Chapter 17

Air Pollution Increases Forest Susceptibility to Wildfires: A Case Study in the San Bernardino Mountains in Southern California

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Abstract

Many factors increase susceptibility of forests to wildfire. Among them are increases in human population, changes in land use, fire suppression, and frequent droughts. These and other factors have been exacerbating forest susceptibility to wildfires over the past century in southern California. We report on the significant role that air pollution has had on increasing forest susceptibility to wildfires, based on a 1999–2003 case study in the San Bernardino Mountains. Air pollution, specifically ozone (O_3) and wet and dry deposition of nitrogenous (N) compounds as a by-product of fossil fuel combustion, has significantly increased since urbanization and industrialization of the region after 1945. Ozone and elevated N deposition cause specific changes in forest tree carbon (C), N, and water balance that enhance individual tree susceptibility to drought, bark beetle attack, and disease, and when combined, contribute to whole ecosystem susceptibility to wildfire. For example, elevated O_3 and N deposition increase leaf turnover rates, leaf and branch litter, and decrease decomposability of litter, creating excessively deep litter layers in mixed-conifer forests affected by air pollutants. Elevated O_3 and N deposition decrease the proportion of whole tree biomass in foliage and roots, thereby increasing tree susceptibility to drought and beetle attack. Because both foliar and root mass are compromised, carbohydrates are stored in the bole over winter. Elevated O_3 increases drought stress by significantly reducing plant control of

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water loss. The resulting increase in canopy transpiration, combined with O_3 and N deposition-induced decreases in root mass, significantly increases tree susceptibility to drought stress, likely contributing to successful host colonization and population increases of bark beetles. Phenomenological and experimental evidence is presented to support the role of these factors contributing to an increase in the susceptibility of forests to wildfire in southern California.

17.1. Introduction

Historically, the forests of southern California were created, adapted to, and maintained by regular episodes of wildfire. This agent of ecosystem disturbance paradoxically functioned to maintain forests in a resilient state by better preparing them to withstand severe episodes of wildfire, drought, and bark beetle colonization. However, periodic extreme drought stress (affecting an individual tree within a dense stand) and bark beetle outbreaks can also increase forest susceptibility to wildfire. Under particular current forest conditions, there are many compounding factors, some of which were set in motion decades ago, that increase the susceptibility of southern California forests to severe wildfire and often result in stand-replacing fires. These factors include a rapid increase in human population and resulting resource use, a shift in management goals during the early part of the 20th century from timber utilization to recreational use, and successful fire suppression with subsequent forest densification.

Despite the level of attention given to the causative factors for increased wildfire activity (Westerling et al., 2006), a largely ignored contributing factor is air pollution. Chronic nitrogen (N) deposition contributes to increased forest densification by stimulating aboveground biomass production and enhances litter accumulation through increased needle production, turnover rates, and depressed long-term decomposition rates (Fog, 1988). Elevated ozone (O_3) exposure increases tree susceptibility to drought stress through direct effects on loss of stomatal control with subsequent increased canopy transpiration, and increased successful bark beetle colonization through both increased tree drought stress and pollutant-induced redistribution of carbohydrates to the bole. The effects of these air pollutants, combined with the human and ecological changes in the fire-adapted ecosystem, have increased forest stand susceptibility to wildfire in southern California (Fig. 17.1). This chapter presents a case study for the San Bernardino Mountains in the
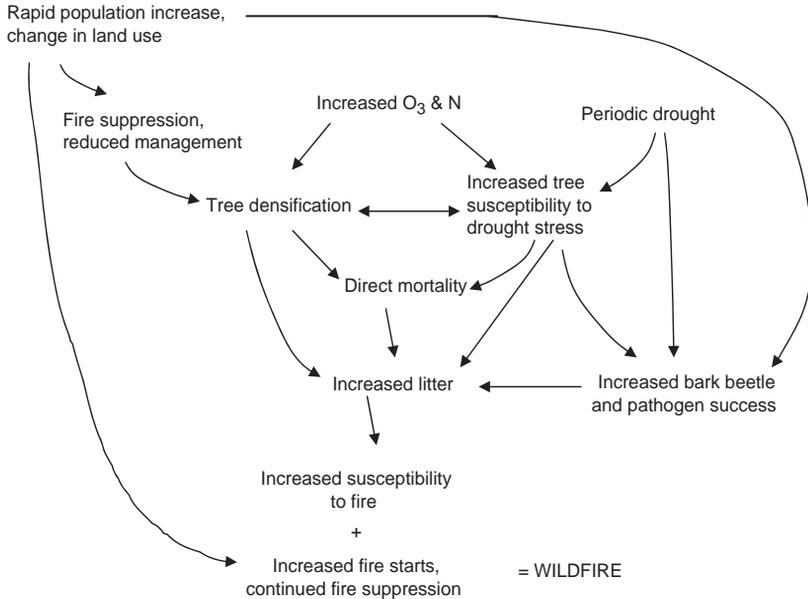
Figure 17.1. Diagram of multiple factors contributing to forest susceptibility to wildfire.

eastern Transverse Range, east of Los Angeles (LA), California that focuses on pollutant effects on ponderosa pine (*Pinus ponderosa* Laws)— an ecologically, socially, and economically important species throughout the western U.S.—that result in forest susceptibility to wildfire.

17.2. Historical effects of land development

The San Bernardino National Forest (SBNF) was established in 1908 and covers about 331,838 ha within San Bernardino and Riverside Counties in California. It includes the eastern end of the Transverse Range and the northern part of the Peninsular Range (San Jacinto Mountain and adjacent areas). Of this area, about 65,558 ha are in private, county, state, or other type of federal ownership.

During the late 19th century, settlers fundamentally altered the mountain landscape in southern California. Gold and other valuable minerals were discovered, and the population rapidly increased in surrounding low elevation areas as well as in the mountains (Minnich, 1988). The forest was logged to provide construction materials for

buildings, mine shaft timbers, and for fuel. In 1899, a severe drought occurred (Fig. 17.2), water was rationed in the communities, and a premium was placed on reservoir development (Lake Gregory, Lake Arrowhead, and Big Bear Lake). As the reservoirs were established, they became the focus for recreational use in the 1920s. With the shift from resource utilization to recreation, forest thinning was suppressed, incursions of fire from the chaparral into the forest were repressed, and forest density increased on the mountaintop. In the 1950s, an attempt was made to thin the forests, but the mountain community councils were strongly opposed to both branch trimming and stand thinning for aesthetic reasons: these were now resort destinations for the rapidly increasing population in post-1945 LA. As a consequence, forest density continued to increase, and with in-growth and lateral canopy expansion, more trees were in physical contact with each other as well as structures, increasing fire hazard. An example of increasing canopy cover of individual trees through time can be observed in the sequence of aerial photos taken from 1938 through 1994 from the western San Bernardino Mountains (Fig. 17.3).

In 1980, the SBNF adopted a new set of forest plans, which addressed in part how to manage for fire on the National Forests surrounding and adjacent to the mountain communities. Due to the high percentage of private land ownership, National Forest personnel participated in community councils and solicited their support for fire-safe activities that would benefit both the private landowner and the National Forest. In response, mountain community councils, in conjunction with the SBNF, drew up their own plans, which included raking leaves, branch trimming, and thinning of trees within 30 m of valued structures (Asher & Forrest, 1982). The community's fire-safe plans were not implemented effectively, nor were they enforced. As a result of these human-induced changes over the past century, the region was, and is, highly susceptible to fire.

17.3. Mountain community behaviors related to fire-safe activities

The consensus of opinion is that either mountain community residents started to follow through on those practices and then stopped, or did not start at all, or did not implement these practices in a coordinated fashion so as to reduce the fire hazard on private property. There are a number of reasons why residents might not have implemented changes for their own (fire) safety. Some of the reasons have to do with demographic changes. Examination of California state census data (www.dof.ca.gov/html/demograp/calhist2a.xls) from 1980 to 2000 indicates population shifts in
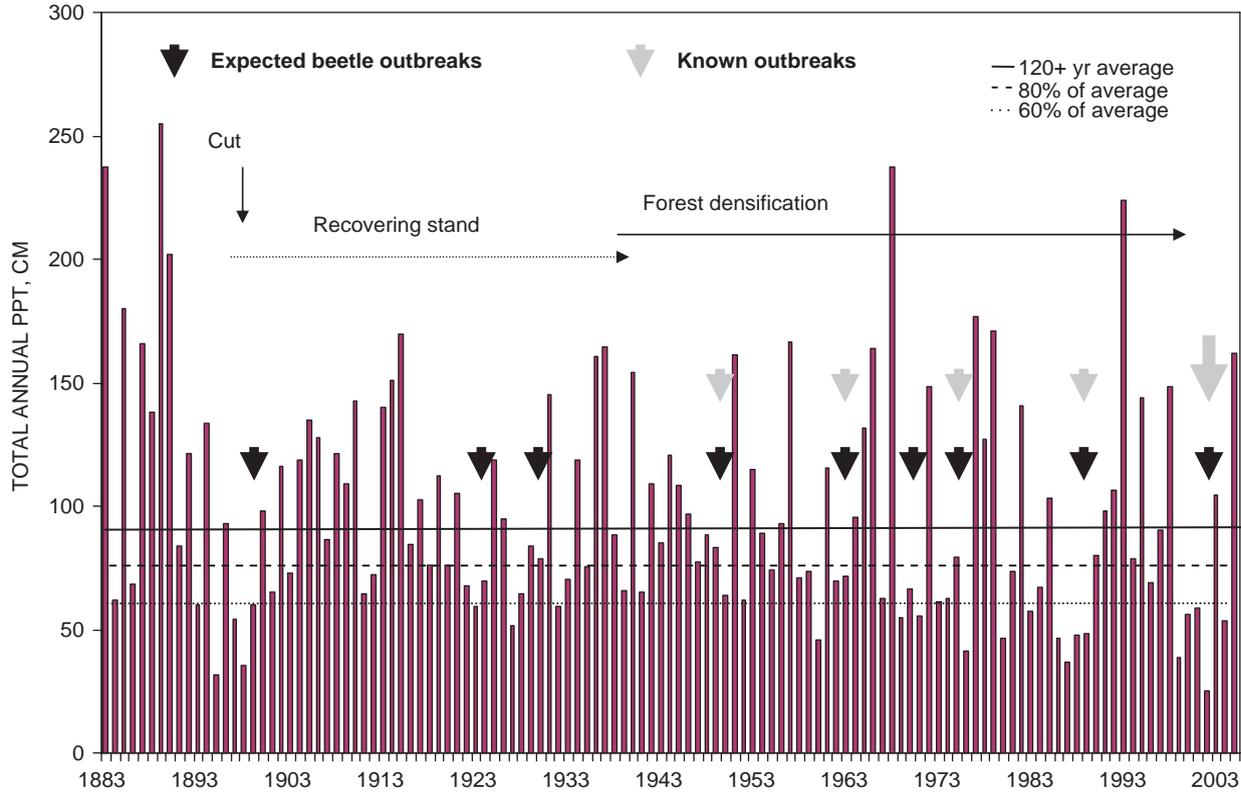
Figure 17.2. Long-term record of regional precipitation at Big Bear Dam, San Bernardino County, California. Total annual precipitation (*y*-axis in centimeters) from October 1 to September 30 was accumulated over each year and plotted. The overall average is denoted by a solid line (96 cm), with the 80% of average (below which moderate drought stress is incurred using physiological definitions) and the 60% of average (below which extreme drought stress is incurred) denoted by dashed and dotted lines, respectively.
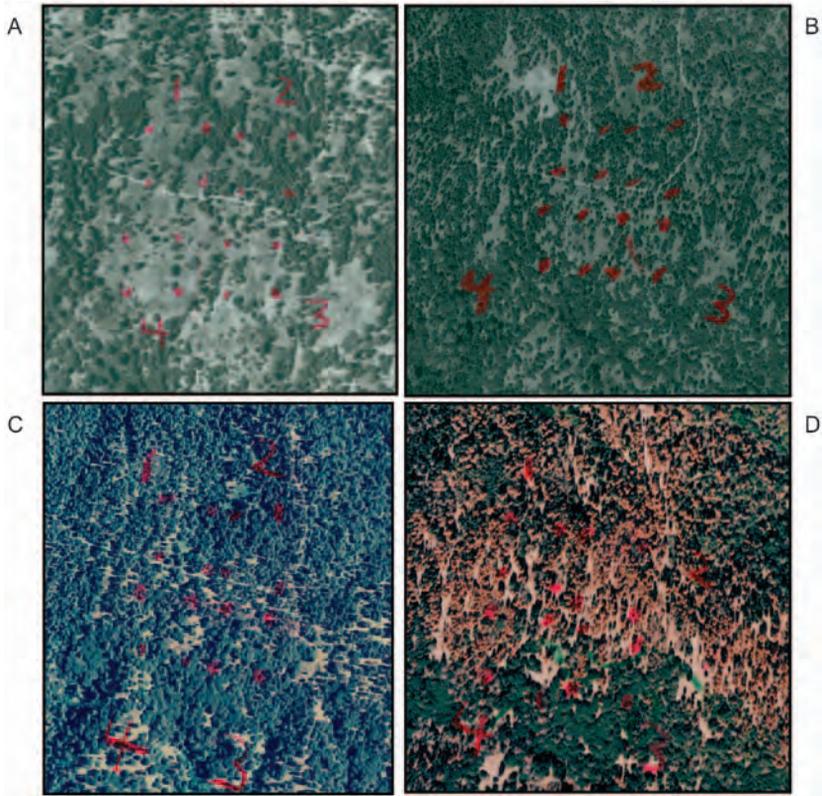
Figure 17.3. Repeat aerial photographs of mixed conifer forest dominated by *Pinus ponderosa* demonstrating forest densification (near site 1, western San Bernardino Mountains; see Fig. 17.5) in (A) 1938, (B) 1965, (C) 1994, and (D) 2003. Photograph sources are San Bernardino County Flood Control (A), San Bernardino National Forest (B,C), and the U.S. Geological Survey, SCAMP program, Department of Earth Sciences, University of California, Riverside (D).

