn state, with the bigcone Douglas fir layer scorched or unburned by surface fires. Scorched stands recover by epicormic sprouting (Plumb 1979). The mixed-aged population structure of bigcone Douglas fir reflects incremental mortality of old stems and their replacement by maturing subcanopy trees. In the high-intensity end-member, stand-replacement burns cause fatal injury to bigcone Douglas fir. Burned forests are covered by basal resprouts of canyon live oak, *Q. wislizenii* var. *frutescens*, and *Cercocarpus betuloides*, as well as dense thickets of *Ceanothus integerrimus*, *C. leucodermis*, *C. oliganthus*, and *C. palmeri* that established from seed banks.

After 30 years, shrubby thickets of canyon live oak develop canopy closure with corresponding dieback of *Ceanothus* spp. Bigcone Douglas fir recruitment densities are <10 ha⁻¹ even in stands as old as 50 years. Saplings appear to be poorly adapted to heat and drought conditions in the shrub phase (Bolton and Vogl 1969; Minnich 1999). Establishment may be delayed by long-range seed dispersal lag times. Trees establish most frequently on disturbed soils, road cuts, cliffs, and steep slopes where they take root in bedrock fractures. Members of *Pseudotsuga* are known for aggressive establishment in disturbed mineral soils. The niche of *P. macrocarpa* appears to be a combination of fire-resistant terrain and high erosion rates that permit continuous recruitment.

Ghost Pine and Coulter Pine Woodlands

Borchert et al. (2002) found that ghost pine sustains high mortality rates, even though the primary fuel is exotic annual

grassland. In the Liebre Mountains, stands in chaparral exhibit even-aged structure due to stand-replacing chaparral burns, the recruits apparently establishing from seed released by serotinous cones (Minnich and Everett 2001). Mortality rates in Coulter pine woodlands decrease with increasing altitude as understory fuels shift from chaparral to black oak or canyon live oak (Vale 1979; Minnich 1980; Borchert 1985; Minnich 1999; Wells 2002). Borchert et al. (2002) found that the probability of survival of Coulter pine and ghost pine decreased with increasing percentage of crown scorch and increasing height of bole bark char. A trend for decreasing serotiny in Coulter pine along an understory gradient from chaparral to oak woodlands suggests that strong selection may exist for natural variation in cone habit (Borchert 1985).

There are few studies on postfire successions. Ghost pine grows in mixed stands, reflecting both partial survivorship of fires and continuous recruitment (Borchert et al. 2002). Coulter pine woodlands form mixed-aged stands as trees establish continuously in grassland, and continuous seed dispersal is encouraged by reduced cone serotiny in these populations (Borchert 1985), similar to stands in the Santa Lucia Mountains of central California (Griffin 1976; Vale 1979). Wells (2002) observed pulsed cohort regeneration with extended recruitment after fire in Coulter pine woodlands at Cuyamaca State Park and proposed a “bet hedging” model in which recruitment failures in chaparral stands are recolonized by seed dispersal from permanent Coulter pine woodlands. However, the interaction between Coulter pine chaparral versus oak woodland stands must account for long-range dispersal among these assemblages, and inefficient intraburn recruitment in dense chaparral.

Mixed-Conifer Forest

The most fundamental observations that form the basis of fire research on mixed-conifer forest are the densification of formerly open forests and massive buildup of fuels during twentieth-century fire suppression. Early writings and ground photographs (Fig. 18.6) in southern California record open stands of mature trees with few polesize stems (Minnich 1988). VTM survey quadrat data for 1929 to 1934 in the SBM (Figs. 18.6) reveal that most stems were >60 cm dbh with stand densities ranging from 150 ha⁻¹ in white fir forest to 79 ha⁻¹ in monotypic Jeffrey pine forest (Minnich et al. 1995). Harvested forests of ponderosa pine had densities of 230 ha⁻¹ with most stems <30 cm dbh. VTM maps depict forests dominated by ponderosa or Jeffrey pine, with white fir dominating north-facing slopes. Early settlers and foresters explicitly describe open forests in relation to ground fires (Minnich 1988). Leiberg (1900) wrote: “The fires which run in the forests are low, having only a small amount of litter to feed on.” The damage to the western yellow pine . . . consists chiefly in the fire scars on the basal portions of the trunks.” Sterling (1904) writes that in SJM: “In the timber belt . . . the absence of shrubby ground cover reduces the severity of fire to such an extent that large trees

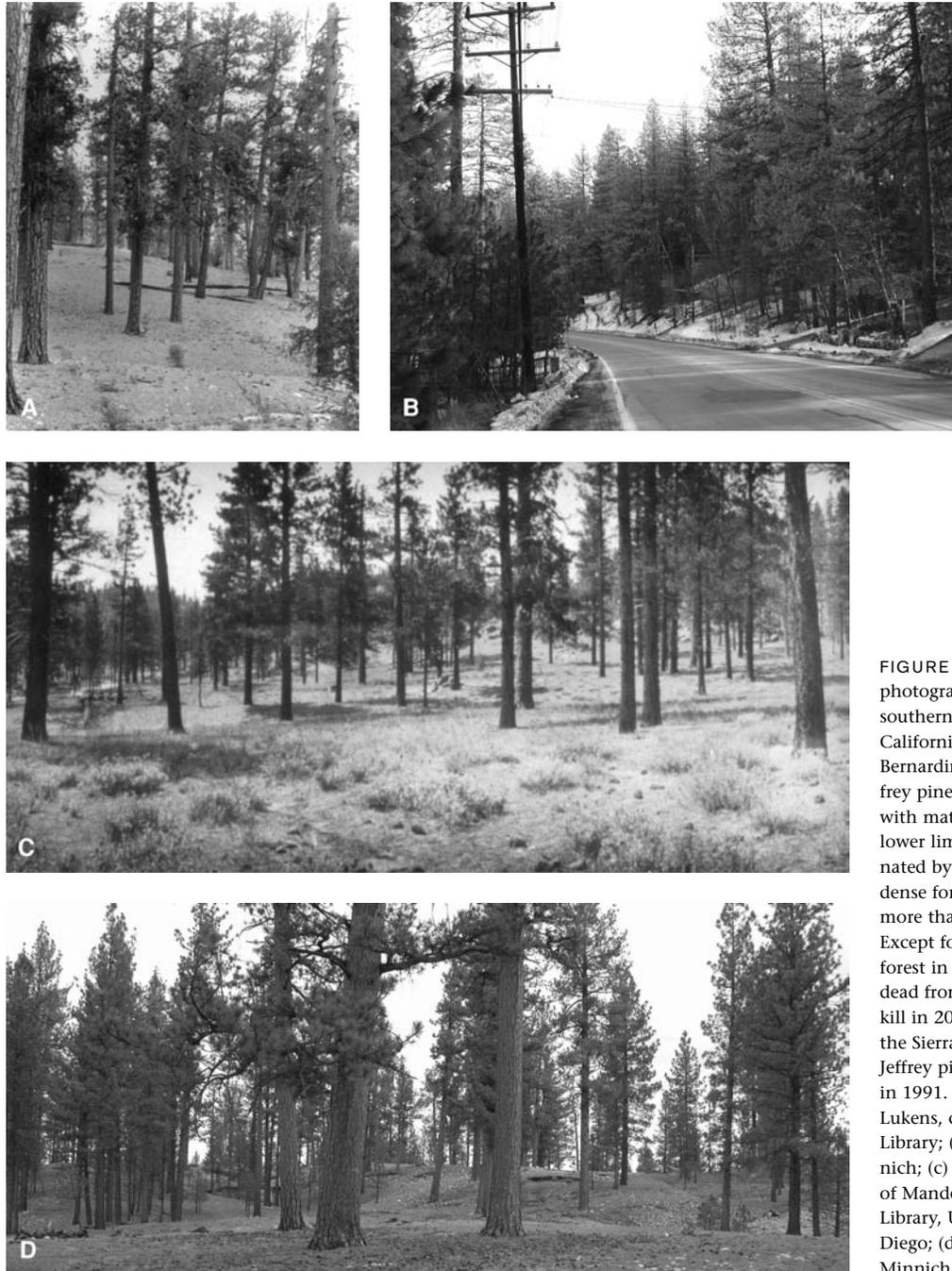


FIGURE 18.6 Mixed-conifer stands photographed a century apart, in southern California (a, b) and Baja California (c, d). In the San Bernardino Mountains: (a) open Jeffrey pine forest near Big Bear in 1900, with mature trees >60 cm dbh and lower limbs (and younger trees) eliminated by intense surface fires; (b) dense forest at Lake Arrowhead after more than 100 years without fire. Except for young trees in the left, the forest in this photograph is entirely dead from drought and bark beetle kill in 2002. At Arroyo San Rafael in the Sierra San Pedro Martir: (c) open Jeffrey pine in 1903; (d) the same area in 1991. Photographs: (a) by T.P. Lukens, courtesy of the Huntington Library; (b) courtesy of Victoria Minnich; (c) by Ford Carpenter, courtesy of Mandeville Special Collections Library, University of California, San Diego; (d) courtesy of Richard Minnich.

survive . . ." Homans (1910) wrote ironically: ". . . the destructive element of the ground fire is that it kills all reproduction, leaving only a stand of mature trees."

In the SSPM, recurrent surface fires maintain open, mixed-aged parks of mature trees forming an umbrella-like canopy 10 to 15 m above the ground. The open forest structure has been photographed since 1903 (see Fig. 18.6; Nelson 1921; Minnich and Franco-Vizcaino 1998). Overstory tree densities (Fig. 18.7) range from 50–100 ha⁻¹ in monotypic Jeffrey pine to 70–120 ha⁻¹ in mixed Jeffrey pine forest and 130–200 ha⁻¹ in mixed white fir forest, with most stems >50 cm dbh.

Forest densities also increase with elevation (Savage 1997; Minnich et al. 2000; Maloney and Rizzo 2002; Stephens 2003). Pole-size and sapling densities are ca. 10–15 ha⁻¹ in all types and across all elevations (Minnich et al.). Forest densities (stems >10 cm dbh), species composition, and diameter frequency distributions are close to those of a forest survey of SSPM in 1886 (Minnich and Franco-Vizcaino 1998; Minnich et al.), as well as the 1929 to 1934 VTM survey in SBM (Fig. 18.8). Vegetation maps (Minnich 2001) also show similar patterns of tree dominance by slope and aspect as mapped by the VTM survey in SCA.