several San Bernardino Mountain communities (Table 17.1). In mountain communities with population increases, some portion of the residents must have moved into the area and were never a part of the mid-1980s community council discussions on fire-safe actions for their property. New residents may have brought a different set of social values, such as the expectation of less, not more regulation, even if the activity improved their own survival or protection of property. New mountain residents arriving from urban areas often bring with them an expectation that fire is an emergency, not a way of life. The perception

Table 17.1. Population statistics for permanent residents in San Bernardino Mountain communities from 1980 to 2000

Place/Town/City	1980	2000	Change (%)
Big Bear City	11,151	5779	−52
Big Bear Lake	4896	5438	+11
Idyllwild-Pine Cove	2959	3504	+18
Lake Arrowhead	6272	8934	+42
Wrightwood	2511	3837	+53

that emergencies are handled by the fire department, not themselves, could have had an effect on their sense of control over the fire hazard. New residents may also have had a different level of trust in or experience with adjacent landowners (e.g., federal, state, or private) in carrying out fire-safe activities.

On the other hand, the population of Big Bear City was halved over the last two decades. If some of the reduction in residential population was due to seasonal use of homes, the level of property care by owners may have also declined, and some residents who originally agreed to participate may no longer reside in the area and are not on site to conduct or adequately maintain fire-safe activities. Interestingly, a single study (Vogt, 2003) suggests a moderate level of fire-safe activities among seasonal ($n = 176$) and permanent homeowners ($n = 119$) in the northeastern U.S. In their study, permanent homeowners had a greater level of compliance of defensible space ordinances (68%) relative to seasonal homeowners (52%). If the age of the property owner has increased, this could also play a role in the reduced level of property care observed.

There are no data available to quantify what proportion of the residents participated in the 1980 mountain community forest plan discussions. The current residents in the San Bernardino Mountains may not have been involved in community decision making or agreements that were in place before their arrival. In the study in the northeastern U.S., only about one-third (30%) of the permanent and fewer (6%) seasonal homeowners attended a public meeting about wildland fire (Vogt, 2003). In another report on the same data set, Vogt and Cindrity (2003) found that the majority of respondents had purchased their property with the help of a realtor or sales office (75% of permanent and 70% of seasonal homeowners). Less than 2% of the permanent residents and 7% of the seasonal homeowners acquired their property through their family. Property transfer outside of the family could reduce the exchange of information on fire-safe activities that could occur from generation to generation, and this emphasizes the importance of the community in

fire-safety education. Currently, efforts to educate new residents to mountain communities about fire-safe activities focus on delivering messages through communication tools that reach both permanent and seasonal, as well as long- and short-term residents.

There are other sociological and experiential reasons for not maintaining fire-safety practices. For example, some of the original participants may have initially agreed to implement fire-safe practices, but had a dispute with other participants, or the activities requested were perceived as ineffective, or ineffective relative to the magnitude of the risk. For example, if mountain residents observed a lack of fire-safe activities on adjacent properties, they may see no value in maintaining fire-safe activities on their own property. Perhaps the importance of peer pressure has declined in the past two decades. It is also possible that there are too many changes and burdens imposed on the residents. There could be other regulations that have been imposed that made fire-safe activities an overburden.

It is possible that homeowners may not have direct experience with wildfires. In one study from the northeastern U.S., 82% of permanent residents experienced smoke from a wildfire, compared to 45% of seasonal homeowners (Vogt, 2003). The homeowners were also questioned about their involvement in fire-education activities. Three-quarters of the permanent homeowners had read information on home protection from wildland fires, as had 70% of the seasonal homeowners. Residents who may have been motivated to implement fire-safe actions by the experience of living through a fire in recent history may be less likely to remain a resident of the community because of the experience itself. Fire is a motivating factor only for those who choose to stay in a fire-prone community. New residents may or may not have experienced a fire and thus have no context that would influence a decision to take action.

It is difficult or impossible to pinpoint the multiple causes for a lack of compliance with fire-safe actions on private land. Generally, mountain community residents and seasonal owners, historically and currently, influence the susceptibility of their properties to wildfire through knowledge, attitudes, observations and sense of risk, physical presence in the community, and level of action on community fire-safe activities. Regardless of causation, and whether intentional or not, private property owners in the San Bernardino Mountains have significantly contributed to the current state of high fire hazard that exists today. They have an equally significant opportunity to influence the future susceptibility of their properties and the forest as a whole to future wildfires through implementing fire-safe practices on their property.

17.4. Air pollution deposition

Pollutants generated by urban residents in the greater LA metropolitan area are transported 60–100 km downwind and affect mid-elevation forests in the San Bernardino Mountains (Bytnerowicz, et al., in press). The primary source of air pollution is fossil fuel combustion, whether it is from vehicular exhaust, residential production, or industry. Approximately half of the air pollution in the LA Air Basin is generated from mobile sources including trucks, trains, cars, ships, and buses (South Coast Air Quality Management District, 1997). On the western end of the San Bernardino Mountains, nearly half of the nitrogen deposition is in reduced forms (Fenn & Poth, 2004), most of which is believed to originate from dairy farms in the Chino/Norco area. Agricultural sources of ammonia are expected to decrease in coming years as farmland is converted to residential uses.

Fossil fuel combustion emits nitrogen oxide, which is converted to other nitrogen oxides (NO_x) and O_3 in the presence of high-energy ultraviolet (UV) light. Both NO_x and O_3 are strong oxidizing agents and damage living cells. These pollutants also react with biogenic volatile organic compounds like terpenes in the airspace of forested ecosystems facilitating the formation of organic aerosols (Atkinson & Arey, 2003; Cahill et al., 2006). Although O_3 is highly reactive and disintegrates through time, sufficient concentrations are generated in urban and agricultural areas (from NO_x emissions from fertilized soils) and transported long distances. For example, from west (nearer the pollutant source) to east (farther from the source) in the San Bernardino Mountains, O_3 concentrations were high at Camp Paivika (80 ppb h^{-1}, averaged over 24 h, from April 15 through October 15, from 1993 through 1995; Grulke et al., 1998), moderately high (72–74 ppb h^{-1}) 5 km further east near Rim Forest, and moderate (62–64 ppb h^{-1}) 45 km east of Camp Paivika at Barton Flats (Figs. 17.4, 17.5).

Because O_3 is a product of photolysis of nitrogen oxides, if O_3 is present at moderate concentrations, there is also concurrent N deposition. Deposition occurs from a wide variety of nitrogen species in gaseous, wet, and dry forms to vegetation and soil surfaces (nitric oxide [NO], nitrous oxide [NO_2], nitric acid vapor [HNO_3], nitrous acid vapor [HNO_2], particulate nitrate [NO_3^-]). Ammonium (NH_4^+) can also be transported moderate distances from feedlots for cattle and poultry (Bytnerowicz et al., 2002). Along the same west to east gradient in the San Bernardino Mountains (Fig. 17.5), N deposition averages 71 kg ha^{-1}yr^{-1} at Camp Paivika and declines to 9 kg ha^{-1}yr^{-1} at Barton Flats (Breiner et al., 2007). Because air pollution has been high since 1945 in the LA Air Basin (Lee et al., 2003), N deposition is in excess of plant and microbial
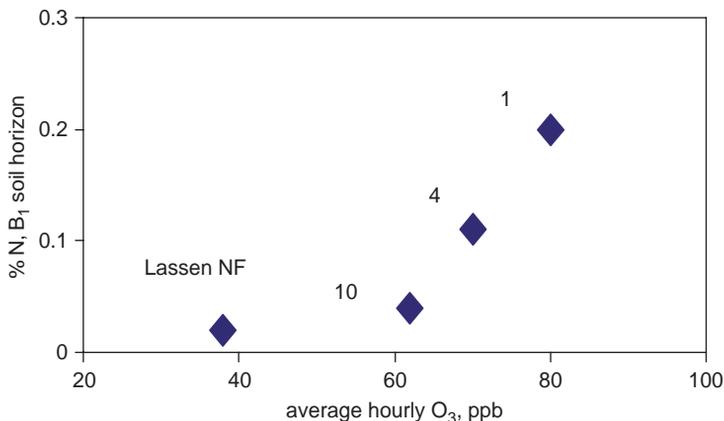
Figure 17.4. Relationship between O_3 exposure (averaged across the summers of 1993–1995; Grulke, 1999) and incorporation of long term, excess nitrogen deposition within the upper 5 cm of B_1 mineral soil (Grulke et al., 1998). Site numbers correspond to those given in Fig. 17.4. The atmospherically "clean" site is 1 mile west of the Guernsey Creek Campground (Hwy 38), Lassen National Forest, in northern California.

demand (Fenn et al., 1996). The cardinal symptom of excess N is the export of high nitrate levels in streamwater, which is well demonstrated for areas with N deposition above $15 \, kg \, ha^{-1} yr^{-1}$ in the San Bernardino and San Gabriel Mountains (Breiner et al., 2007; Fenn & Poth, 1999; Michalski et al., 2004; Riggan et al., 1985).

In the mid 1990s, soil N in the mineral horizon was 0.2% at Camp Paivika, 0.1% near Rim Forest, and 0.04% in the Barton Flats area (Fig. 17.4; Grulke et al., 1998). This represents a considerable increase over background levels expected from weathered granitic bedrock substrates and when compared to atmospherically "clean" sites (e.g., 0.02% N, Lassen National Forest). The effects of O_3 and excess N deposition are evaluated here as contributing factors to forest susceptibility to wildfires. Although O_3 concentrations have declined in the last decade due to increased regulation (Lee et al., 2003), soil N is still in excess and continues to influence plant response (Tingey et al., 2004).