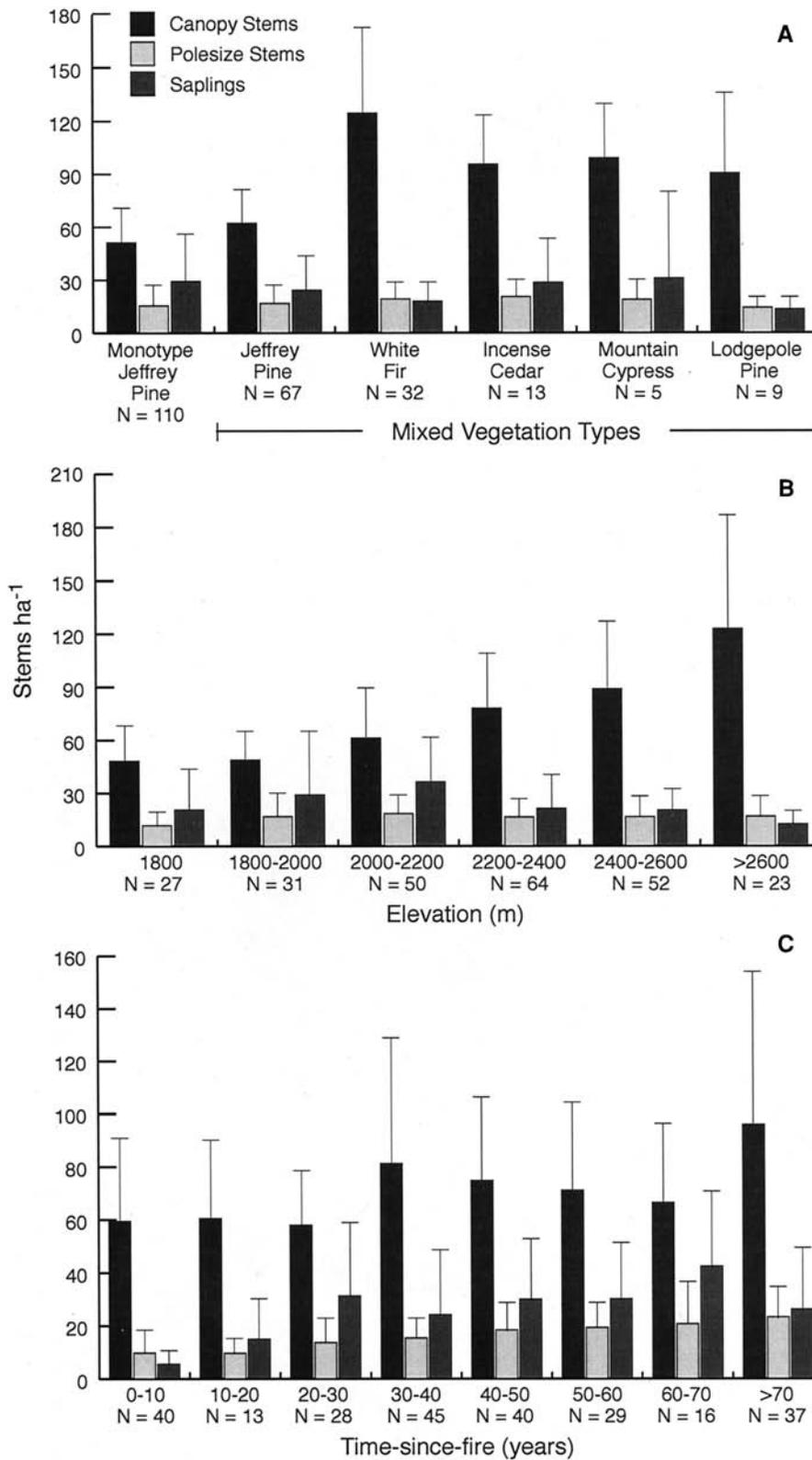
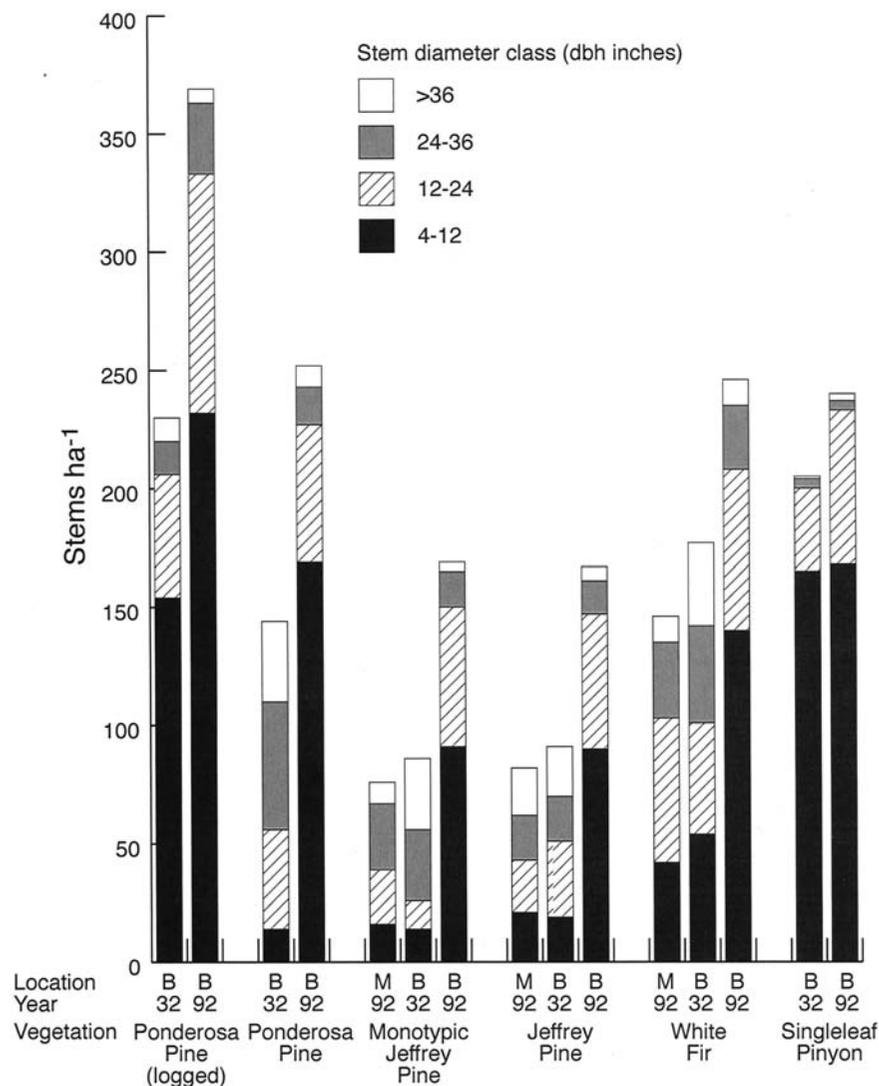


FIGURE 18.7 Densities of canopy trees, polesize trees (trunks 0.25–0.50 × diameter of canopy trees), and saplings (trunks <0.25 × diameter of canopy trees) in Sierra San Pedro Martir by vegetation type, elevation, and years since fire.

FSD studies in SCA reveal that trees were scarred by fires at rates of several times per century, but few trees were scarred since 1900 (McBride and Laven 1976; Everett 2003). Extensive forests have reached canopy closure, with dominance shifting from sun-tolerant ponderosa and Jeffrey pine to

shade-tolerant white fir and incense cedar in the subcanopy. Replication of VTM plots in SBM show that stem densities (>10 cm dbh) had doubled since 1929 to 1932, ranging from 260 ha⁻¹ in white fir to 160–180 ha⁻¹ in other assemblages (Fig. 18.6; Minnich et al. 1995). Densification rates are

FIGURE 18.8 Tree-stem diameter distributions for various montane forest stands in the San Bernardino Mountains (B) and in the Sierra San Pedro Martir (M) in 1932 and 60 years later in 1992.



proportional to gradients in average annual precipitation (AAP), with increases of 300% in forests with AAPs of 100 cm, and no increase in forests with AAPs of 40 cm. The highest densities (380 ha^{-1}) occur in logged ponderosa pine forest where harvest disturbance resulted in abundant recruitment beginning in 1850 to 1870, whereas densification began after 1900 in unharvested forests (Minnich 1988; Minnich et al. 1995). The density of stems $<10 \text{ cm dbh}$ in harvested forests reach $1,000\text{--}2,000 \text{ ha}^{-1}$ (Albright 1998), similar to the Sierra Nevada (Roy and Vankat 1999).

Not all forests experienced species changes. The composition of postsuppression cohorts in SBM is similar to the overstory in white fir forest on north-facing slopes and monotypic Jeffrey pine forests in interior basins (Minnich et al. 1995). A decline in the density of stems $>60 \text{ cm}$ since 1932 may be related to competition from younger cohorts that weaken large trees, making them susceptible to infestations of bark beetles, pathogens and air pollution (Minnich et al. 1995; cf. Stone et al. 1999).

Elsewhere in SCA, modern forest structure varies with topography and climatic gradients (Fig. 2.17 in Stephenson and Calecarone 1999). Open forests are widespread in the rugged SGM and most leeward slopes of the Transverse Ranges. Dense forests grow on moist windward slopes such as Pine Mountain Ridge, Idyllwild, Mt. Palomar, and Mt. Cuyamaca.

Few studies have quantified presuppression fire regimes in SCA. A FSD study in SBM, based on 15 samples of single trees at 1.0-km intervals, estimates that fire intervals were 15 to 29 years (McBride and Lavin 1976). Everett (2003) working on two 280-ha grids in SJM and SBM found that fires scarred at least one tree in each grid every 5 years. Spatially reconstructed rotation periods—the interval between scars of each tree—was 32 years on Black Mountain and 49 years at Big Pine Flat. Aerial photographs in 1938 to 1939 show presuppression stand-replacement burns on steep slopes and ridges with subcanopy of brush and canyon live oak as well as dense harvested forests near Lake Arrowhead

(Minnich 1988). Stand-replacement burns were mostly <20 ha and collectively comprised 4.2% of the forest.