17.5. O_3 exposure and excess nitrogen deposition effects on forest health

17.5.1. Tissue, cellular, and subcellular levels

Ozone is primarily deposited and decomposes on surfaces in the forest such as leaves, branches, bark, soil, and litter. In a ponderosa pine
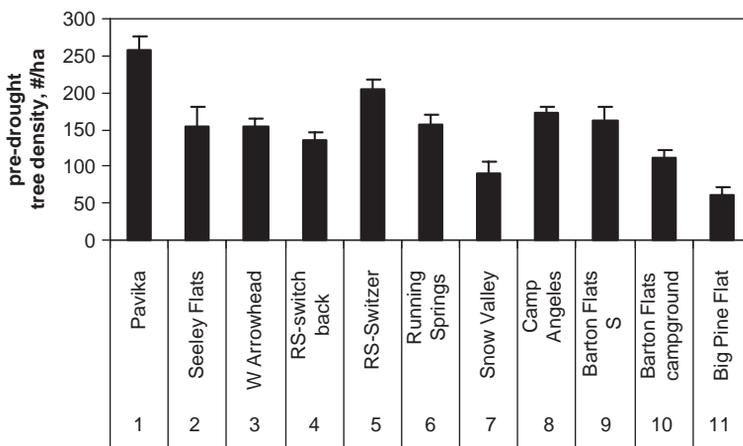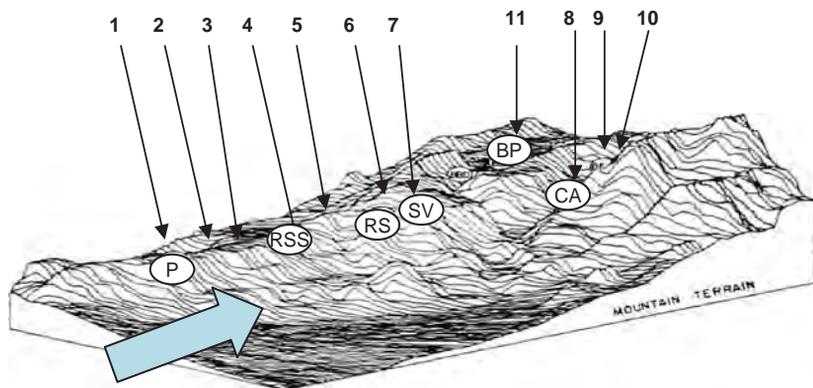
Figure 17.5. San Bernardino Mountains pollution gradient from west to east based on historic data (intermittent databases from 1977 to 1995). Recent data (2001; Grulke et al., 2004) suggest a more consistent, high O_3 concentration across these sites, with higher nighttime O_3 concentrations experienced in the area around sites 4 and 5 during the growing season. Since nitrogenous deposition is not transported as far (i.e., the west side of the San Bernardino Mountains has higher N deposition than the east side), and because it has accumulated in these ecosystems since post-1945, an N gradient in the soil still persists from west to east (see Fig. 17.3). Nitrogen deposition has contributed to significant densification of forest stands in the western San Bernardino Mountains.

plantation, approximately one-third of the O_3 was absorbed into the leaf via stomata (Bauer et al., 2000). When plants take up carbon dioxide (CO_2) during photosynthesis (the carbon capturing mechanism), they also inadvertently take up O_3 (from the air into the leaf, down a concentration

gradient). Once O_3 enters the leaf, it reacts with a thin film of water (apoplastic water) that surrounds cells, where it may be decomposed by ascorbate to oxidative derivatives, which in turn initiate signaling of oxidative stress through receptors in the plasmalemma. The decomposition of O_3 in the apoplastic water requires energy, and the regeneration of oxidized ascorbate with glutathione in the cytosol (De Kok & Tausz, 2001). Once oxidative derivatives are formed, membrane pH and permeability is altered such that ions that should be retained by the cell leak out and other ions influx along a chemical as well as charge gradient (Zhang et al., 2001). Other mechanisms of ion transport such as calcium (Ca^{+2}) channeling can also be blocked with O_3 exposure (McAinsh et al., 2002). Also, the oxidative derivatives may initiate signaling of stress (Pei et al., 2000), which could stimulate a chain of metabolic steps that launch an antioxidative defense, or cell death if redox regulation in the cell is overwhelmed.

Drought stress that is sufficient to reduce stomatal conductance, while the leaf is experiencing moderately high light levels ($> 1000\,\mu mol\,m^{-2}\,s^{-1}$), may also induce oxidative stress. Under these conditions, there is sufficient light to drive photosynthesis, but CO_2 may be limited by lower stomatal aperture. Instead of passing light-excited electrons to CO_2, it may be passed to O_2 (which is in abundance if photosynthetic rate is high under nonlimiting light levels), forming a highly reactive oxygen radical ($\bullet O$), which then reacts with O_2 to form O_3 within the chloroplast. An antioxidant signature of this process was presented for Jeffrey pine in xeric versus mesic microsites (Grulke et al., 2003b). When strong oxides degrade photosynthetic pigments in the chloroplast, the pigments must be reconstructed into functional arrays, requiring additional nutrients and energy.

One of the first measurable effects of O_3 in plants is a decrease in the efficiency of photosynthesis. Carbon–carbon bonds store energy in plants for later use. Because O_3 damages tissue, there is a metabolic cost in energy, C, and nutrient resources to repair tissues (Matyssek & Sandermann, 2003). That metabolic cost is reflected in an increase in respiration and decrease in the total C stored by the plant. Lower total C stored and greater requirements for N (to rebuild photosynthetic pigments) results in retranslocation of materials from older to younger needles.

In general, a reduction in leaf water loss (transpiration or stomatal conductance to water) accompanies the reduction in photosynthesis in low to moderate O_3 exposures (for ponderosa pine seedlings; Weber et al., 1993). Both moderate or lower O_3 exposure, and a low level of drought stress have been shown to reduce stand level O_3 uptake (for ponderosa

pine; Panek & Goldstein, 2001). Although drought is considered to protect plants via a reduction in O_3 uptake, under moderate O_3 exposure and greater levels of drought stress, the two stresses were synergistically deleterious for C acquisition (for ponderosa pine in 1994 at Barton Flats; Grulke et al., 2002).

17.5.2. Whole tree and stand levels

At the whole plant (tree) level, O_3 exposure and excess N deposition results in premature senescence and loss of needles (within whorl loss of needles, fewer needle age classes) (Grulke, 2003; Grulke & Balduman, 1999). The greater the O_3 exposure and N deposition, the more needles are lost. One of the reasons this may occur is that with ample nitrogen availability, older needles may not be needed as storage organs for nitrogen. In a moderately polluted site such as Barton Flats, up to nine needle age classes were retained in ponderosa pine. At a high pollution site such as Camp Paivika, only four needle age classes were retained, but there were few needles retained in the older needle age classes. When air pollution was combined with moderate drought stress in the following year, less than three needle age classes were retained at Camp Paivika, whereas five were retained at Barton Flats (Grulke & Balduman, 1999). In an atmospherically "clean" site on the Lassen National Forest, seven needle age classes were retained even in a drought year. Because premature needle senescence of older needles can be extreme in high pollution sites (Camp Paivika), 95% of the total canopy biomass can be found in current-year foliage (Grulke & Balduman, 1999). In contrast, canopy foliar biomass was more or less evenly distributed across four to five needle age classes in Lassen National Forest.

Self-pruning of older (lower) branches is accelerated in O_3-exposed trees (Miller et al., 1996). First, lower branches are more likely to be shaded, and shaded branches have greater transpiration (water loss through stomata from foliage) per unit C uptake but inadvertently also take up more O_3. Second, because lower branches are more shaded and are more injured due to O_3 uptake, the net C balance is lower. Presumably when net C balance drops below zero, the branch is excised (Sprugel et al., 1991; but see Reiter et al., 2005).

As a result of the combined effects of O_3 exposure and chronic N deposition, needle and branch production and loss are increased and may contribute to greater litterfall (Fig. 17.6). In addition to pollutant stressors, other factors could contribute to differences in litterfall, such as stand density, composition, leaf area index, and differences in forest floor
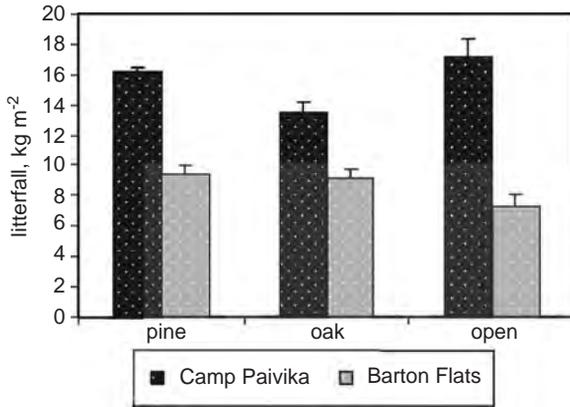
Figure 17.6. Difference in forest floor litter layer between a high and moderate pollution site (Camp Paivika [upper photo] and Barton Flats [lower photo], respectively). Arrows depict the decomposed O_2 litter layer. Annual litter accumulation ranged from 50 to 125% greater in the more polluted site. The large difference in litter build up at Camp Paivika was likely due to both higher litter deposition (O_3 exposure, N deposition, and drought) and lower litter decomposability due to O_3-induced high lignin content (Dizengremel, 2001) and the effects of N enrichment on long-term deposition (Fog, 1988; data from tabular data presented graphically from Fenn et al., 2005).

microenvironment (lower temperatures may be associated with higher stand density, and thus result in lower decomposition rate). Simulations using the CENTURY model predicted greater long-term needle fall with the combination of O_3 and N deposition (Arbaugh et al., 1999).

Litter accumulation is further enhanced by the retarding effects of these pollutants on litter decomposition. Higher lignin content is found in needles produced in high O_3 exposure environments (Dizengremel, 2001), and greater lignin content reduces decomposability (Kimmins, 1997). As a result of N deposition, litter N concentrations are significantly higher in the more polluted areas of the San Bernardino Mountains. The higher N levels in litter result in higher litter decomposition rates in the initial stages of decomposition (Fenn & Dunn, 1989; Persson et al., 2000). However, many studies have demonstrated that long-term decomposition rates are retarded by high N concentrations in litter (Berg, 2000; Fog, 1988; Persson et al., 2000; Swanston et al., 2004), particularly in high lignin content litters (Carreiro et al., 2000; Knorr et al., 2005), and that litter accumulates to a greater degree in N-enriched forests (Kuyper, 1994; Nilsson, 1995; Nohrstedt et al., 1989). In the western San Bernardino Mountains experiencing high pollution, the O_2 litter depth averaged 15 cm compared to 1 cm in the eastern San Bernardino Mountains experiencing moderate pollution (Fig. 17.6). The mass of litter in the forest floor is typically 50–125% greater in the more polluted site. The large difference in litter accumulation between the high and low pollution sites is a result of greater tree densities, high leaf turnover rates, and inhibited long-term decomposition at the high pollution site.

Perhaps because of the increased repair costs for aboveground tissues, less biomass is retained in roots of ponderosa pine exposed to high O_3 concentrations, which is exacerbated by lower allocation to root mass with N-enrichment (Haynes & Gower, 1995). From the western to the central San Bernardino Mountains, both O_3 and N deposition contributed to significantly lower fine and medium root biomass at depths of -10, -30, and -50 cm. Root biomass at these sites was 6–14 times lower than that at a moderate pollution site (Fig. 17.7; Grulke et al., 1998). Lower root biomass alone significantly increases the susceptibility of ponderosa pine to drought in this Mediterranean-type climate.

In addition to lower leaf and root mass (Grulke et al., 1998), ponderosa pine also had lower carbohydrate concentrations of both leaf and root tissue (Grulke et al., 2001) at the high pollution sites relative to the moderate pollution site. In general, carbohydrates for spring growth are stored in the roots over winter. However, because of the lower leaf and
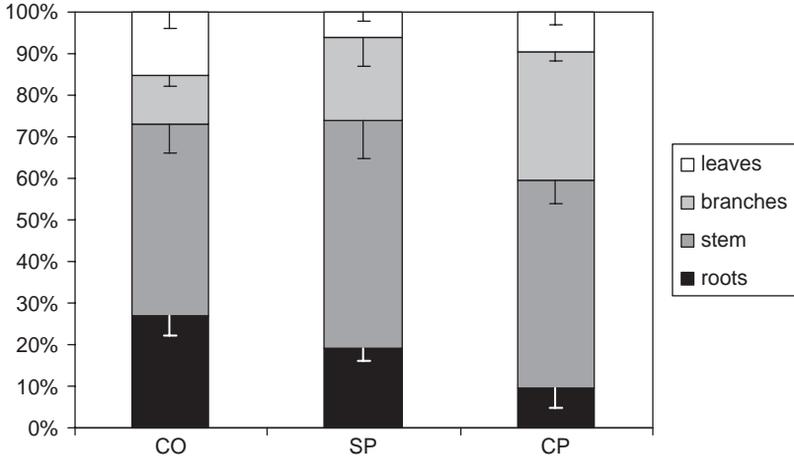
Figure 17.7. Exposure to high O_3 concentrations and excess N deposition alters biomass allocation (*y*-axis, in %) within ponderosa pine (Grulke & Balduman, 1999). CO is Camp Osceola, a site in eastern Barton Flats, in the eastern San Bernardino Mountains (less polluted site); Strawberry Peak is a site between sites 4 and 5 (see Fig. 17.4); and CP is Camp Paivika (highly polluted site).

root mass in ponderosa pine at highly polluted sites, overwintering carbohydrate was stored in tree boles, and potentially in branches (as seen in Fig. 17.7 at Camp Paivika). Hypothetically, increased carbohydrate storage as found in the bole subcortex, which includes phloem, cambium, and xylem, may enhance fecundity of bark beetles that feed and create galleries for their eggs and larvae in this area of the tree (see later).

At the scale of the stand, N deposition, associated with high to moderately high O_3 concentrations, increased stand density, as has been shown by Miller et al. (1989) for the period from 1973 to 1988, and subsequently by Arbaugh et al. (1999). Stand densification was especially promoted on north-facing slopes and in microsites with more water availability or lower evapotranspiration (topographic lows). When more stringent regulatory controls were imposed limiting O_3 concentrations in the early 1990s (Lee et al., 2003), ponderosa pine diameter growth increased in the western San Bernardino Mountains (Arbaugh et al., 1999; Tingey et al., 2004). In these stands, historically high O_3 exposure was also associated with high N deposition, which was not regulated and persists in the soil. Current N deposition fluxes in throughfall in the western San Bernardino Mountains are 30–470 kg N ha^{-1} yr^{-1} (Breiner et al., 2007). Excess N promotes tree growth, especially with reduced

oxidant exposure. Dense forest stands and rapid canopy growth further increase susceptibility to drought because of the greater total demand for water at the stand level.