Minnich et al. (2000) reconstructed a spatially explicit fire history of the SSPM for 1925 to 1991 using time-series aerial photographs. They found that forests were burned in intense subcanopy burns about twice per century. Most burning was accomplished by fires ranging from 200 to 6,400 ha in self-organized sequences similar to chaparral (Minnich and Chou 1997); that is, the movement of fire lines in old stands were constrained by young stands in a shifting patch mosaic. Burn perimeters elongate west-to-east parallel to prevailing anabatic upslope winds that dominate in summer (Minnich 1983). Fires caused mortality to >10% of canopy layer trees in 22% of forests, but only 3% of forests were denuded in stand-replacement burns. Forest stand-replacement gaps were mostly <16 ha in size (Minnich 2001). Forests exhibit bole char to 5 m and crown scorch to 10–15 m above ground (Minnich et al.). Basal crown height is typically 10 to 20 m throughout SPM forests, with lowest live boughs retaining fire scars. To explain the predominance of high intensity surface fires, it is hypothesized that the complete combustion of the litter layer is dependent on the energy release of the overstory tree layer. Recurrent upward “fire pruning” of lower canopy creates a raised tree layer detached from surface fuels. In early postfire successions, littercast supports mostly microburns with intensities insufficient even to burn shrubs. In later successions fire hazard increases gradually as the crown base “lowers” with the build up of first-generation conifer recruits combined with the development of the shrub layer.

High intensities are consistent with the findings of Stephens and Finney (2002) that mixed-conifer forests can survive fires that produce crown scorch as high as 45% to 90%. The removal of lower canopy reduces transpiration demand, thereby increasing photosynthate production in the upper canopy. Sapling and polesize densities increase with time since fire (see Fig. 18.7). One stand last burned >75 years ago had densities of 410 stems ha⁻¹, comparable to densified forests of SCA. They hypothesize that open forests are maintained by intense selective elimination of sapling and polesize trees from subcanopy fires, with few midsize trees incrementally joining the canopy layer between fire sequences, producing mixed-aged overstory.

The rate of entry into the overstory class is balanced by low mortality rates in the overstory class. The density of standing dead trees and logs indicate intrafire mortality rates in the canopy layer of one to five trees per hectare. Periodic burning maintains species dbh class composition in a steady-state population of mixed-age overstory trees, where few understory trees survive burning to attain canopy dominance and express reproductive fitness. In effect, mature trees represent a few remnants from cohorts scaling in hundreds or thousands of individuals. Discrete age mosaics from stand-replacement burns in the canopy layer are rare.

In an FSD study of SSPM, Stephens et al. (2003) estimated that fire intervals are 25 years, with fires occurring fre-

quently to 1790, then abruptly declining to 50-year intervals thereafter. Increased fire-rotation intervals were attributed to the removal of flammable herbaceous cover by livestock introduced to the region by Spanish missionaries. The position of scars on annual growth rings occurred primarily in early wood, similar to that in Arizona, that is, before the arrival of the North American monsoon in early July. Studies northward through California show ever-later fires in the ring growth cycle, that is, late wood (summer–fall) in SCA (Everett 2003) and southern Sierra Nevada (Stephens and Finney 2002), and dormant wood (fall) in northern California (Beatty and Taylor 2001). However, annual ring cycles do not represent a calendar due to interannual and geographic variation in growth rates and phenology. Summer ambient temperatures between 850 and 700 mb (1,500–3,000 m elevation) along the Pacific Coast are isoclinal, whereas the elevational zonation of mixed-conifer forests is inversely related to latitude (1,000–1,500 m in northern California to 2,000–2,500 m in BCA). As a result, the growth flushes occur earlier at high temperatures in northern California than in mild temperatures in BCA. Hence, dormancy-latewood scars in the north could be simultaneous with early wood scars in the south.

Stand-densification and fuel ladders have led to extensive stand-replacement burns in SCA, similar to that in the Sierra Nevada (Weatherspoon, Husari, and Van Wagtenonk 1992; McKelvey and Johnston, 1992; SNEP 1996). In SGM and SBM, >30% of forests within fire perimeters have sustained stand-replacement burns, or an order of magnitude greater than in BCA (Minnich 1999) where stand-replacement burns are rare in open forests on gentle terrain, but occur locally on slopes with understory shrub cover that promotes a passive crown fire.

Postfire succession following surface burns was characterized by a slight increase in cover of shrub species and establishment of forest tree seedlings, especially ponderosa and Jeffrey pines (McBride and Laven 1999). In stand-replacement fires, postfire succession is dominated by a shrub phase of species establishing from seedbanks (*Ceanothus integerrimus*, *C. palmeri*, *C. cordulatus*, *Arctostaphylos patula*) or recruit continuously from seed cached by fauna (*Rhamnus californica*, *Arctostaphylos pringlei*, *A. pungens*). *Rhamnus californica* and *Ceanothus cordulatus* resprout and *Chrysolepis sempervirens* establishes new stems from rhizomatous roots. Canyon live oak and black oak respond by epicormic sprouting after surface fires, and basal sprouting after severe burns (Plumb 1979). Black oak recruitment and resprouting promote dense thickets in forest openings (cf. Kauffman and Martin 1990, 1991). Stand-replacement burns as early as 1919 and 1922 have persisted as canyon live oak and black oak woodlands (Albright 1998). On leeward slopes *Cercocarpus ledifolius*, a nonsprouter, is replaced by *Chrysothamnus nauseosus* and *Artemisia tridentata*, both species establishing from seed dispersed by wind. *C. ledifolius* recruitment gradually establishes a subcanopy in 30 to 50 years. Conifer recruitment occurs continuously from

seed dispersed by wind or fauna. Studies of long-term conifer succession have not been undertaken.

PATCH MOSAIC FOREST MODEL—SUBALPINE FOREST AND PINYON-JUNIPER WOODLAND

Stand-replacement fires periodically denude pinyon-juniper woodland and subalpine forests, but only at intervals of centuries due to low primary productivity rates (Minnich 1988; Wangler and Minnich 1996; Minnich and Chou 1997; Minnich et al. 2000; see Table 18.1). Stand-replacement burns result in stepwise increases in fire intervals to an order of centuries because the removal of the tree layer discourages short-term fire recurrences. Postfire shrub successions yield low fuel accumulation rates compared to the chaparral on coastal slopes. Even partly burned trees perish because the thin bark permits fatal cambium damage. Fires leave discrete patch structures that fade after ca. 100 years when trees develop mature stature and subcontinuous canopy closure. Stand-replacement fires eliminate carryover biomass that potentially contribute to short-interval fires, and low annual precipitation limits fuel buildup rates in postfire shrub successions compared to coastal chaparral.

Using FSD analysis, Sheppard and Lassoie (1998) found that fires in lodgepole-limber pine forest on Mt. San Jacinto were single tree events. Ancient limber pine forests at this site, Mt. Baden-Powell (Thorne 1988) and Mt. San Gorgonio, have robust twisted boles and bark striping reminiscent of bristlecone pines (*Pinus longaeva*) in the Great Basin ranges due largely to single tree burns. Lightning detection densities predict that virtually every tree is struck by lightning by the time it reaches 1,000 years age. Aerial photographs in 1938 record linear treeless gaps in dense timberland chaparral on south-facing slopes, the gaps apparently an outcome of terrain-channeled fire runs (Minnich 1988). Dense forests on north-facing slopes exhibit discrete even-aged patches from stand-replacement fires that collectively account for 10% of forests. It is unknown whether presuppression burns were crown fires or surface fires causing fatal cambium injury. Lodgepole pine forests undergo variable fire patterns from low intensity ground fires to canopy fires in extreme weather (Kilgore and Briggs 1972; Kilgore 1981; Parker 1986; Agee 1993).

The trend for stand-replacement fires in pinyon-juniper of SBM and SJZ (Wangler and Minnich; Minnich and Chou 1997; Minnich et al. 2000) supports fire-regime studies in dense forests of the Southwest (Erdman 1970; Koniak 1985; Floyd, Romme, and Hanna 2000). Fire sequences show evidence of nonrandom patch turnover as cumulative fuel buildup with gradual densification of canopy appears to be more significant in fire occurrence than short-term fluctuation in fuels due to climatic variability.

Stand-replacement burns in subalpine forests are replaced by timberland chaparral of *Ceanothus cordulatus*, *Arctostaphylos patula*, and *Chrysolepis sempervirens* (Minnich 1978). Lodgepole pine recruitment reaches preburn densities in ca. 20 years, the trees establishing from wind-dis-



FIGURE 18.9 A nineteenth-century stand-replacement fire in subalpine forest on Charleton Peak near Mount San Gorgonio, in 1885. Photograph courtesy of the Smiley Library, Redlands, CA.

persed seed from unburned stands. Forest gaps recorded in photographs taken a century ago (Fig. 18.9) now host young trees of mature stature (Minnich 1988). Both lodgepole and limber pine are shade intolerant, limiting recruitment in stands with canopy closure. Limber pine has thicker bark and is more tolerant of surface fires than lodgepole pine, possibly explaining its greater longevity in harsh habitats.

Early pinyon-juniper successions are dominated by a shrub layer of species establishing by long-range seed dispersal (*Artemisia tridentata*, *Chrysothamnus* spp.) and soil seedbanks (*Ceanothus greggii*, *Fremontodendron californicum*), as well as from resprouting (*Purshia tridentata*, *Quercus john-tuckeri*, canyon live oak; Wangler and Minnich 1996). Although pinyon seed and juniper berries are widely dispersed by birds and mammals (Van der Wall and Balda 1977; Van der Wall 1997), recruitment appears to be delayed 20 to 30 years until the establishment of the shrub layer which acts as nurse plants that protect seedlings from high soil temperatures, soil heaving, and predation by rodents (Wangler and Minnich; cf. Chambers 2001). The first pinyon recruits establish within shrub canopies, often within 2 cm of root axes. The development tree canopy reduces freeze-thaw processes after ca. 75 years, followed by spatially random recruitment throughout burns. The development of tree canopy after 100 to 150 years is accompanied by a decline in the shrub layer. Mature stands are mixed-aged due to continuous recruitment typical of white pines, with densities of 150 to 250 stems ha⁻¹.

In semiarid woodlands of Joshua Tree National Park (Minnich 2003), conifers perish largely from flames lines generated by a understory shrub layer. Woodlands are replaced by recruitment of *Hymenoclea salsola*, *Salazaria mexicana*, *Viguiera parishii*, *Eriogonum fasciculatum*, and *Eri-cameria cooperi*. Obligate sprouters (*Lycium* spp., *Ephedra* spp.) persist at low densities. Fires correlate with wet episodes of climate due to abundant fuels provided by herbaceous bunch grasses (*Pleuraphis rigida*, *Achnatherum*

speciosa) and shrubs, as well as annual wildflowers, which apparently increase canopy in wet episodes and die back in drought. The role of invasive annuals *Bromus rubens* and *B. tectorum* that have proliferated the past three decades is unclear. In the 6,000-ha fire complex of 1999, bromes had little effect in old-growth woodlands that burned at comparable intensities as chaparral. In reburn zones, bromes supported only creeping, low-intensity flame lines that left shrubs unburned or scorched; that is, postfire successions were not breached. Mediterranean exotics do not represent novel herbaceous fuel hazard in deserts.

Suppression appears to have little impact in pinyon-juniper and subalpine forests because fire-free periods are longer than the suppression era. Increases in fire intensity may not change fire mortality rates because stand-replacement fires characterize these ecosystems. Forest densities and diameter frequency distributions of pinyon-juniper woodlands have not significantly changed since the VTM survey (Wangler and Minnich 1996).

Fire and Biogeography of Southern California Conifer Forests

The “real world” of forest fires, of course, does not play out in discrete fire regimes in lock step with forest distributions. Instead, it is best to view fire relationships as gradients in properties in a continuum of environmental change that exert intense selective pressure on the species composition and spatial pattern on the landscape. In southern California, forests distribute along a corresponding “pecking order” of resilience. High-resilience assemblages (i.e., species with life traits that include rapid establishment, short generation times, and short life spans) grow in productive chaparral on windward slopes, recycled by frequent severe fires, and grow on steep, undissected concave slopes subject to intense fire behavior. Low-resilience forests (slow recolonization, long generation times, long-lived) survive surface fires in low chaparral fuel loads in mesic productive environments on gentle surfaces or steep convex canyons, or occur on unproductive leeward slopes from middle elevations to the highest summits.

Successive fires, of course, leave a unique overprint of range expansions and contractions resulting from stochastic variability of fire regime properties. It should be expected that forest distributions and stand properties over multiple fire cycles would oscillate around steady-state distributions as a function of random fire occurrence with weather, ignitions, and patch mosaic status. However, we can only dream of century-scale time-series empirical data necessary to assess forest equilibria. The following statements—based on space-for-time substitutions of disturbance and succession patterns—can be treated as hypotheses for future research.

The limit of mixed-conifer forest on moist windward slopes is a conspicuous ecotone in which tree cover with sparse chaparral understory is replaced by dense cover of chaparral (Minnich 2001). Intense chaparral fire cycles selec-

tively eliminate mixed conifers in favor of treeless zones, or colonies of serotinous conifers with vigorous establishment traits. Competitive exclusion processes are suggested by the observation that mixed-conifer forest grows as low as 1,300 m in shrub free basins, and are absent from steep, undissected chaparral slopes to 2,400 m, across large gradients in climate. Trees must also compete with chaparral for soil water. Intense fires selectively eliminate mixed conifers colonizing bigcone Douglas fir forest, which persist by resprouting (Minnich 1988). Above 2,000 m, mixed conifers coexist in open montane chaparral and arboreal canyon live oak because ground fires leave the tree layer. Intense fires convert canyon live oak into shrublands, eliminate mixed conifers and selectively favor Coulter pine over bigcone Douglas fir. This hypothesis is consistent with the distribution of bigcone Douglas fir in fire-resistant canyons and Coulter pine on concave slopes and ridgelines. The sprouting habit of bigcone Douglas fir may be a “last resort” life trait that maintains small groves in a hostile regime of frequent intense chaparral fires below ca. 1,200 m.

Low-intensity fires select for downslope expansion of mixed-conifer forest, the permanent tree canopy selectively displacing shade-intolerant chaparral and serotinous conifers. Bigcone Douglas fir stands expand into arboreal cover of canyon live oak, with selective elimination of serotinous conifers. It appears that bigcone Douglas fir does not invade mixed-conifer forests except on rapidly eroding slopes vital to its establishment. Suppression policies have already selected for the displacement on ponderosa and Jeffrey pine by shade-tolerant white fir and incense cedar. The scarcity of Coulter pine—oak woodlands suggests that this assemblage may be unstable over long time scales because the pine is short-lived and shade intolerant. A succession of nonfatal surface fires many encourage its replacement by long-lived mixed-conifer forests. Emerging stand replacement fire cycles may reverse this trend by selecting for replacement of mixed conifers by short-lived serotinous conifers.

The mixed-conifer/subalpine forest ecotone coincides with a discontinuous shift from frequent surface burns to infrequent stand-replacement burns. The permanent canopy of mixed-conifer forest discourages the establishment of lodgepole pine, which is selectively eliminated by recurrent surface fires fueled by cumulative litter buildup. High-intensity fires select for the downslope displacement of subalpine forest into mixed-conifer forest. Mineral seedbed conditions favor lodgepole pine establishment, resembling successions in the Rocky Mountain subalpine forest. The destruction of the tree layer increases the chance for long fire intervals due sparse litter in mature subalpine forests. A discontinuity in fire intervals also occurs at the mixed-conifer forest-pinyon-juniper woodland ecotone (Minnich and Chou 1997; Minnich et al. 2000). Recurrent surface fires sustained by continuous litter-fall from surviving tree canopy selectively eliminate pinyons in mixed-conifer forest. The removal of canopy in pinyon-juniper woodland precludes short interval fires. Drought-tolerant mixed-conifers, especially Jeffrey pine, readily establish

in pinyon-juniper woodlands. However, mixed-conifers are preferentially extirpated in extreme drought (see below).

The distribution of pinyon-juniper woodlands overlap with extensive areas of open desert chaparral assemblages but rarely extend into contiguous chaparral on coastal slopes. Desert chaparral comprises long-lived species including *Quercus turbinella*, *Q. cornelius-mulleri*, *Arctostaphylos glauca*, *A. glandulosa*, *Cercocarpus betuloides*, *Rhus ovata*, *Prunus ilicifolia*, and *Rhamnus crocea*. The longevity of shrubs diminishes the importance of seed reservoirs in stand maintenance. Although members of *Ceanothus* subg. *Cerastes* and *Fremontodendron californicum* establish local thickets in early postfire succession, fire intervals are longer than the life span of these shrubs. Hence, they do not contribute as fuels in fire sequences. The low productivity and open-stand structure of desert chaparral assure long fire intervals compatible with pinyon-juniper colonization. Short fire intervals select against pinyon-juniper, enhance recruitment of obligate seeding shrubs in *Adenostoma* and *Ceanothus*, and increase chaparral cover. Pinyon-juniper is most extensive on leeward slopes >1,500 m, with cool climate, low annual precipitation and productivity. It is absent from low passes or mountain crests with high lee slope precipitation and productivity.

Establishing a Presuppression Baseline

A fundamental goal in fire ecology is to establish a presuppression baseline to assess how natural fire is integrated into forest systems and how suppression has changed them. There is evidence that several forest types have been little affected by twentieth-century fire control. In subalpine forest and pinyon-juniper woodland, fire-free periods are far longer than the suppression era. The earliest aerial photographs record virtually the same forest of stems as at present and suggest limited population turnover, even as a scale of a century. They also give a clear record of presuppression stand-replacement burns in long-lived pinyon-juniper and subalpine forests, but provide only one generation of fires. In the chaparral belt, cohort regeneration after stand-replacing fires appears to characterize closed-cone conifer forest before and during suppression (Minnich 1988). Early aerial photographs reveal that presuppression patch structure in chaparral and closed-cone conifer forest was already emplaced by suppression era burns. However, enormous change has occurred in mixed-conifer forest. Dense "dog-hair" forests are now pervasive in southern California. Unfortunately, the fire process shaping dispersed forest structure of course was not rigorously documented at the time.

Ideally, the reconstruction of baseline structure and dynamics of mixed-conifer forest requires spatially explicit data over long time scales. Spatially explicit data include fire perimeter histories, but the data begin in 1910 with the establishment of the National Forests, i.e., records began only when suppression was initiated (Minnich 1988). Perimeters accurately depict the removal of biomass in stand-replacing events, but they provide no information on

fire severity and tree mortality in surface fires. Time-series aerial photographs have the advantage of providing raw records of forest status over large regions, including the limits of burns, removal and survival of canopy, population dynamics, and intraburn successions. Mixed-conifer forests were already in incipient densification (Minnich et al. 1995). In BCA, time-series photographs record uncontrolled fire regimes only to the early twentieth century.

Studies have utilized space for time substitutions, such as synoptic analyses of time-series aerial photographs. This approach assumes that spatial and temporal variation are equivalent, but this assumption cannot account for transient effects such as shifting climate (Pickett 1985). The most widely used method for mixed-conifer forest is fire scar dendrochronology (FSD), which has the primary advantage of capturing fire records over many centuries, but it is a site-specific methodology limited to forest systems with surface fire regimes. Likewise, time for space substitutions, such as FSD studies, assume the same equivalency but cannot account for spatial effects (see also Baker and Ehle 2001).

A centerpiece of the FSD method is the estimation of mean fire return intervals (FRI) from ring counts between successive fire scars on tree bole catfaces. Studies have sampled scar records of single trees and multiple tree samples as small aggregates of point samples (Agee 1993; Taylor 2000; Grissino-Mayer 2001; Morgan et al. 2001). Recently FSD methods employed spatial sampling protocols to reconstruct fire histories at scales of thousands of ha (e.g., Brown, Kaufmann, and Shepperd 1999).

A key issue in FRI reconstructions is how fire scars represent other fire regime properties in broad spatial scales. The assumption that FRIs can be substituted for spatial pattern must take into account scarring efficiency, relationships between fire size and intensity, and how scarring correlates with fire size frequency distributions. How does scar data extrapolate to the landscape when fire size frequency distributions are skewed?

Time-for-space substitutions are valid only if a sample represents a discrete event. But fire scars represent multiple events of unknown distribution except specifically to the sample sites, and spatial extrapolation is invalid because the skewed fire size frequency distribution does not permit it. Single tree samples are considered to conservatively underestimate past fire occurrence for a given point on the assumption that many fires do not scar trees, i.e., intervals are shorter than measured (Skinner and Chang 1996). Alternatively, trees may scar easily once they form catfaces because heartwood ignites more readily than bark. An important step in the interpretation of FSD would be inductive experimentation. There are no studies in which scarring efficiency has not been independently tested against field burn experiments, where fire extent and severity are known.