17.6. Air pollution effects on the incidence of forest tree diseases

Ozone injury has been shown to predispose ponderosa pine to annosus root disease (*Heterobasidion annosum*; James et al., 1980) and black stain root disease (*Leptographium wageneri*; Fenn et al., 1990). The effects of elevated soil N levels on disease has not been studied in the San Bernardino Mountains, although N-enrichment has been shown to increase fungal and bacterial diseases of foliage (Snoeijers et al., 2000). Annosus root disease was most severe in Norway spruce (*Picea abies* (L.) H. Karst.) in N-rich soils (Boyce, 1961). Nitrogen fertilization has also been shown to increase root rot of eucalyptus (Marks et al., 1973) and crown and root rot of apple trees (Utkhede & Smith, 1995), both caused by *Phytophthora* species.

Ponderosa and Jeffrey pine stands are frequently infected with Western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.), but possible relationships between air pollution and the severity of mistletoe infestations in the San Bernardino Mountains have not been studied. It has long been assumed that reduced tree vigor from dwarf mistletoe infection, plus the debilitating effects of O_3, is additive in the least, and results in greater host mortality (Pronos et al., 1999). We hypothesize that greater allocation of plant carbohydrates and biomass aboveground as a result of O_3 exposure and N deposition may enhance mistletoe parasitism by providing a greater pool of available nutrients at infection points. Severe infections with mistletoe increase tree mortality rates and predispose trees to attack by insects (Hawksworth & Shaw, 1987), suggesting that if O_3 and N deposition do in fact predispose pine trees to more severe mistletoe infestations, the additional factor of air pollution stress will likely lead to enhanced tree mortality. Even though O_3 injury and possibly increased N fertility are known to increase tree diseases, including the major diseases occurring in the San Bernardino Mountains, it has not been shown that tree diseases are more common or severe in the more polluted sites within this mountain range (Pronos et al., 1999).

17.7. Effects of periodic extreme drought on forest health

Ponderosa pine frequently experiences drought stress in the Mediterranean-type climate of California. Although there is an increase in

evapotranspiration from west to east, weather that results in precipitation
in the San Bernardino Mountains is generally a regional phenomenon. The
longest record of precipitation for the range has been collected over the past
123 years at Big Bear Dam (San Bernardino County Water Resources
Division, www.sbcounty.gov/transprtn/psw/; Fig. 17.2) in the eastern
San Bernardino Mountains. The seasonal distribution of precipitation
begins with the onset of the hydrological year on October 1 (Fig. 17.8).
Regardless of the total annual precipitation (low, average, or high), 90% of
the annual precipitation accumulates by April 1. Summer precipitation
occurs when occasional monsoonal incursions from the Gulf of California
travel north into California, but these events are generally insufficient to
relieve late summer drought stress in pine for more than a few days
(Franco-Vizcaino et al., 2002). An exception was a mid-July precipitation
event in 1992 that wetted soils to $-15\,cm$ and increased stomatal
conductance for 10 d (Temple & Miller, 1998). Such events in 1993 and
1994 had little influence on stomatal conductance. By relating the level of
physiological stress that develops in ponderosa pine to the total annual
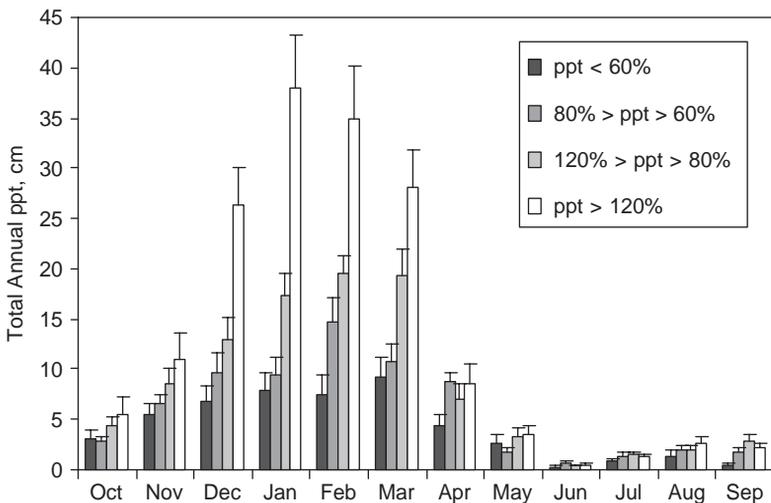precipitation received in that year, we have a means for estimating how

Figure 17.8. Seasonal distribution of annual precipitation in extreme drought years
($<60\%$), drought (61–80%), average precipitation (81–120%), and above-average
precipitation ($>120\%$) relative to the 123-year record from Big Bear Dam, San Bernardino
County, California (given in Fig. 17.2). Regardless of the total annual precipitation, 90% of
the annual precipitation accumulates by April 1. Sixteen percent of the years had extreme
drought, 26% had drought years, and 26% had above average precipitation ($>120\%$).

frequently ponderosa pine historically has experienced moderate or extreme drought stress.

Moderate drought stress is defined physiologically as reduced cell turgor, which lowers stomatal conductance (reduced water loss from the leaf), and lowers cellular water potential, which in turn allows the tissue to hold more tenaciously to the water that is in the leaf (Levitt, 1980). In 1994, a year of 80% of the average precipitation (preceded by an above average precipitation year), ponderosa pine experienced moderate drought stress by mid-July, which was extended through the end of the growing season until the onset of autumn precipitation (Fig. 17.9; Grulke, 1999).

Extreme drought stress is also accompanied by reduced cell turgor, stomatal conductance, and cell water potential. However, extreme drought stress also exhibits increased cell solute concentrations sufficient to disrupt enzymatic function. Cell turgor is reduced sufficiently and, for a long enough duration, that elongation growth is limited. Needles produced in years of extreme drought stress are much shorter (e.g., 2002; Fig. 17.10). In 1996, a year of 60% of the average precipitation (preceded by an above average precipitation year), ponderosa pine experienced
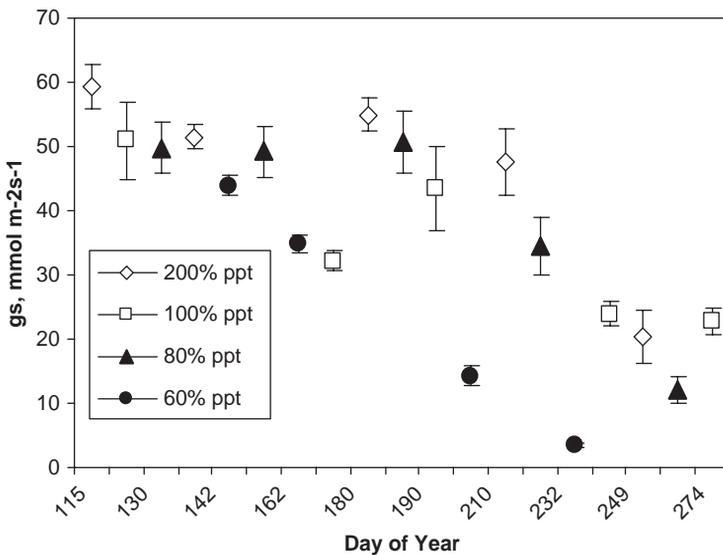

Figure 17.9. Seasonal change in stomatal conductance in years with 200% (1993), 100% (1995), 80% (1994), and 60% (1996) of the long-term precipitation record from Big Bear Dam, San Bernardino County, California. This site, eastern Barton Flats, was 10 km south-southeast of the dam.
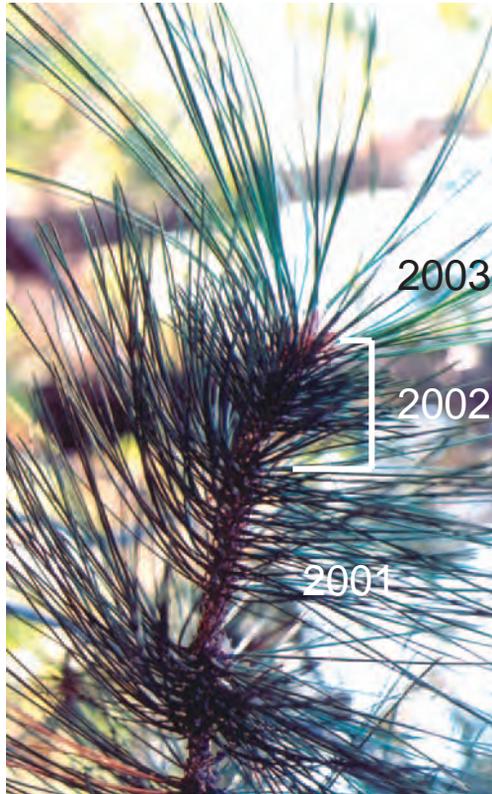
Figure 17.10. Illustration of reduced elongation growth in needles during extreme drought (2002) for ponderosa pine near Silverwood Lake, San Bernardino Mountains, California.

extreme drought stress from the end of June through the end of the growing season (Fig. 17.9), with reduced elongation growth.

Factors that strongly affect the level of physiological drought stress experienced include how precipitation is delivered in each storm, the level of antecedent moisture, and the depth of both the litter layer and mineral soil, by horizon above the bedrock. The San Bernardino Mountains were formed from a granitic dome, with the western half more weathered than the eastern half. However, similar to the Sierra Nevada, the litter layer and the soil depth (to bedrock) are highly variable. Mature pine can grow successfully from cracks in the bedrock, with only thin seams of soil in the cracks, because they have adequate access to moisture in the rock interstices (Hubbert et al., 2001). For example, an intense, single, summer precipitation event of 2 cm did not penetrate the deep litter layer at Camp

Paivika (Franco-Vizcaino et al., 2002). The same storm intensity at Barton Flats with little litter percolated 5 cm into the mineral horizon (Temple & Miller, 1998). At Camp Paivika, that precipitation event positively affected pine water status for a couple of hours, whereas at Barton Flats, pine water status was improved for several days (via reduced evapotranspiration; Temple & Miller, 1998). Until we understand how effective single precipitation events are in contributing to replenishing groundwater reserves, the level of physiological drought stress cannot be adequately modeled in these western ecosystems.

For the purposes of discussion, the following is a rough estimate of the frequency and degree of severity of physiological drought stress in forests of this region. Using the long-term precipitation record (Fig. 17.2), 15% of the years had low enough total annual precipitation to cause extreme drought stress in ponderosa pine, 30% of the years had low enough precipitation to result in moderate drought stress, and 26% of the years had above average precipitation ($> 120\%$). Using this rough index of the level of physiological stress, ponderosa pine experienced drought stress 45% of the years since 1883 when precipitation records were initiated (Fig. 17.2). Multiple years of drought, of course, would intensify the level of physiological stress experienced, but cannot be quantified in this example.

Because O_3 exposure and nitrogen deposition reduce root biomass, pines in the San Bernardino Mountains are already predisposed to drought stress independent of precipitation inputs. In general, low to moderate O_3 exposures (< 60 ppb) reduce water loss from trees. O_3 reduces photosynthetic rates, less CO_2 is required, and stomatal apertures are reduced to conserve water. However, under moderate, high, or above concentrations, O_3 exposure modifies stomatal behavior in ways that increase drought stress. For example, sugar maple was exposed to O_3 concentrations of 70 ppb during daylight hours (Tjoelker et al., 1995). By mid-season of chronic exposure, there was a significant decrease in water-use efficiency: at the same level of carbon gain, seedlings growing in chronic O_3 exposure had twice the level of water use as control seedlings grown in charcoal-filtered air. In a field study of O_3-sensitive and -tolerant genotypes, sensitive Jeffrey pine had lower water loss under moist, favorable conditions and higher water loss under dry, unfavorable conditions (Patterson & Rundel, 1989). Under favorable conditions, sensitive Jeffrey pine had less water loss, but because the stomatal apertures were smaller, there was also less photosynthetic carbon gain for reparation activities. Under unfavorable conditions (most of the day in the Sierra Nevada), sensitive Jeffrey pine had higher water loss, which results in greater desiccation.

Although physiologists generally report plant response under "steady state" (stable) conditions, the light environment in the forest is dynamic. Understanding stomatal responses under rapidly changing environmental conditions with concurrent O_3 exposure may help explain why trees exposed to moderately high and higher concentrations of O_3 lose more water. In typical forest environments, foliage on a primary branch, on the southern aspect of an open-grown tree experiences "flecky" light two thirds of the time (Grulke, 2000). In experimental simulations of "sunflecks," stomatal closure in response to abruptly reduced light level was slower in plants without nitrogen amendment: nitrogen amendment partially mitigated the desiccating effects of high O_3 exposure (in California black oak, *Quercus kelloggii*, at Camp Paivika; Grulke et al., 2005).