Fire intensity has not been directly evaluated from fire scars. Hence scarring efficiency cannot be directly estimated using FSD methods. Moreover, intensity estimates from stand age frequency distributions are not possible because forests

represent survivorship; that is, there is no direct evidence of fire processes that selectively remove canopy. However, stand-replacement burns can be inferred from the spatial pattern of the oldest trees ("age caps"; e.g., Brown, Kaufmann, and Shepperd 1999). Fire spread models predict that small fires have low intensity because energy release is below thresholds required to maintain flame lines (Rothermel 1972; Scott and Burgan 2005). Above this threshold there is uncertainty as to whether flame front intensities continue to increase with fire size (fractal; Minnich et al. 2000). Fire size cannot be estimated from FSD methods because studies are site specific. Spatially based sampling studies are smaller than the fires that account for most regional burn area (e.g., Kilgore and Taylor 1979; Beaty and Taylor 2001). Area estimates from stand structure (e.g., Kilgore and Taylor) cannot differentiate actual burn size and local fire behavior within burns. A tree may survive because it lies beyond the limit of a burn, or because of a shift in intensity within a burn.

If fire intensity was proportional to fire size, the combination of long-tailed fire size frequency distributions (Minnich and Chou 1997; Malamud et al. 1998) and low scarring efficiency would yield a record of intense major burns exclusively. Alternatively, with perfect scarring, fire scars would reflect both mass burns and local microburns that collectively add to small fire area; that is, any randomly selected FSD sampling site may record the full range of fire sizes and intensities. In such case, *regional burning rates may not covary with scarring rates*. Large transient fluctuations may arise from the interannual variation in lightning discharge rates, anthropogenic starts, and fuel moisture, rather than from the regional rate of burning at the landscape scale.

SIERRA SAN PEDRO MARTIR: GRAZING, CLIMATE CHANGE, OR MICROBURNS?

The SSPM is a rare example where fire-interval estimates of FSD studies can be empirically tested against a spatially explicit fire history from aerial photographs. Estimates of fire intervals from perimeters (Minnich et al. 2000) are twice that estimated from FSD methods (Stephens, Skinner, and Gill 2003). Minnich et al. found that large fires are intense and self-organizing. Forests outside perimeters show fixed spatial arrangement of trees and shrubs over scales of decades; that is, no fires removed woody biomass. Microburns are abundant, but leave only ash beds of consumed needle litter, with little effect on forests. One important unanswered question is whether microburns leave scars on tree bole catfaces.

The interpretation of site-specific FRIs to the landscape assumes covariance between scarring and landscape burning rates. However, scarring may also reflect transient variation in local ignition rates. For example, to explain the decline in scarring rates after 1790, Stephens (2003) proposes that the introduction of cattle reduced dry herbaceous cover, thereby increasing fire intervals (a landscape interpretation). This view requires that herbaceous cover contributed significant

fuel. However, annual and perennial forbs form <10% cover and remain green in summer. Exclosures show no significant effect of cattle grazing on herbaceous cover (Minnich et al. 1997). Alternatively, the decrease in scarring may have been caused by the decimation and dislocation of Kiliwa Indians with the establishment Mission San Pedro Martir in 1794, thereby eliminating a source of abandoned campfires (a site-based interpretation). Stephens asserts that there is no historical record for fire use in the SSPM, but indigenous cultures there are poorly studied. Native Americans doubtless set fires for cooking and warmth, and for ceremonial rituals (Kroeber and Lowie 1929). For example, the extraordinary 2- to 4-year fire intervals in Sierra Nevada *Sequoiadendron* groves (Swetnam 1993) is very likely an outcome of Native American cooking fires.

In summary, FSD methods provide little direct evidence of fire regime properties other than FRIs. Hence, the deduction of fire regime properties (intensity, selective removal of biomass, population dynamics) is dependent on the accuracy of FRI estimates at broad spatial scales. The grass extirpation hypothesis is circular because an assumption (former herbaceous cover) is used to affirm a conclusion. No paleobotanical studies have been undertaken in the area. Similarly, in the southwestern United States the assertion that variable scarring rates correlates with interannual precipitation variability due to the El Niño cycle (Swetnam and Betancourt 1990) could also be reasonably explained by variable establishment of microburns due to changing fuel moisture of the litter layer rather than changes in landscape scale burning. The hypothesis that fires decreased because of reduced El Niño frequency and herbaceous cover between 1790 and 1840 (e.g., Stephens, Skinner, and Gill 2003) could also be explained by the decimation of Native Americans (Cook 1937, 1940, 1943). Given poor spatial sampling protocols to present, the effects of microburns from drought, and Native American burning practices cannot be differentiated.

The inconsistencies in FSD chronologies and spatially explicit reconstructions of fire regimes from time-series aerial photography leads to a number of important questions: What is the long-term ecological role of small fires across landscapes, given that lightning strike rates are 1–3 strikes $\text{ha}^{-1} \text{yr}^{-1}$ and any hectare of forest contains several stems with bark stripped off by lightning? As first discussed in Minnich et al. (2000), do microburns leave scars in cat faces, thereby influencing fire-scar dendrochronologies, or is scarring exclusively an artifact of landscape-scale fires? At present, there is a lack of synoptic studies that incorporate plot data and spatial fire records. Indeed, to date there is not one FSD study where fire scars are correlated with independent spatially explicit evidence.

Perhaps most significant is whether FRIs underestimate spatial fire intervals because the method cannot differentiate mass burns from a cloud of microburns with little collective impact on forests (Minnich et al. 2000; Baker and Ehre 2001). Even at scales of a few hectares, fire scars may be created both by mass burns and microburns within a

TABLE 18.2
Major Forest Pests in Southern California

Tree Species/Pest Species	Ponderosa					Pinyon Pine
	Coulter Pine	Pine	Jeffrey Pine	Sugar Pine	White Fir	
Western pine beetle (<i>Dendroctonus brevicornis</i>)	X	X	–	–	–	–
Mountain pine beetle (<i>Dendroctonus ponderosae</i>)	X	(X)	–	X	–	(X)
Jeffrey pine beetle (<i>Dendroctonus jeffreyi</i>)	–	–	X	–	–	–
Red turpentine beetle (<i>Dendroctonus valens</i>)	x	x	x	x	–	x
Pine engraver beetles (<i>Ips</i> spp.)	x	x	x	x	–	–
Pinyon pine engraver (<i>Ips confusus</i>)	–	–	–	–	–	–
California flatheaded borer (<i>Melanophyla californica</i>)	x	X	X	x	–	–
Fir engraver (<i>Scolytus ventralis</i>)	–	–	–	–	x	–
Flatheaded fir borer (<i>Melanophyla drummondi</i>)	x	x	–	–	X	–
Dwarf mistletoe (<i>Arceuthobium</i> spp.)	X	X	X	X	–	X
Leafy mistletoe (<i>Phoradendron pauciflorum</i>)	–	–	–	–	x	–
Annosus root disease (<i>Heterobasidium annosum</i>)	x	x	x	x	x	–
Blackstain root disease (<i>Leptographium wagneri</i>)	–	–	–	–	–	X

NOTE: X = high ability to kill vigorously growing trees, x = less mortality, (X or x) only an occasional host. Note that Jeffrey pine bark beetle does not occur in the San Jacinto Mountains nor in the peninsular range.

single mass burn fire cycle. Other fire regime parameters deduced from FSD studies are not constrained. Studies that correlate fire occurrence with climatic variability in annual time scales cannot be applied to ecosystems where fires occur in response to cumulative fuel buildup over long time scales. Time-series climate correlations with fire should be scaled as a running average of the process tied to the cumulative build-up of vegetation architecture and fuels, rather than annual time-series statistics (Lovell, Mandondo, and Moriarty. 2002). Fire models based exclusively on fire-interval estimates, a number, nothing else has empirical basis. Any error in fire-interval estimates affects all other fire-regime properties reconstructed by deduction. The entire model can fall like a house of cards. The bottom line is that the empirical basis of FSD methods is poor at best. The human mind is capable of extraordinary concepts, but needs a “reality check” from nature, the best teacher, which will always provide the unexpected.

Disturbance from Insects, Pathogens, and Air Pollutants

Native insect herbivores and pathogens, including bark beetles, mistletoes, and root diseases, perform an important

function in conifer forests including killing decadent trees and nutrient cycling (Pronos et al. 1999). Pine beetles are either host specific or generalists (Table 18.2). Among those that kill trees in southern California, *Dendroctonus jeffreyi* breeds almost exclusively in Jeffrey pine, *Dendroctonus pseudotsugae* is exclusive to Douglas firs, *Dendroctonus brevicornis* attacks ponderosa and Coulter pine, and *Scolytus ventralis* attacks white fir. *Dendroctonus ponderosae* breeds in many pine species (Wood et al. 2003).

Beetles and engravers are opportunists that attack trees in a weakened or dying state due to root erosion, snow breakage, advanced age, lightning strikes, drought, and other factors that compromise tree vigor. With only a few rare exceptions, either the host tree is killed by the colonizing bark beetles or the host resistance of the tree kills the attacking adults. To kill a tree, large numbers must successfully colonize in a relatively short period of time (Paine, Stephen, and Taha 1984; Paine, Raffa, and Harrington 1997). Adults emerge from the larval host tree and search for susceptible hosts. Healthy pines and firs respond by exuding pitch, which either “pitches out” the adults or blocks its progress. In weak trees with reduced resin pressure, the adults are able to initiate colonization and produce aggregation pheromones that attract other colonizing adults. Pheromone production ceases when the host tree

ceases resin flow (Raffa and Berryman 1983) signaling the death of the tree. Eggs are laid in the inner bark and the larvae excavate galleries in directions generally perpendicular to the adult galleries. Pupation occurs either in the inner bark or in the outer bark, depending on the species of beetle. Western pine beetle can produce up to 4 generations in a year in southern California due to the mild thermoclimate permitting the populations to expand rapidly when there is an abundance of susceptible host material available for colonization.

There is a threshold of attacking beetles required to kill trees, and that threshold is a function of the vigor of the host; a smaller number of beetles is necessary to kill stressed trees than vigorously growing trees (Paine, Stephen, and Taha 1984). Under normal conditions when background populations of beetles are low, tree mortality is usually at low levels when stands have a few weak trees. However, under drought conditions when there are large numbers of highly stressed trees, a relatively small population of beetles can kill many trees. As a result, the population of beetles will increase in those drought stressed trees, and many more trees will be at high risk because more vigorous trees can be killed by the larger number of adults that respond to the aggregation pheromones (Paine, Stephen, and Taha).