Moderate to high O_3 exposure can also maintain partially open stomata at night. In experimental O_3 exposures, this was first observed in Norway spruce (*Picea abies*; Weiser & Havranek, 1993) and in birch (*Betula pendula*; Matyssek et al., 1995). They reported nighttime water losses of 25% of that of full daytime rates of water loss. This was corroborated in ponderosa pine across the San Bernardino Mountain pollution gradient, with higher O_3, NO_2, and HNO_3^- exposure. In the latter case, nighttime water losses were 10% of that of full daytime rates of water loss (Grulke et al., 2004).

Because these studies were largely phenomenological, a new gas exchange system was designed and built to directly test the effects of known levels of O_3 concentrations on single leaves. Chronic, moderate O_3 exposure (70 ppb O_3 for 8 h day^{-1} for 1 month) significantly increased nighttime foliar water loss in California black oak and blue oak, *Quercus douglasii* (Grulke et al., 2006). Nighttime water losses were attributable directly to O_3 exposure and were 30% and 20%, respectively, that of daytime rates of foliar water loss in these species. Moderately high (or higher) O_3 exposure increases foliar water loss, and increases tree susceptibility to drought stress. This has been observed at the watershed level in the western Appalachians: on days of high O_3 exposure, less water flow was observed at the watershed level, presumably due to increased canopy transpiration (McLaughlin et al., 2007).

The mechanisms responsible for modified stomatal response ("sluggish" resulting in increased foliar water loss) during O_3 exposure are not wholly understood. Ozone exposure mediates increases in apoplastic hydrogen peroxide H_2O_2, which alters membrane permeability, specifically to cation influx (Castillo & Heath, 1990; McAinsh et al., 2002; Pei et al., 2000; Torsethaugen et al., 1999). Increased guard cell cation concentration is associated with increased pH, decreased potassium (K^+)

and chloride (Cl^-), decreased guard cell turgor, and thus decreased stomatal aperture (e.g., reduced g_s or stomatal closure; Zhang et al., 2001). Also, if poor stomatal control in a moderately high O_3 environment resulted in a net increase in transpiration, abscissic acid (ABA) would further modify the H_2O_2-mediated, membrane hyperpolarization and cation influx (Pei et al., 2000). Guard cell zeaxanthin modulates CO_2-dependent changes in stomatal aperture (Zhu et al., 1998): its oxidation state and activity are directly modified by O_3 exposure. In Norway spruce, sluggish stomatal response to O_3 exposure was attributable to reduced cell wall lignification. Reduced cell wall lignification resulted in greater g_s, but also in slower stomatal movement because cellulose has a higher affinity for water than lignin (Maier-Maercker & Koch, 1992). These responses describe primary effects of O_3 exposure on the guard or subsidiary cells, or on the surrounding epidermal cells from physical collapse.

We believe that the mechanism of increased loss of water from the leaves in high O_3 environments occurs regularly at the stand level in the western San Bernardino Mountains. The historic (1938–2004) changes in stand cover and tree mortality rates are given for a subset of the plots (Fig. 17.11). The highest mortality rates were observed at the high pollution site, Camp Paivika, at 160 trees ha^{-1} detected after the 1999–2002 drought. Two sites with moderate air pollution (plot 9, Barton Flats, and plot 10, Snow Valley; Fig. 17.11) that had been thinned (9 in the mid-1960s) or succumbed to a wildfire (10, in 1970) had low tree cover, and low mortality. An additional site with moderately high pollution exposure, but lower tree cover due to logging in the mid-1960s (8, Camp Angelus), also had lower mortality rates. This is substantiated by higher mortality rates reported at three of the four sites with the highest pollution (Camp Paivika, Dogwood Campground (near Rim of the World-Switzer), and Camp Angelus; in Arbaugh et al., 1999) prior to the 1999–2002 drought. Combined, high predrought tree density was correlated (adjusted $r^2 = 0.56$) with postdrought tree mortality (Fig. 17.12). Because of high tree density, the light environment for most of the canopy is likely to be dynamic, not stable. Poor plant water control due to direct effects of O_3 exposure on guard cell control may have exacerbated drought stress and mortality at high O_3 exposure sites.

17.8. Susceptibility to successful bark beetle attack

Ultimately, plant health is determined by plant access to, and accumulation of, C, water, and nutrient resources. Environmental factors
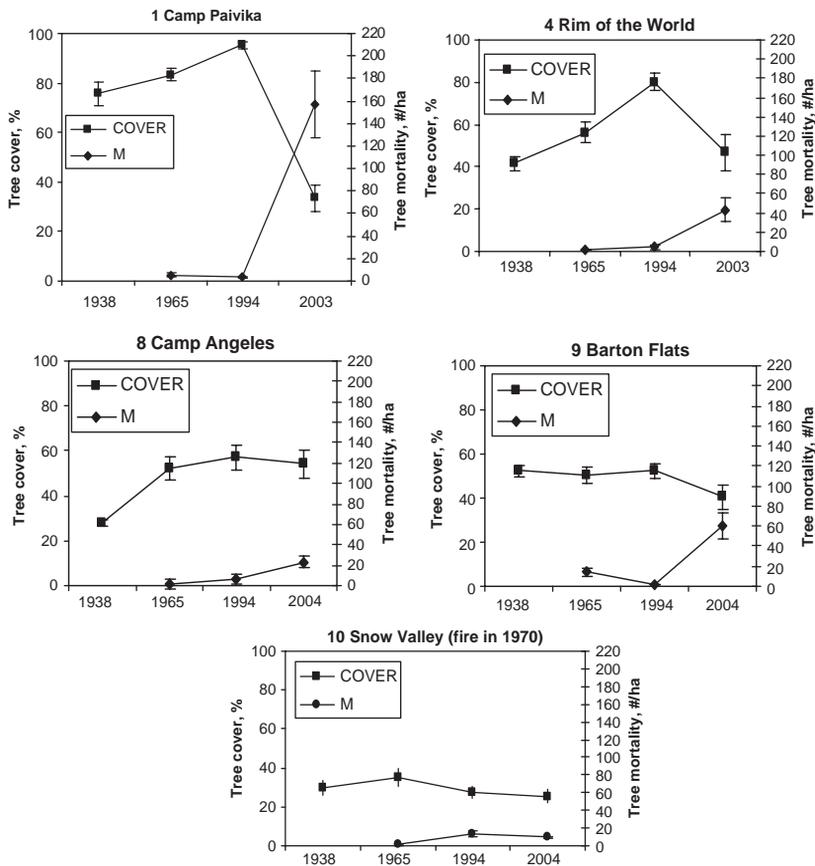
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Figure 17.11. Development of tree canopy cover and associated tree mortality rate estimated from four to eight 1-ha plots at each of the five sites. Location of sites is given in Fig. 17.4. Across a pollution gradient in the San Bernardino Mountains (1: Camp Paivika is the most polluted site; 9: Barton Flats is the least polluted site in this sequence; 10: Snow Valley is an example of a site with moderate air pollution and wildfire in 1970).

such as drought that reduce stomatal aperture consequently reduce both C acquisition in the short term (daily, cumulative) and nutrient flow in the transpirational stream to the foliage over the long term (months). Nearly all species of bark beetles are opportunists that attack trees in a weakened state. Host colonization, and more specifically, host selection behavior in bark beetles is a complex process involving both long-range and proximal behavioral components (Fig. 17.13). With only a few exceptions, either the host tree is killed by the colonizing bark beetles, or the host resistance
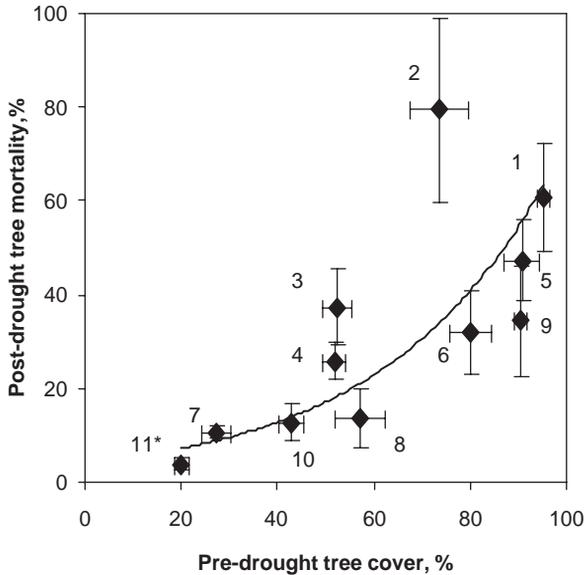
Figure 17.12. In the San Bernardino Mountains in southern California, predrought canopy cover (*x*-axis) in ponderosa pine-dominated mixed-conifer stands appears to influence the level of postdrought tree mortality (*y*-axis), largely due to successful bark beetle attack in these stands. Numbers correspond to plot numbers in Fig. 17.5. The upper four points are unmanaged stands. The lowest two points represent stands with prescribed burns (marked with a sun). Managed stands with thinning are indicated with arrows.

of the tree kills or otherwise repels the attacking adults. To kill a tree, large numbers of beetles must successfully colonize in a relatively short period of time (Paine et al., 1984, 1997). However, fewer beetles may be sufficient to kill a compromised tree (Paine et al., 1984). In a recent study in the San Bernardino Mountains, bark beetle activity and mortality of ponderosa and Jeffrey pine were positively related to O_3 injury and N deposition or experimentally amended N level (Eatough-Jones et al., 2004). Earlier studies also demonstrated that bark beetle damage was more severe, and host resistance decreased, in O_3-injured pines in the San Bernardino Mountains (Stark et al., 1968).

The primary bark beetles responsible for ponderosa pine mortality in the western San Bernardino Mountains are the western pine beetle, *Dendroctonus brevicomis* LeConte, and the mountain pine beetle, *D. ponderosae* Hopkins. Western pine beetle can produce up to four generations in a year in southern California due to the mild climate. As observed in the San Bernardino Mountains in 2003 through 2005
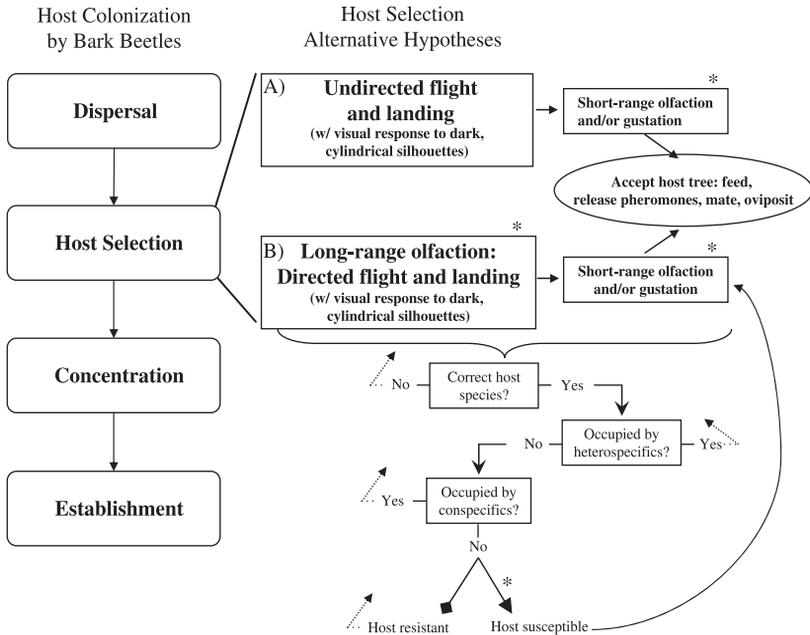
Host Colonization
by Bark Beetles

Host Selection
Alternative Hypotheses

Figure 17.13. Host colonization by bark beetles is subdivided into four phases (dispersal, host selection, concentration (aggregation), and establishment) according to Wood (1982). Two major hypotheses to describe host selection are based on (A) undirected flight or (B) directed flight based on long-range olfactory signals (Borden, 1997; Byers, 2004; Campbell & Borden, 2006; Pureswaran & Borden, 2005; Wood, 1982). Both of these alternatives may also integrate vision with olfaction, as some species respond well in flight to dark, cylindrical silhouettes (Strom et al., 1999, 2001). Both hypotheses may also include short-range olfaction and gustatory (tasting) behavior (McNee et al., 2000, 2003) after landing on the stem of a host or nonhost. Prior to (long range) or after landing, a bark beetle may undergo a series of binary decisions to evaluate the suitability or susceptibility of a host (Borden, 1997). Host selection decision nodes likely to be affected by air pollution, drought, and wildfire are indicated by (∗). (This figure was developed with the assistance of A.D. Graves, University of Minnesota, Department of Entomology.)

(Fig. 17.14), beetle populations increase rapidly, and the spatial extent of groups of dead trees expands annually when there is an abundance of susceptible trees.

Bark beetles aggregate and feed on the phloem, cambium, and outer xylem (subcortical tissue) in the tree bole. Eggs are laid in the phloem, and the larvae excavate galleries in this tissue. For most species, the larvae and pupae occur only in the phloem. Western pine beetle is unusual in that larvae of the second of the four instars (stages) migrate to the outer bark to complete their development (Miller & Keen, 1960). Thus,
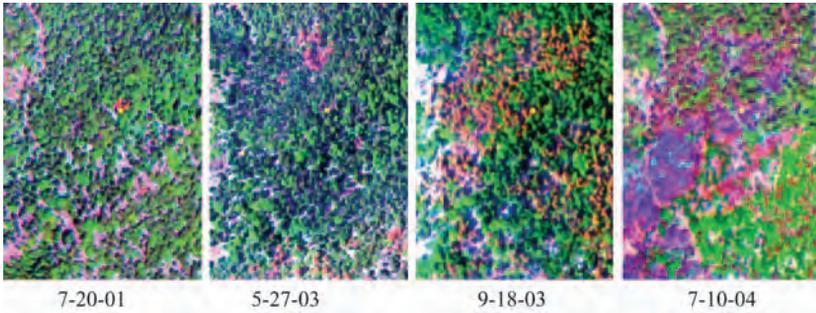
Figure 17.14. Remote imagery of Camp Paivika, San Bernardino National Forest, California. This forest stand is most affected by ozone and N deposition in North America. The sequence of remote imagery above was constructed from red, near-infrared, and thermal wavelengths at 5 km above the forest canopy. The yellow dot denotes the same location in each image. The forest stand is a mix of ponderosa pine, California black oak, white fir, incense cedar, and sugar pine. A dirt road and bare soil or dead herbaceous vegetation is indicated in fuchsia. On July, 20, 2001, the third year of a chronic drought, the first sign of bark beetle attack occurred on the site near the yellow dot (copper-colored trees). On May 27, 2003, after three years of chronic drought and an acute drought (2002), additional points of bark beetle infection were observed, including some possible drought-induced mortality (more scattered, individual dead ponderosa pine near the bottom of the image). On September 18, 2003, after the drought years plus the wet year (2003), tree mortality continued to accelerate, primarily ponderosa pine, white fir, and some sugar pine. On July 7, 2004, tree mortality was further increased (purple and fushia-colored areas) after the Old Fire swept through the area on October 12, 2003. At the stand level, the tree mortality for the first three dates, respectively, was 0%, 5%, and 42%. Observed mortality (estimated from proportion of pixels) declined to 32% in the July 7, 2004 image due to needle loss on standing dead trees.

pupation occurs either in the inner bark or in the outer bark, depending on the species of beetle. Adults emerge from the larval host tree and disperse to select new susceptible hosts (Fig. 17.13).

When attacked, healthy pines respond by exuding resin that either "pitches out" the adults, or blocks their progress. Resin production provides both a physical and chemical impedance to bark beetle attack. This response by pines is both constitutive and inducible after attempted colonization by the beetles (Franceschi et al., 2005; Langenheim, 2003; Nebeker et al., 1993). However, pines rely heavily on the preformed (i.e., constitutive) resin-based defense relative to other conifers (Nebeker et al., 1993). Oleoresin pressure, related to the turgor potential of cells lining the resin ducts, forces preformed resin to the site of injury or invasion. The cell turgor is derived from the transpirational stream; thus, if the tree is under drought stress, the cells lose turgor, the resin pressure is

reduced, and the effectiveness of the preformed resistance is compromised (Vité, 1961).

In weak trees with reduced resin pressure, adult beetles are able to successfully colonize and produce specific pheromones that attract other colonizing adults (concentration phase, Fig. 17.13). In 2000 (an average precipitation year based on a 68-yr record), Jeffrey pine was under sufficient drought stress so that the outer 1–2 cm of xylem tissue was < 50% water content in August and September versus 95% earlier in the growing season, and the transpirational stream was nearly 0 in xeric microsites (in Sequoia National Park; Grulke et al., 2003a). Of 32 Jeffrey pine in xeric microsites, 4 had succumbed to bark beetle by 2006 versus 2 out of 32 Jeffrey pine in mesic microsites (Grulke, unpublished data; mortality due to bark beetle, John Wenz, pers. comm.).

Extreme drought and other stresses reduce the photosynthetic capacity of trees and the levels of carbohydrates used for growth, defense, and tissue repair. This can have significant impact on the ability of the tree to induce an effective response to invasion (Mattson & Haack, 1987; Paine & Stephen, 1987a,b), as plants have only a limited amount of resources to partition between growth and defense (Herms & Mattson, 1992). Environmental factors such as drought stress also alter within-plant allocation of carbohydrates (Kozlowski & Pallardy, 2002). As mentioned previously, the high pollution site (Camp Paivika) had elevated carbohydrate content in just the bole (stem) due to changes in within-plant allocation relative to sites with lower stress levels (Grulke et al., 2001). Such a change in subcortical tissue concentration of carbohydrates may be a "tipping point" for increases in bark beetle populations. Trees with elevated bole carbohydrate levels at Camp Paivika sustained the highest rates of tree mortality due to both drought and bark beetle in the San Bernardino Mountains (see Fig. 17.12, site 1). In the 1960s, a multidisciplinary team of scientists concluded that ponderosa pines in this area that had been exposed to atmospheric pollutants were predisposed to bark beetle infestation (Stark et al., 1968). Highly drought-stressed plants are also known to exhibit increased levels of free amino acids (such as proline; Ain-Lhout et al., 2001; Lei et al., 2006), which are thought to increase cellular solute concentration, and thus lower osmotic potential and increase the ability of the cell to retain water under drought stress (but see discussion in Hare et al., 1998). However, an increase in free amino acids in subcortical tissue may also improve nutritional value for bark beetles, but is as yet untested. Once mature bark beetles emerge from the galleries by tunneling through the outer bark, they begin searching for a host. Although they appear to be able to discriminate host from nonhost, while in flight it is unclear

whether they can determine from a distance whether a host is susceptible or not (Fig. 17.13; Borden, 1997). Interestingly, conifers under moderate drought stress produce jasmonate, a plant hormone that stimulates resin production (for Norway spruce; Zeneli et al., 2006). There is no evidence that jasmonate itself elicits electrophysiological or behavioral responses from bark beetles. However, dense stands of pine, overgrown from excess N deposition and historic land management practices, may produce ample signal (terpene production), which could alter nonolfactory aspects of short-range host selection behavior (Fig. 17.13). During the extreme drought experienced in 2002, trees likely had insufficient turgor pressure in subcortical cells to exude resin. Thus, these trees may have been chemically competent, but physically incapable of exuding the resin as defense. Pollutant-exposed trees, already compromised and susceptible to drought stress, may be primed for successful bark beetle colonization.

17.9. Stand demographics across the San Bernardino Mountains

The type, timing, and magnitude of multiple stressors across the San Bernardino Mountains are presented in Table 17.2, which qualify the environmental conditions that led to bark beetle infestations. There were nine periods in the past 123 years that may have had sufficient tree drought stress to precipitate beetle epidemics. We can find evidence for five such events in the California Pest Reports that were first published annually in 1949. Prior to that, letters of the Forest Entomologist to the Regional Forester were used (written annually) to ascertain level of bark beetle infestation. Bark beetle was not considered significant (designated with a "+" in Table 17.2) unless more than four areas of 2000 ha or more were reported. Because the same areas were not inspected aerially and/or reported on each year, we report infestation qualitatively.

Since the forest in the San Bernardino Mountains had been thinned early in the late 19th century by commercial logging, we would not expect to observe an epidemic beetle infestation early in the 20th century, despite the drought stress experienced (Minnich et al., 1995) because tree density was low (Fig. 17.11). Human population in the Los Angeles Basin significantly increased after 1945, but air pollution levels were not quantified (or reconstructable) until 1963. From 1963 through 1980, peak 1-h O_3 concentrations averaged 250–425 ppb (Lee et al., 2003). From 1980 on, peak 1-h O_3 concentrations were still high (>250 ppb), but cumulative O_3 exposures over the growing season began to decline. Through strong regulatory controls, O_3 concentrations declined further

Table 17.2.   List of drought years experienced regionally, bark beetle outbreaks, pollution levels, and stand density in the western San Bernardino Mountains. The years of moderate or extreme drought, the average percent of total average annual precipitation (based on the 120-yr record), the percent of total average annual precipitation in the year following drought, and whether a bark beetle epidemic occurred after the sequence of drought years is also presented

1st year of drought	Dates of aerial photos	% of 123-yr record[a]				3–4 year average	Bark Beetle[b]	Pollution SUM06[c]	Tree cover %[d]
		1	2	3	4				
	1860								(Logged)
1897		54	35	60		50			
1922		68	60	70		66			
1927		51	65	84	79	70			
	1938								76±5
1947		78	88	84	64	79			
1958		71	73	46		63	++		
	1965							100	83±3
1969		55	66	55		59	+++	170	
1973		61	63	79	42	61	++	140	
1986		47	37	48	48	45	++	160	
	1994							150	95±1
1999		39	56	59	25	45	++++	110	
	2004								34±5

[a]San Bernardino County Water Management District database, site 6032 Big Bear Dam, from 1983 to present.
[b]California Pest Reports, Annual, USDA Forest Service, San Francisco, California; 1949 to present for the San Bernardino Mountains area in general.
[c]Air pollution reconstructed for the Camp Paivika area, as an example from Lee et al. (2003).
[d]Changes in stand cover from Camp Paivika estimated from eight 1-ha plots drawn on aerial imagery (this chapter).

to tens of occurrences to only isolated occurrences of hourly concentrations exceeding 95 ppb from the mid-1990s to present. However, N continued to accumulate in these ecosystems, and drought stress was exacerbated by chronic O_3 exposure.

The effect of multiple stressors (pollutant deposition, stand densification, drought stress, effects of bark beetle infestations) on stand demography were evaluated across the San Bernardino Mountains at 11 sites (Fig. 17.5) using historic aerial photographs from 1938, 1965, 1994, and 2004 (archived at the SBNF Supervisor's Office, San Bernardino, California). These years were chosen with regard to prior multiple-year droughts and photographic quality. Stand demography (tree cover and density, recruitment, and mortality) was measured from four to eight 1-ha plots sampled sequentially from the aerial photographs taken in (Fig. 17.3). In the western San Bernardino Mountains (plot 1) and at other high pollutant exposure sites (plot 5, 6, 8) along the southern and western front of the range, tree density was especially high (as high as 160 trees ha^{-1}). Tree density increased the most from the mid-1960s to 1994 (Fig. 17.11). The highest mortality rates were observed between 1994 and 2004 at the sites with the highest initial density or tree cover (sites 1, 2, and 5, Fig. 17.12). At sites with the lowest canopy cover or tree density resulting from wildfire (1970 in Snow Valley, site 7, Figs. 17.5, 17.11, 17.12) or prescribed fire (1987 in Big Pine Flat, site 11, Fig. 17.5), mortality was <10 trees ha^{-1} (Fig. 17.12). Despite the high predrought tree density at Seeley Flats (site 2), we believe that mortality was lower than expected due to more consistent groundwater availability relative to other sites in the western San Bernardino Mountains. We cannot explain the high tree density development at Barton Flats (site 9), a moderate pollution site, but this is also reported by Miller et al. (1989) and Arbaugh et al. (1999) for plots located in the same area.

Although aerial photography illustrated decadal or multiple decadal changes in forest density and mortality rates, we were able to capture the specific effects of chronic drought (1999–2001), the acute drought (2002), the development of epidemic bark beetle infestation (2003–2004), and the incursion of the October 2003 Old Fire from the chaparral into the mixed-conifer forest (Fig. 17.14) at one of the sites (site 1, Camp Paivika, the high pollution site). A sequence of images was taken at 5 km above the forest canopy and constructed from the intensities of red, near-infrared, and thermal wavelengths.