Root diseases and dwarf mistletoes account for most of pathogen-caused growth loss and tree mortality in the western United States (Pronos, Merrill, and Dahlsten. 1999). Dwarf mistletoes (*Arceuthobium* spp.) place more stress on host trees than true mistletoes. Lacking chlorophyll, dwarf mistletoes reduce the amount of water and photosynthates available for tree survival and growth. True mistletoes take water from their host and produce their own photosynthates. Western dwarf mistletoe (*Arceuthobium campylopodum*) attacks Coulter, Jeffrey, and ponderosa pine. A true mistletoe (*Phoradendron pauciflorum*) attacks white fir. Annosus root disease (*Heterobasidium annosum*), black-stain root disease (*Leptographium wagneri*), and armillaria root diseases (*Armillaria* spp.) are somewhat host specific and do not generally kill trees directly. They do predispose trees to subsequent attack by bark beetles. In annosus root disease, microscopic airborne spores land on recently cut stump surfaces or bole wounds, grow into root system, reducing water absorption (annosus root rot). Annosus may persist and spread among root systems for years. Mistletoes also tend to weaken trees reducing survival due to beetle infestations. Black stain root disease fungus, which attacks primarily single-leaf pinyon pine, colonizes the water-conducting vascular tissues and interferes with water movement, but does not destroy living tissues as with annosus.

Sugar pine forests in northern and central California are extremely susceptible to the introduced white pine blister rust (*Cronartium ribicola*), but the pathogen has yet to spread into southern California (Kliejunas 1985). Bishop pine has recently sustained heavy mortality from needle blight caused by *Dothistroma septospora* (Ades et al. 1992).

The exposure of coniferous trees to oxidant air pollution in SCA results in lower photosynthetic rates and production of carbohydrates, as well as changes in plant priorities in

resource acquisition, allocation, and partitioning (Gulke 2003). Nitrogen deposition also modifies the effects the oxidant exposure. Although the physiological response of trees to oxidant pollution is well documented, the long-term impact of air pollution is complex in relation to other factors such as stand-densification, drought, and insect attack. Summaries of air pollution impacts in forests of SCA and the Sierra Nevada are given in McBride and Miller (1999) and Bytnerowicz et al. (2003).

The amount of air pollution transported to SCA forests depends on the distribution of pollution sources—primarily oxidant and nitrate from automobiles and power-generation plants as well as ammonia and nitrous oxides from agricultural areas—and transport due to onshore flows and anabatic winds during the summer pollution season (Edinger et al. 1972; Lu and Turco 1995; Padgett et al. 1999). The plume of highest oxidant and nitrate concentration moves from Los Angeles to SGM and SBM. The Orange-Riverside County plume moves to the eastern SBM and northern SJM, whereas the San Diego County plume moves into the Cuyamaca and Laguna Mountains and southward into far northern SJZ of BCA. Lacking upwind sources, low pollution concentrations occur in the mountains of Ventura and Santa Barbara Counties, the southern SJM, and Palomar and Hot Springs Mountains. The air is still pristine south of ca. lat. 32° in BCA.

Air pollution is stably stratified in the marine layer during transport across the SCA coastal plains with onshore flows, but anabatic winds move pollutants upslope through the marine inversion along coastal front of the mountains. Pollutants in anabatic flows also stratify into the overlying inversion layer where they have longer residence times than in the marine layer (Edinger et al. 1972). The highest forest pollution levels have been recorded in the western SBM where trees grow as low as 1,300 m and are exposed day and night to oxidant transported by anabatic winds and flows in the inversion layer (Watson et al. 1999). The marine inversion normally dissipates on the desert side of the mountains, with oxidant and nitrates mixing and diluting into upper air layers. Hence, pollution levels normally decrease from windward to leeward slopes, although ozone transports more readily than nitrogen (Bytnerowicz et al. 1999). Because oxidant exposure is also dependent on wind speed (advection), trees in exposed ridges and summits sustain greater flux of ambient pollution than in sheltered canyons and basins.

The physiological impact of ozone is the reduction of net photosynthesis, stomatal conductance, production of carbohydrates, and nutritional content of tissues (McBride and Miller 1999; Gulke 2003). Foliage develops chlorotic mottle on older needles of each whorl, which accelerates necrosis leaf senescence. Crown injury includes the reduction of needle whorls, needle length, and percentage of live crown. Reduced photosynthetic capacity limits the carbohydrates available for the growth of the tree. Ozone injury assessments show that ponderosa and Jeffrey pine are most sensitive;

bigcone Douglas fir and Coulter pine are moderately sensitive, whereas lodgepole pine and sugar pine are moderately tolerant. White fir and incense cedar are visually the least affected (Miller et al. 1983). A model simulation of white fir response to elevated ozone and drought stress reduced branch and bole growth similar to field responses found in the SJM (moderate pollution) and SSPM (Retzlaff et al. 2000). Time-series data show that ring width and cross-sectional growth are reduced where ponderosa pine, Jeffrey pine, and bigcone Douglas fir are exposed to chronic levels of oxidant air pollution (Arbaugh, Peterson, and Miller 1999).

Oxidant exposure alters within plant priorities for resources as less carbon is allocated to roots and less foliar biomass is retained (Gulke 2003). Compared to herbs, conifers have lower stomatal conductance, and lower O₃ uptake. However, the total O₃ exposure and uptake is larger over the lifetime of a leaf because foliage is longer lived and active or longer period of the year than herbs. Cumulative O₃ exposure, high radiation, and drying of the upper soil horizons (insufficient uptake of N to replenish damaged pigments) may all contribute to chlorotic mottle. The period of the highest gas exchange rates and presumably the greatest air pollutant uptake takes place during the growth flush in early summer (Gulke et al. 2002). Stomatal conductance decreases with increasing pollution levels, with normal stomatal function being lost at the most polluted sites. Environmental factors that decrease stomatal conductance also decrease ozone uptake. The seasonal course of stomatal conductance, as regulated by water availability, is a key process controlling injury development each summer. Ozone injury is low in early summer, when fine root mass is wet. Chlorotic mottle increases by midsummer when drying trees rely on deep roots for water (Hubbert et al. 2001a). If significant rains occur in autumn, fine roots and mycorrhizae grow in the near surface soils, and chlorotic mottle can significantly decrease. Polesize and large trees can mitigate reductions in carbon acquisition with carbon assimilation in unpolluted days in winter.

Oxidant pollution levels peaked in the 1970s and have decreased since that time due to air pollution control measures. The crown condition of pines improved slightly in the 1980s but no significant change has occurred in the 1990s (Miller and Rechel 1999). The effect of bark beetles from pollution injury are smaller than nonpolluted trees due to reduced cambial thickness; that is, reduced growth also reduces food reserves for bark beetles. However, it takes smaller number of beetles to kill weakened trees (Pronos et al. 2001).

Ambient nitrogen deposition, mostly dryfall (Byrtneowicz et al. 1999), decreases carbon allocation to roots (Gulke, Andersen, and Hogsett 2001), further exacerbating the effects of oxidant exposure to roots (Gulke et al. 1998). Ambient nitrogen deposition accelerates needle loss by increasing foliar nitrogen content, producing redundant nitrogen with too high carbon cost for maintenance (Gulke 2003). Drought stress reduces both the number of

needle age classes and needles within each age class, which acts synergistically with O₃ exposure to promote premature senescence of foliage. This can occur as excess nitrogen saturation (Fenn, Poth, and Johnson 1996). Increased nitrogen availability also exacerbates O₃ exposure effects on foliage turnover: fewer needle age classes are retained (Gower et al. 1993). Nitrogen deposition counteracts the effect of oxidant exposure on photosynthesis by increasing nitrogen available for photosynthetic pigments and enzymes, increasing stomatal conductance, but deleteriously resulting in increased O₃ uptake (Gulke 2003). Nitrogen deposition may also mitigate the degree of foliar injury from oxidant pollution by increasing nitrogen available for reparation of photosynthetic pigments.

Ozone induces premature foliar senescence and abscission, and N stimulates the production of foliar biomass, the net result of which is greater litterfall (Arbaugh, Peterson, and Miller 1999; Fenn et al. 2003). Carbon allocation to fine roots is significantly lower with increased pollution (Fenn and Poth 1999). Thus, the combination of drought stress inhibition of aboveground litter decomposer microbes, sustained litter production in trees capable of accessing deep water, greater C allocation above ground, and N stimulation of litter production (reduced decomposition rates) are factors that likely contribute to long-term C storage in above-ground detritus, as well as increasing fuel buildup in stands already at fire risk due to long-term fire suppression (Gulke et al. 1998, 2001; Arbaugh 1999; Gulke and Balduman 1999; Fenn et al. 2003). The greater C storage in above ground woody tissue (Gulke et al. 1998, 2001) and reduction of fine root biomass and carbohydrate allocation belowground increase the risk of conifers to drought stress (Gulke et al. 1998, 2001). Over long time scales, ambient pollution may favor stand composition toward ozone-tolerant and fire-sensitive species like white fir and incense cedar (McBride and Miller 1999). Selection pressures from stand densification will also increase the abundance of these shade-tolerant conifers. In areas of high ambient pollution, multiyear drought can reduce O₃ uptake, but can also reduce carbon and nutrient acquisition, reducing resource allocation to defenses (antioxidants, resins against insect infestation).

Catastrophic Dieback in Record Drought

Drought reduces the photosynthetic capacity of trees and the levels of carbohydrates used for growth and tissue repair. Although the stress incurred by the dry conditions may kill trees directly, the reduction in resin pressure also predisposes these trees to attack by bark beetles and pathogens, and increases fire hazard (McBride and Miller 1999). Tree-ring analysis for last 1,000 year shows that every decade has several years of pronounced reduction in tree growth due apparently to drought (Graumlich 1993). The correlation between beetle attacks and climate can be diffuse because bark beetles may delay or prolong the exact time of tree mortality. However, mortality tends to increase in multiyear

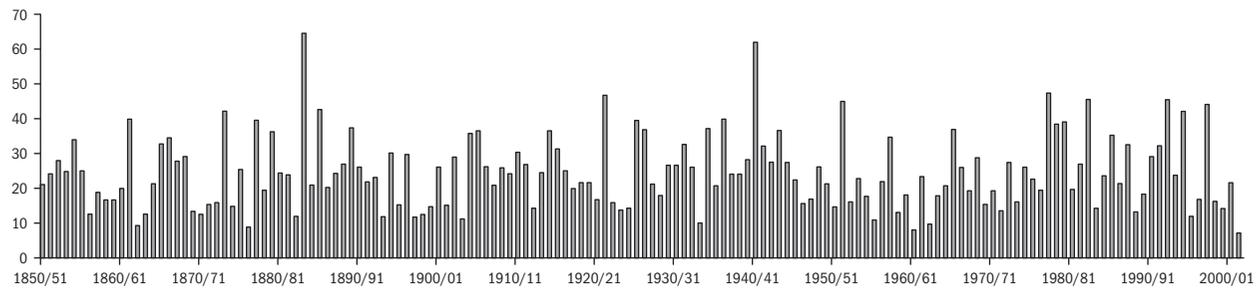


FIGURE 18.10 Annual precipitation (in centimeters) for San Diego during 1850–2002. Notice that the driest year of record (6 cm,) was 2001–2002. Data are from the National Weather Service.