After 3 years of chronic drought at this polluted site, clusters of tree mortality due to bark beetle attack were apparent in the July 20, 2001, imagery (red trees, Fig. 17.14). Based on imagery analysis, the mean stand tree mortality rate was 0% based on subsamples of four, 0.25 ha plots

(Fig. 17.14). After both chronic and acute drought, tree mortality due to both bark beetles and drought was 5% at the stand level (mostly ponderosa pine) based on the same imagery analysis (May 27, 2003). A field measure of mortality at this site yielded 9.5% mortality, also assessed in spring 2003 (based on a total of 62 yellow pine trees (ponderosa and Jeffrey pine combined); Eatough-Jones et al., 2004). In the spring following the wet winter, bark beetle populations reached epidemic proportions, and 42% of the trees had died (ponderosa pine, white fir, and sugar pine) by September 18, 2003 (proportion of imagery with "dead tree" signature of red, near-infrared, and thermal, Fig. 17.14). Estimates of mortality from true-color aerial photographs (42.7%) were very similar. Field assessments in the previous spring estimated that a total of 55.6% of the ponderosa pine had been affected by bark beetle activity (Eatough-Jones et al., 2004), suggesting that most of the tree mortality at the site was attributable to successful bark beetle colonization of ponderosa pine (assuming all ponderosa pine colonized in spring 2003 were destined to die by fall 2003). Discrepancies between field counts and imagery analysis are likely due to inability to count dead trees under large canopies (field count predicted higher mortality), the patchy distribution of beetle colonization (see Fig. 17.14), total sample size (aerial photos: 2920 trees in eight 1-ha plots; field count: 60 trees in three plots), and time lag between bark beetle colonization and tree death.

The stand was at high risk for an intense fire with high litter layers, high numbers of standing dead trees, and susceptible live trees exacerbated by drought stress. In autumn of that year, the Old Fire swept through the stand (imagery taken the following summer, July 10, 2004 Fig. 17.14). Interestingly, not all of the "red trees" (standing dead with needles retained) were consumed in a crown fire because the highly dense understory was not in contact with the lower branches of the ~ 100-yr old trees. The effects of O_3 exposure, excess nitrogen deposition, and drought had promoted lower branch abscission so that the lowest branches were attached at 20 m or higher. Trees continue to be colonized by bark beetles and die at this site, but the rate of change is below statistical detection. We assume that the timing of most of the mortality observed between 1994 and 2004 follows that presented for site 1—that mortality occurred primarily between 2003 and 2004.

17.10. Conclusions

The role of air pollutants in increasing tree susceptibility to drought, successful bark beetle attack, disease, tree mortality, and thus to wildfire

has been largely ignored by land managers. Elevated levels of photochemical oxidants and N deposition as described for the San Bernardino Mountains also occur over the western and southern regions of the Sierra Nevada. Ozone injury to pines and elevated nitrate export in streams have also been reported from these areas, suggesting that air pollution in these regions may be sufficient to predispose the most polluted forest stands in the Sierra Nevada to greater mortality and wildfire risk. In the San Bernardino Mountains air pollutants, specifically strong oxidants and nitrogen deposition, contribute to increased litter accumulation and increased tree susceptibility to drought stress. It is well known that drought-stressed trees are more susceptible to successful colonization by bark beetles. The combined chronic drought in 1999–2001 and acute drought in 2002 resulted in a bark beetle epidemic in the western San Bernardino Mountains. The evidence from our research shows that the severity of tree mortality in the western San Bernardino Mountains was significantly exacerbated by the higher air pollutant deposition in this region.

REFERENCES

Ain-Lhout, F., Zunzunegui, M., Diaz-Barradas, M.C., Tirado, R., Clavijo, A., and Garcia-Novo, R. 2001. Comparison of proline accumulation in two mediterranean shrubs subjected to natural and experimental water deficit. Plant Soil 230, 175–183.

Arbaugh, M.J., Peterson, D.L., and Miller, P.R. 1999. Air pollution effects on growth of ponderosa pine, Jeffrey pine, and bigcone Douglas-fir. In: Miller, P.R., and McBride, J.R., eds. Oxidant air pollution impacts in the montane forests of Southern California: A case study of the San Bernardino Mountains, Ecological Studies 134. Springer-Verlag, New York, pp. 179–207.

Asher, J.E., and Forrest, D.W. 1982. Lake arrowhead communities forest management plan's "State of the Forest" report. Lake Arrowhead Property Owners Association, Lake Arrowhead, CA.

Atkinson, R., and Arey, J. 2003. Gas-phase tropospheric chemistry of biogenic volatile organic compounds: A review. Atmos. Environ. 37, S197–S219.

Bauer, M.R., Hultman, N.E., Panek, J.A., and Goldstein, A.H. 2000. Ozone deposition to a ponderosa pine plantation in the Sierra Nevada Mountains (CA): A comparison of two different climatic years. J. Geophys. Res. 105, 123–136.

Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22.

Borden, J.H. 1997. Disruption of semiochemical-mediated aggregation in bark beetles. In: Cardé, R.T., and Minks, A.K., eds. Insect pheromone research: New directions. Chapman & Hall, New York, pp. 421–438.

Boyce, J.S. 1961. Forest pathology (Third ed.). McGraw-Hill, New York.

Breiner, J., Gimeno, B.S., and Fenn, M. 2007. Calculation of theoretical and empirical nutrient N critical loads in the mixed-conifer ecosystems of southern California. ScientificWorldJournal 7(S1), 198–205, doi: 10.1100/tsw.2007.65.

Byers, J.A. 2004. Chemical ecology of bark beetles in a complex olfactory landscape. In: Lieutier, F., Day, K.R., Battisti, A., Gregoire, J.-C., and Evans, H.F., eds. Bark and wood boring insects living in trees in Europe, a synthesis. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 89–134.

Bytnerowicz, A., Arbaugh, M., Schilling, S., Fraczek, W., and Alexander, D. in press. Ozone distribution and phytotoxic potential in mixed conifer forests of the San Bernardino Mountains, southern California. Environ. Pollut.

Bytnerowicz, A., Tausz, M., Alonso, R., Jones, D., Johnson, R., and Grulke, N. 2002. Summer-time distribution of air pollutants in the Sequoia national park, California. Environ. Pollut. 118, 187–203.

Cahill, T.M., Seaman, V.Y., Charles, M.J., Holzinger, R., and Goldstein, A.H. 2006. Secondary organic aerosols formed from oxidation of biogenic volatile organic compounds in the Sierra Nevada Mountains of California. J. Geophys. Res. 111, D16312, doi: 10.1029/2006JD007178.

Campbell, S.A., and Borden, J.H. 2006. Close-range, in-flight integration of olfactory and visual information by a host-seeking bark beetle. Entomol. Exper. Applic. 120, 91–98.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., and Parkhurst, D.F. 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81, 2359–2365.

Castillo, F., and Heath, R.L. 1990. Ca^{2+} transport in membrane vesicles from pinto bean leaves and its alteration after ozone exposure. Plant Physiol. 94, 788–795.

De Kok, L.J., and Tausz, M. 2001. The role of glutathione in plant reaction and adaptation to air pollutants. In: Grill, D., Tausz, M., and De Kok, L.J., eds. Significance of glutathione to plant adaptation to the environment. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 185–205.

Dizengremel, P. 2001. Effects of ozone on the carbon metabolism of forest trees. Plant Physiol. Biochem. 39, 729–742.

Eatough-Jones, M., Paine, T.D., Fenn, M.E., and Poth, M.A. 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. Forest Ecol. Manag. 200, 67–76.

Fenn, M.E., and Dunn, P.H. 1989. Litter decomposition across an air-pollution gradient in the San Bernardino Mountains. Soil Sci. Soc. Am. J. 53, 1560–1567.

Fenn, M.E., Dunn, P.H., and Wilborn, R. 1990. Black stain root disease in ozone-stressed ponderosa pine. Plant Dis. 74, 426–430.

Fenn, M.E., and Poth, M.A. 1999. Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California. J. Environ. Qual. 28, 822–836.

Fenn, M.E., Poth, M.A., and Johnson, D.W. 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. For. Ecol. Manag. 82, 211–230.

Fenn, M.E., and Poth, M.A. 2004. Monitoring nitrogen deposition in throughfall using ion exchange resin columns: A field test in the San Bernardino Mountains. J. Environ. Qual. 33, 2007–2014.

Fenn, M.E., Poth, M.A., Terry, J.D., and Blubaugh, T.J. 2005. Nitrogen mineralization and nitrification in a mixed-conifer forest in southern California: controlling factors, fluxes, and nitrogen fertilization response at a high and low nitrogen deposition site. Can. J. For. Res. 35, 1464–1486.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63, 433–462.

Franceschi, V.R., Krokene, P., Christiansen, E., and Krekling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytol. 167, 353–376.

Franco-Vizcaino, E., Escota-Rodriguez, M., Sousa-Ramirez, J., and Minnich, R.A. 2002. Water balance of the southern limit of the California mixed conifer forest and implications for extreme deficits watershed. Aridland Res. Manag. 16, 133–147.

Grulke, N.E. 1999. Physiological responses of ponderosa pine to gradients of environmental stressors. In: Miller, P.R., and McBride, J., eds. Oxidant air pollution impacts in the Montane Forests of southern California: A case study of the San Bernardino Mountains, Ecological Studies 134. Springer-Verlag, New York, pp. 126–163.

Grulke, N.E. 2000. An analysis of short-, medium-, and long-term O_3 exposure in influencing stomatal conductance of ponderosa pine. Proc., IUFRO Working Group 7.04, Air Pollution Effects, 28–31 May, Michigan Technical University: Houghton, MI.

Grulke, N.E. 2003. Physiological basis of ozone injury assessment in Sierra Nevadan conifers. In: Bytnerowicz, A., Arbaugh, M., and Alonso, R., eds. Assessment of ozone distribution and its effects on Sierra Nevada ecosystems. Dev.Environ. Sci. 2, 55–81. Elsevier Publishers, The Hague, The Netherlands, pp. 55–82.

Grulke, N.E., Andersen, C.P., Fenn, M.P., and Miller, P.R. 1998. Ozone exposure and N deposition reduces root biomass in ponderosa pine across the San Bernardino Mountains, California. Environ. Pollut. 103, 63–73.

Grulke, N.E., and Balduman, L. 1999. Deciduous conifers: High nitrogen deposition and ozone exposure effects on ponderosa pine. Water, Soil, Air Pollut. 116, 235–248.

Grulke, N.E., Andersen, C.P., and Hogsett, W.E. 2001. Seasonal changes in carbohydrate pools of ponderosa pine in stands under differing environmental stress. Tree Physiol. 21, 173–184.

Grulke, N.E., Preisler, H.K., Rose, C., Kirsch, J., and Balduman, L. 2002. O_3 uptake and drought stress effects on carbon acquisition of ponderosa pine in natural stands. New Phytol. 154, 621–631.

Grulke, N.E., Johnson, R., Esperanza, A., Jones, D., Nguyen, T., Posch, S., and Tausz, M. 2003a. Canopy transpiration of Jeffrey pine in mesic and xeric microsites: O_3 uptake and injury response. TREES 17, 292–298.

Grulke, N.E., Johnson, R., Jones, D., Monschein, S., Nikolova, P., and Tausz, M. 2003b. Variation in morphological and biochemical O_3 injury attributes of Jeffrey pine within canopies and between microsites. Tree Physiol. 23, 923–929.

Grulke, N.E., Alonso, R., Nguyen, T., Cascio, C., and Dobrowolski, W. 2004. Stomata open at night: Implications for pollutant uptake in ponderosa pine. Tree Physiol. 24, 1001–1010.

Grulke, N.E., Dobrowolski, W.L., Mingus, P., and Fenn, M.E. 2005. California black oak response to N-amendment at an N-saturated site. Environ. Pollut. 137, 536–545.

Grulke, N.E., Paoletti, E., and Heath, R.A. 2006. Direct measurements of foliar ozone uptake in crop and tree species. Environ. Pollut. 146, 640–647.

Hare, P.D., Cress, W.A., and Van Staden, J. 1998. Dissecting the roles of osmolyte accumulation during stress. Plant Cell Environ. 21, 535–553.

Hawksworth, F.G., and Shaw III, C.G. 1987. Damage and control of major diseases of ponderosa pine. In: Baumgartner, D.M., and Lotan, J.E., eds. Symposium proceedings, ponderosa pine: The species and its management, 29 September 29 to 1 October. Spokane, Washington, USA. Dept. Nat. Res. Sci., Coop. Ext., Washington State University, Pullman, WA, pp. 99–108.

Haynes, B.E., and Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15, 317–325.

Herms, D.A., and Mattson, W.J. 1992. The dilemma of plants: To grow or defend. Qtr. Rev. Biol. 67, 283–335.

Hubbert, K., Beyers, J.L., and Graham, R.C. 2001. Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula*. Can. J. For. Res. 31, 1947–1957.

James, R.L., Cobb, F.W. Jr., Miller, P.R., and Parmeter, J.R., Jr. 1980. Effects of oxidant air pollution on susceptibility of pine roots to *Fomes annosus*. Phytopath 70, 560–563.