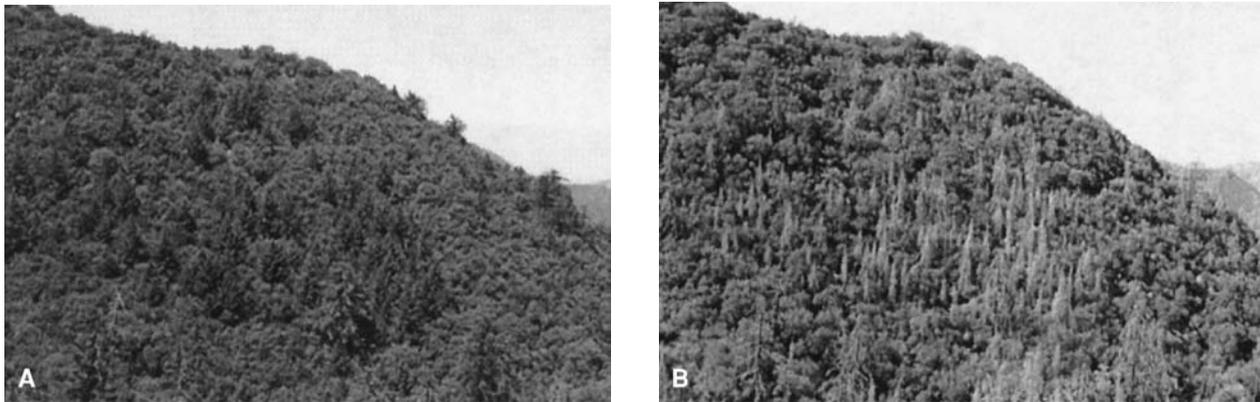


FIGURE 18.11 Whole-stand mortality of bigcone Douglas fir forest at Skinner Creek. (a) 1980; (b) 2003.

droughts (Taylor 1973), particularly in highly resource competitive dense stands, or stands with preexisting damage or stresses (Pronos et al. 1999). Elevated mortality occurred in SCA conifer forests in 1975 to 1977 and 1988 to 1991 (Savage 1994, 1997). Most recently, the 2002 to 2004 conifer dieback is unprecedented.

The winter of 2001 to 2002 was the driest year in SCA since instrumental records began in 1849 (Fig. 18.10). Total precipitation varied from 10 to 25 cm, and 17% to 30% of normal. From SBM to SSPM this record year followed 3 years of subnormal precipitation. By the summer of 2002, conifers and broadleaf trees exhibited failure in leader growth, premature leaf shed, and aborted cones and fruits. Evergreen canyon live oak and chaparral taxa such as *Quercus berberidifolia* and *Cercocarpus betuloides* became virtually deciduous by late summer. Leaf shed and crown dieback was also widespread in *Arctostaphylos* spp., *Ceanothus* spp., and *Adenostoma fasciculatum*; and widespread light mortality occurred among species in *Ceanothus* subg. *Cerastes*. Historically unprecedented conifer mortality took place in 2002 to 2003. Time-series photographs have been taken at ca. 100 localities since the onset of the mortality outbreak in 2002 (Fig. 18.11). Heavy mortality first appeared in Coulter pine by May 2002, and then expanded to incense cedar and Jeffrey pine by early July. Light mortality began in all other

mixed-conifer forest species by late summer. Major insect attack of ponderosa pine developed on the north side of Lake Arrowhead and locally at Idyllwild. Defoliation of bigcone Douglas fir was first observed in September 2002.

In spite of wet ground from normal precipitation in the winter of 2002 to 2003, mortality continued in Jeffrey and Coulter pine until the early summer of 2003, then declined only after trees began uptaking soil water in warm temperatures. Although Coulter pine mortality in 2002 was zonally distributed, mortality in this species the following summer was patchier in association with expanding populations of bark beetles. Mortality virtually ceased in incense cedar. Widespread mortality from bark-beetle attack developed in ponderosa pine by July 2003, especially dense forests at Lake Arrowhead, Idyllwild, and Cuyumaca (see Fig. 18.6 and Fig. 18.11). Drought-compromised trees were apparently unable to rehydrate before terminal attack by bark-beetles. A low frequency of defoliated bigcone Douglas fir stems began resprouting from epicormic buds along the bole and largest branches. In the eastern SBM, populations as large as 100 ha sustained whole-stand mortality.

In 2004, mortality had decreased in nearly all species, after 65% of normal precipitation but several soaking rains the previous winter. Surviving trees had improved growth flushes and resistance to insect predators compared to 2003 due

apparently to resaturation of soils in combination with tree rehydration. There were also fewer surviving trees competing for water. The decline in mortality shows that precipitation departures inclusively are a poor predictor of conifer health status. Subnormal precipitation years resaturate soils because the mean annual precipitation exceeds soil field capacities, with ca. 30% of annual precipitation contributing to runoff (Franco et al. 2002). In 2004, ponderosa pine bark-beetle infestations expanded to more open stands beyond the urban forests of Lake Arrowhead. There was little mortality at Idyllwild. The highest levels of white fir mortality occurred in the summer of 2003 and continued into the winter of 2003 to 2004.

At broad scales, forest mortality is manifested in predictable spatial pattern in complex terrain. Dead trees tend to concentrate on well-drained convex surfaces and south-facing exposures. Rates of survival were greater in deep canyons, north-facing slopes, old erosion surfaces and valley floors subject to soil water convergent flow. Mortality is highest in short-lived closed-cone conifer forests, especially Coulter pine, and lowest in long-lived pinyon-juniper woodland and subalpine forest. This outcome should be expected because long-lived species have a greater probability of experiencing drought as extreme as 2002 than short-lived species. In addition, the longevity of trees translates into greater environmental space from which to obtain resources; that is, stems integrated into the habitat over long time scales have a large proportion of resources are carried over long time scales and buffer them from environmental variability (Grulke 1999, 2003). At the short-lived end of the continuum, Coulter pine sustained the highest mortality among coniferous species in the drought of 1988 to 1991 (as high as 50 ha⁻¹) in SJM, and lower rates among mixed-conifer species (Savage 1994). Coulter pine sustained whole-stand mortality in the order of hundreds of ha, and the order of 1,000 ha in the San Bernardino and Hot Springs Mountains. Apparently, selection for rapid growth results in the production of soft wood that is vulnerable to insect attack and disease. At the long-lived end of the continuum, subalpine forests sustained virtually no impact from the 2002 to 2003 drought. Even in extreme drought of 2001 to 2002, soils were replenished by snowmelt as late as May and cool summer temperatures may have limited drought stress. In pinyon-juniper woodland, light mortality is associated with low AAP and absolute water deficits.

In all forest types, mortality increased with time-since-fire due apparently to increasing leaf area, transpiration demand, and tree stress in successions. The majority of Coulter pine and bigcone Douglas fir perished in watersheds last burned >60 years ago but few trees perished in burns <35 years age. The covariance in the defoliation of bigcone Douglas fir and canyon live oak is evidence that high transpiration demand was a primary factor in the spatial pattern of leaf shed. To date, postdrought re sprouting of bigcone Douglas fir, from epicormic buds along the bole and largest branches, was <10% of stems compared to postfire sprouting of >90% of trees (Minnich 1999).

It appears that carbohydrate reserves are more depleted by the gradual defoliation of canopy than from "instant" defoliation by fires. Fires in surrounding chaparral watersheds also increase available soil water for resprouting bigcone Douglas fir, whereas high water demand persists in old-growth chaparral. Arbaugh, Peterson, and Miller (1999) showed that more than 80% of bigcone Douglas fir have reduced recent growth, with trees with high-ozone exposure having larger growth decreases than sites with low ozone, especially in western SBM (Watson et al. 1999). However, low drought mortality in this region suggests that increasing tree vigor due to reduced ET demand of young chaparral may have compensated for stresses of air pollution.

Preliminary aerial survey estimates are that 10% to 30% of mature mixed-conifer forest stems have perished in 100,000 ha of SBM and SJM (20–100 dead trees ha⁻¹). The highest levels occurred in areas of highest densification (Lake Arrowhead and Idyllwild) and longest fire intervals. Mortality is 1 to 2 orders of magnitude greater than reported for SJM in the 1988 to 1991 drought (Savage 1994). Mortality in ponderosa pine began in discrete nodes of whole-stand mortality that expanded radially to scales of hundreds of hectares, reflecting the behavior of bark beetles. A different pattern emerged in Jeffrey pine forest on leeward south-facing slopes. Stems perished on south-facing slopes exclusively, mortality occurred in open stands, and stems exhibited few signs of insect attack. Trees apparently perished for lack of soil water (cf. Hubbert et al. 2001a,b).

Likewise, mortality in white fir was homogeneously distributed from its lower elevational limit to as high as 2,300 m. Zonal whole-stand mortality in mixed-conifer forest, mostly in the summer of 2002, occurred over an elevation range of 1,800 to 2,200 m in the Santa Rosa Mountains, eastern escarpment of SJM, and southern escarpment of SBM. Few trees died above 2,400 m throughout the drought zone due apparently to increasingly favorable moisture conditions with elevation. The synchronicity and zonal spatial pattern of mortality suggest that trees perished primarily due to drought rather than from insect attack. Low mortality occurred in rare forests maintained in open stands by recent understory fires, including Keller Peak-Snow Valley (burned in 1970) and in prescribed burns at Big Pine Flat (1987) and Barton Flats (late 1990s). Mortality was also light in mostly monotypic Jeffrey pine forest on basin floors subject to convergent soil water flow such as Big Bear and Garner Valley.