Kimmins, J.P. 1997. Forest ecology: A foundation for sustainable management (Second ed.). Prentice Hall, Upper Saddle River, NJ, USA.

Knorr, M., Frey, S.D., and Curtis, P.S. 2005. Nitrogen additions and litter decomposition: A meta-analysis. Ecology 86, 3252–3257.

Kozlowski, T.T., and Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68, 270–334.

Kuyper, T.W. 1994. Fungal species diversity and forest ecosystem functioning in the Netherlands. In: Boyle, T.J.B., and Boyle, C.E.B., eds. Biodiversity, temperate ecosystems, and global change, NATO ASI series. Springer-Verlag, Berlin, Vol. I 20, pp. 99–122.

Langenheim, J.H. 2003. Plant resins—chemistry, evolution, ecology, and ethnobotany. The Timber Press, Portland, OR.

Lee, E.H., Tingey, D.T., Hogsett, W.E., and Laurence, J.A. 2003. History of tropospheric ozone for the San Bernardino Mountains of southern California, 1963–1999. Atmos. Environ. 37, 2705–2717.

Lei, Y., Yin, C., and Li, C. 2006. Differences in some morphological, physiological, and biochemical responses to drought stress in two contracting populations of *Populus przewalskii*. Physiol. Plant. 127, 182–191.

Levitt, J. 1980. Responses of plant to environmental stresses. Academic Press, London.

Maier-Maercker, U., and Koch, W. 1992. The effect of air pollution on the mechanism of stomatal control. Trees 7, 12–25.

Marks, G.C., Kassaby, F.Y., and Fagg, P.C. 1973. Die-back tolerance in eucalypt species in relation to fertilization and soil populations of *Phythophthora cinnamomi*. Aust. J. Bot. 21, 53–65.

Mattson, W.J., and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. BioSci 37, 110–118.

Matyssek, R., Gunthardt-Georg, M.S., Maurer, S., and Keller, T. 1995. Nighttime exposure to ozone reduces whole-plant production in Betual pendula. Tree Physiol. 15, 159–165.

Matyssek, R., and Sandermann, H. 2003. Impact of ozone on trees: An ecophysiological perspective, Progress in Botany 64. Springer-Verlag, Heidelberg, 349–404.

McAinsh, M.R., Evans, N.H., Montgomery, L.T., and North, K.A. 2002. Calcium signalling in stomatal responses to pollutants. New Phytol. 153, 441–447.

McLaughlin, S.B., Wullschleger, S.D., Sun, G., and Nosal, M. 2007. Interactive effects of ozone and climate on southern Appalachian forests in the USA: II. Effects on water use, soil moisture content, and streamflow. New Phytol. 174, 109–124.

McNee, W.R., Wood, D.L., and Storer, A.J. 2000. Pre-emergence feeding in bark beetles (Coleoptera: Scolytidae). Environ. Entomol. 29, 495–501.

McNee, W.R., Bonello, P., Storer, A.J., Wood, D.L., and Gordon, T.R. 2003. Feeding response of *Ips paraconfusus* to phloem and phloem metabolites of *Heterobasidion annosum*-inoculated ponderosa pine, *Pinus ponderosa*. J. Chem. Ecol. 29, 1183–1201.

Michalski, G., Meixner, T., Fenn, M., Hernandez, L., Sirulnik, A., Allen, E., and Thiemens, M. 2004. Tracing atmospheric nitrate deposition in a complex semiarid ecosystem using Δ^{17}O. Environ. Sci. Tech. 38, 2175–2181.

Miller, J.M., and Keen, F.P. 1960. Biology and control of the western pine beetle: A summary of the first fifty years of research. USDA Forest Service Misc. Publ. 800.

Miller, P.R., McBride, J.R., Schilling, S.L., and Gomez, A.P. 1989. Trend of ozone damage to conifer forests between 1974 and 1988 in the San Bernardino Mountains of southern California. In: Olson, R.K., and Lefohn, A.S., eds. Effects of air pollution on western forests. Trans., Air, Waste Manag. Assoc., June. Anaheim, CA. Air, Waste, Manag. Assoc.: Pittsburgh, PA, pp. 309–324.

Miller, P.R., Stolte, K.W., Duriscoe, D., and Pronos, J. 1996. Methods for monitoring air pollution: Effects on western conifers. USDA Forest Service PSW-GTR-155.

Minnich, R.A. 1988. The biogeography of fire in the San Bernardino Mountains of California: A historical survey, Geography 28. University of California Publication, Riverside, CA, 128 pp.

Minnich, R.A., Barbour, N.G., Burk, J.H., and Fernau, R.F. 1995. Sixty years of change in California conifer forest of the San Bernardino Mountains. Conserv. Biol. 9, 902–914.

Nebeker, T.E., Hodges, J.D., and Blanche, C.A. 1993. Host response to bark beetle and pathogen colonization. In: Schowalter, T.D., and Filip, G.M., eds. Beetle-pathogen interaction in Conifer Forests. Academic Press, London, pp. 157–173.

Nilsson, L.-O. 1995. Forest biogeochemistry interactions among greenhouse gases and N deposition. Water, Air, Soil Pollut. 85, 1557–1562.

Nohrstedt, H.-Ö., Arnebrant, K., Bååth, E., and Söderström, B. 1989. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. Can. J. For. Res. 19, 323–328.

Paine, T.D., Stephen, F.M., and Taha, H.A. 1984. Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. Environ. Ent. 13, 619–624.

Paine, T.D., and Stephen, F.M. 1987a. Influence of tree stress and site quality on the induced defense system of loblolly pine. Can. J. For. Res. 17, 569–571.

Paine, T.D., and Stephen, F.M. 1987b. The relationship of tree height and crown class to the induced plant defenses of loblolly pine. Can. J. Bot. 65, 2090–2092.

Paine, T.D., Raffa, K.F., and Harrington, T.C. 1997. Interactions among scolytid bark beetles, their associated fungi and live host conifers. Ann. Rev. Entomol. 42, 179–206.

Panek, J.A., and Goldstein, A.H. 2001. Response of stomatal conductance to drought in ponderosa pine: Implications for carbon and ozone uptake. Tree Physiol. 21, 337–344.

Patterson, M.T., and Rundel, P.W. 1989. Seasonal physiological responses of ozone-stressed Jeffrey pine in Sequoia National Park, California. In: Olson, R.K., and Lefohn, A., eds. Effects of air pollution on western forests. Air Waste Manag. Assoc., Pittsburgh, PA, pp. 419–427.

Pei, A.-M., Murata, Y., Benning, G., Thomine, S., Klüsener, B., Allen, G.J., Grill, E., and Schroeder, J.I. 2000. Calcium channels activated by hydrogen peroxide mediate abscisic acid signalling in guard cells. Nature 406, 731–734.

Persson, T., Karlsson, P.S., Seyferth, U., Sjoberg, R.M., and Rudebeck, A. 2000. Carbon mineralisation in European forest soils. In: Schulze, E.-D., ed. Carbon and nitrogen cycling in European forest ecosystems, Ecological Studies 142. Springer-Verlag, Berlin, pp. 257–275.

Pronos, J., Merrill, L., and Dahlsten, D. 1999. Insects and pathogens in a pollution-stressed forest. In: Miller, P.R., and McBride, J.R., eds. Oxidant air pollution impacts in the Montane Forests of southern California: A case study of the San Bernardino Mountains, Ecological Studies 134. Springer-Verlag, New York, pp. 317–337.

Pureswaran, D.S., and Borden, J.H. 2005. Primary attraction and kairomonal host discrimination in three species of *Dendroctonus* (Coleoptera: Scolytidae). Agric. For. Entomol. 7, 219–230.

Reiter, I.M., Haberle, K.-J., Nunn, A.J., Heerdt, C., Reitmayer, H., Grote, R., and Matyssek, R. 2005. Competitive strategies in adult beech and spruce: Space-related foliar carbon investment versus carbon gain. Oecologia 146, 337–349.

Riggan, P.J., Lockwood, R.N., and Lopez, E.N. 1985. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. Environ. Sci. Tech. 19, 781–789.

Snoeijers, S.S., Perez-Garcia, A., Joosten, M.H.A.J., and De Witt, J.G.M. 2000. The effect of nitrogen on disease development and gene expression in bacterial and fungal plant pathogens. Eur. J. Plant Path. 106, 493–506.

South Coast Air Quality Management District. 1997. The Southland's war on smog: 50 years of progress toward clean air. www.aqmd.gov/news1/Archives/History/marchcov.html

Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The theory and practice of branch autonomy. Ann. Rev. Ecol. Sys. 22, 309–334.

Stark, R.W., Miller, P.R., Cobb, F.W. Jr., Wood, D.L., Parameter, J.R. Jr., and Zavarin, E. 1968. Photochemical oxidant injury and bark beetle (Coleoptera: Scolytidae) infestation of ponderosa pine. Hilgardia 39, 121–152.

Strom, B.L., Roton, L.M., Goyer, R.A., and Meeker, J.R. 1999. Visual and semiochemical disruption of host finding in the southern pine beetle. Ecol. Appl. 9, 1028–1038.

Strom, B.L., Goyer, R.A., and Shea, P.J. 2001. Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. Entomol. Exp. Appl. 100, 63–67.

Swanston, C., Homann, P.S., Caldwell, B.A., Myrold, D.D., Ganio, L., and Sollins, P. 2004. Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochem 70, 227–250.

Temple, P.J., and Miller, P.R. 1998. Seasonal influences on ozone uptake and foliar injury to ponderosa and Jeffrey pines at a southern California site. In: Bytnerowicz, A., Arbaugh, M.J., and Schilling, S.L., eds. Tech. coor., Proc., Internatl Symp. air pollution and climate change effects on forest ecosystems, 1996 February 5–9. Riverside, CA. General Technical Report, PSW-GTR-166. U.S. Dept. Agric., Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 221–228.

Tingey, D.T., Hogsett, W.E., and Lee, E.H. 2004. Stricter ozone ambient air quality standard has beneficial effect on ponderosa pine in California. Environ. Manag. 34, 397–405.

Tjoelker, M.G., Volin, J.C., Oleksyn, J., and Reich, P.B. 1995. Interaction of ozone pollution and light effects on photosynthesis in a forest canopy experiment. Plant, Cell, Environ. 18, 895–905.

Torsethaugen, G., Pell, E.J., and Assmann, S.M. 1999. Ozone inhibits guard cell K^+ channels implicated in stomatal opening. Proc., Natl Acad. Sci. USA 96, 1357–13582.

Utkhede, R., and Smith, E. 1995. Effect of nitrogen form and application method on incidence and severity of *Phytophthora* crown and root rot of apple trees. Eur. J. Plant Path. 101, 283–289.

Vité, J.P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. Contrib., Boyce Thompson Inst. 21, 37–66.

Vogt, C. 2003. Seasonal and permanent homeowners' past experiences and approval of fuels reduction. In: P. Jakes (comp.). Homeowners, communities, and wildfire: Science findings from the National Fire Plan. U.S. Dept. Agric., Forest Service, North Central Research Station, St. Paul, MN, pp. 63–73.

Vogt, C.A., and Cindrity, S.J. 2003. A changing landscape in the wildland-urban interface: Permanent and seasonal homeowners, recreation, and fuel management. In: Schuster, R., (comp). Proc., Northeastern Recreation Research Symposium; 13–16 April, 2002. Bolton Landing, NY. General Technical Report NE-302. U.S. Dept. Agric., Forest Service, Northeastern Research Station: Newtown Square, PA, pp. 208–214.

Weber, J.A., Clark, C.S., and Hogsett, W.E. 1993. Analysis of the relationships among O_3 uptake, conductance, and photosynthesis in needles of *Pinus ponderosa*. Tree Physiol. 13, 157–172.

Weiser, G., and Havranek, W.M. 1993. Ozone uptake in the sun and shade crown of spruce: Quantifying the physiological effects of ozone exposure. Trees 7, 227–232.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313, 940–943.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Ann. Rev. Entomol. 27, 411–446.

Zeneli, G., Krokene, P., Christiansen, E., Krekling, T., and Gershenzon, J. 2006. Methyl jasmonate treatment of mature Norway spruce (*Picea abies*) trees increases the accumulation of terpenoid resin components and protects against infection by *Ceratocystis polonica*, a bark beetle-associated fungus. Tree Physiol. 26, 977–988.

Zhang, X., Zhang, L., Dong, F., Gao, J., Galbraith, D.W., and Song, C.-P. 2001. Hydrogen peroxide is involved in abscisic acid-induced stomatal closure in *Vicia faba*. Plant Physiol. 126, 1438–1448.

Zhu, J., Talbott, L.D., Jin, X., and Zeiger, E. 1998. The stomatal response to CO_2 is linked to changes in guard cell zeaxanthin. Plant Cell Environ. 21, 813–820.

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