The effect of stand-densification is seen in a comparative assessment of forest mortality during a synchronous drought in 1987 to 1991 in SBM and SSPM (Savage 1997). In SBM the percentage of standing dead trees was 14%, compared to 4% in SSPM. Engraver beetle related tree mortality among open-structured forests was limited to few low-vigor individuals in SSPM, as opposed to epidemic engraver beetle related whole-stand mortality among dense closed-forest in SBM. Transpiration stress during drought in association with uniform high tree density promote epidemic engraver beetle population

growth and extensive mortality of large diameter overstory dominant trees in SBM (Savage 1993). A regional assessment of SSPM shows that mortality rates during this drought averaged <5% of stems (Minnich et al. 2000; Stephens and Gill 2005).

The 2002 drought brings new perspective on millennial age trees of limber pine, western juniper, and bigcone Douglas fir in SCA. In each species, trees both survived record drought and rarely sustain stand-replacing fires. Limber pines as old as 2,000 years (Thorne 1988) grow at 3,000 to 3,500 m on Mt. San Geronio where soil water depletion may never reach fatal levels in extreme drought. Multicentury stand-replacing burns seldom visit the barren cliffs of glacial cirques there. The 2002 drought caused virtually no mortality of western juniper. Strong drought-tolerance appears to be a major factor for its longevity in fire-resistant sites (stem dbhs reach 2–3 m) such as Onyx Peak and Sugarloaf Mountain in the eastern SBM. In deep canyons at lower elevations are occasional enormous bigcone Douglas fir growing near streams in fire-resistant habitat. The most notable example is “Old Glory” at Mt. Baldy Village in SGM with a circumference of 7.5 m and height of 60 m.

Forest Decline or Punctuated Equilibrium

The number of mature trees that perished in the SBM, SJM, and San Diego County mountains since 2002 is greater than combined mortality of the past century, in the order of 10×10^7 mature stems over an area ca. 200,000 ha. Additional thousands of ha of forest were stand-replaced during the wind-driven 300,000 ha fire storm of October 2003. This episode may quite possibly become one of the great transformations in California vegetation since the beginning of European settlement, rivaled only by the invasion of European annuals into California coastal plains and valleys.

It is difficult to evaluate the significance of the 2002–2003 event without the “hindsight” of past and future climate and vegetation states. The current dieback episode could be natural perturbation in a stable climate, but tree-ring and instrumental records show little evidence that long-term mean precipitation has changed in recent centuries (Dettinger et al. 1998; Graumlich 1993). Moreover, the interannual variation in precipitation is greater than the absolute value of the mean, diminishing the importance of shifting long-term means. In spite of global warming over the past century, twentieth-century temperatures are cooler than most of the Holocene since the Milankovitch solar maximum (Feng and Epstein 1994); that is, the climate is similar to most of the Holocene, for which paleobotanical records show little corresponding change in vegetation (Feng and Epstein; chap. 2, this volume).

The mass mortality of Jeffrey pine cohorts on leeward south-facing slopes of the SBM is very likely due to climate forcing because these stems did not experience significant stand-densification (Minnich et al. 1995) and air pollution

(Bytnerowicz 1999). Tree-ring counts of the largest dead Jeffrey pine suggests the last drought to extirpate Jeffrey pine at these sites occurred in the mid-eighteenth century. The driest 5-year drought in far western SCA occurred in the 1840s (Haston and Michaelson 1994), but the age of SBM Jeffrey pines suggest the 2002 event was more extreme than the 1840s drought in eastern SCA.

Pinyon-juniper and subalpine forests are least impacted as these unproductive systems respond slowly to suppression and have low exposure to air pollution. Short-lived closed-cone conifer forests are smog-tolerant (Miller, Longbotham, and Longbotham 1983) and serotiny/cohort regeneration constrains stand-densification. Frequent chaparral burns maintain vigorous young age classes that survived extreme water deficits. For example, knobcone pine in SBM sustained light drought mortality apparently because all stands had burned within the past 60 years. Substrate mineralogy anomalies in knobcone pine (Vogl et al. 1988) appear to limit associated chaparral biomass and ET. In contrast, the 2002 drought may produce regional extirpations in Coulter pine, as whole stand mortality is extensive in association with old-growth chaparral of SBM and the Peninsular Ranges. Although live seed persist in serotinous cones, range retreat and local extinction may occur in the absence of fire because cones progressively open and trees drop seeds usually in ca. 5 years, exposing seeds to predation by rodents. Recruits compete poorly in mature chaparral. Heavy Coulter pine mortality may have been inevitable in a climatic excursion as severe as 2002 because the standing population of patch elements will contain elements of sufficient age and transpiration demand for insect attack. However, mortality in 2003 may have been enhanced by large chaparral patch elements due to suppression, with increasing distance between surviving stands adding to dispersal and recolonization lag times. Alternatively, a range contraction of this magnitude may only be a temporal perturbation in long time scales because droughts as extreme as 2002 are rare. Planned burns in the near-term may possibly encourage cohort regeneration. Fires may have initiated pulsed recruitment cycles in 2003 in Hot Springs Mountain (2,000 ha), the SBM (1,500 ha), and the Julian-Cuyamaca region (2,000 ha). However, posthumously dead forests in the Hot Springs Mountains burned at intensities sufficient to destroy branches, cones, and seeds, possibly extirpating these stands. At present, there are thousands of ha of unburned Coulter pine forest with whole-stand mortality in SCA. Stochastic mass mortality and recruitment failures may explain the fragmented distributions and detached relationship between closed cone conifer forests with local environmental gradients (Vogl et al. 1988; Minnich and Everett 2001).

Failure of postdrought resprouting in bigcone Douglas fir has led to extensive range contraction of stands growing in old-growth chaparral of the eastern SBM. This trend parallels the long-term contraction from stand-replacement burns since the early twentieth century (Minnich 1999;

Minnich and Everett 2001). Minnich (1999) proposed that the increasing incidence of wind-driven fires from suppression selects for stand-replacement extirpations at rates exceeding the regeneration capacity of the species. The conversion of associated canyon live oak stands into shrub thickets encourages recurrent intense fires in a positive feedback. Before suppression, variable fire intensities of summer-long fires (Minnich 1987) may have produced longer intervals between stand-replacement burns. Models that invoke increased fire severity from excessive fuel buildup must take into account that the range of fire intervals in chaparral in BCA overlap with those in SCA (Minnich and Chou 1997), chaparral is not a significant component of the vegetation, and there is little evidence of conifer densification. Alternatively, the range contraction may also be a natural perturbation due to variability in the fire process. Although range fluctuations would be expected at local scales, steady-state models must account for the virtually ubiquitous decline of the species throughout SCA. One factor may be the reduction in growth rates due to air pollution (Arbaugh et al. 1999).

The maintenance of mixed-conifer forest may be compromised by increasing fire intervals (e.g., Swetnam 1993; Minnich et al. 2000), stand densification (Minnich et al. 1995; Albright 1998; Roy and Vankat 1999), and increasingly extensive stand-replacement burns. Forest densification has a dual effect. High tree densities reduce tree vigor against insect attack, and increase tree resource base to host insect pathogens. Trees are further compromised by air pollution effects on photosynthesis and fine-root biomass (Grulke and Balduman 1999). The advantage of longevity is compensated by intrinsic high productivity and rapid response of this assemblage to suppression, and excessive landscape transpiration demand in overstocked forests. Without suppression in SSPM drought-caused mortality rates normally exceed background levels, even in open stands (cf. Savage 1994). However, because the rate of mortality is less than levels in SCA by ca. 2 orders of magnitude, it appears that the open forest structure mitigated against epidemic insect attack.

The transformation of mixed-conifer forests from "standing" to "stand-replacement" fire regimes may result in progressive regional extirpations (Minnich and Everett 2001). The area of stand-replacement fires in SCA is an order of magnitude greater than in SSPM. The October–November 2003, fire storm extirpated the entire mixed conifer forest (4,000 ha) of Cuyumaca State Park. Only ca. 20 ha of seed-bearing white fir, sugar pine, and ponderosa pine survived, and the nearest seed sources are 30 to 70 km distant on Mt. Palomar, Volcan Mountain, and Hot Springs Mountain, where similar islands of dense forests also face potential stand-replacing extirpations.

Areas for Future Research

As a field science, plant ecology has operated at site-specific scales to work out fundamental processes such as transpiration, CO₂ exchange, plant growth, litter fall and decay, soil

processes, species life traits and competitive relationships, population dynamics, and the role of pollutants and pathogens. The interpretation of locally generated data to broad scales is a leap of faith because biological processes do not have universal nor uniform expression on landscapes. Ecologists need to address how local data compares to the complex functioning and dynamics of plant assemblages at broad scales where probabilistic and unpredictable outcomes are expressed in biogeography, disturbance regimes, and vegetation steady-states, processes vital to forest management.

The bridge to the ecology of landscapes requires that research scale up both spatially and temporally which requires sacrifice of data precision and measurement. As discussed in Jackson et al. (2001), it is important to reduce data quality to improve the temporal dimension of science. The choice of baseline to reconstruct historical vegetation also affects the outcome, the "shifting baseline syndrome." For example, with a hypothetical baseline of 1950, studies might have concluded that dense mixed conifer forest exist as a long-term stable state. A 19th century baseline reveals that forests were formerly open due to periodic surface fires that declined during the 20th century.

One invaluable resource is historical aerial photography which are a virtual "time machine." Resolution permitting, time-series georeferenced photographs of southern California forests, dating to as early as the 1920s and 1930s, permit the development of databases on dynamics at the stand or landscape scales on such parameters as growth, recruitment, mortality, stem densities and cover, as well as fire disturbance parameters. Mediterranean ecosystems in Baja California provide a combination of events not possible in California: aerial photograph and satellite platforms permit spatially explicit analysis of landscapes without fire control.

Southern California conifer forests have been unevenly studied, and perhaps this will portend the direction of future studies. Little studied assemblages include four-needle pinyon, gray pine, and subalpine forest as well as pinyon-juniper woodland. Fire ecology will remain a strong theme, but a new theme will be the long-term legacy of catastrophic forest mortality from the drought of 1998–2003, and its relationship to forest fuels, bark beetles and other pathogens. The forest die off may also encourage studies on the potential for comparable catastrophes elsewhere in California, as well as the effects of ozone and nitrogen deposition on forest assemblages. Research of forests in Baja California, a showcase of California's past ecology, will permit the formulation of hypothesis on pre-suppression fire regimes and vegetation dynamics, and how suppression has transformed these ecosystems over the past century.

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