

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

N.E. Grulke, R.A. Minnich, T. Paine, and P. Riggan

N.E. Grulke, research plant physiologist, USDA Forest Service, Pacific Southwest Research Station, Riverside, CA 92507; **T. Paine**, professor, Department of Entomology, and **R.A. Minnich**, professor, Department of Geography, University of California, Riverside, CA 92521; and **P. Riggan**, research soil scientist, USDA Forest Service, Pacific Southwest Research Station, Riverside, CA 92507.

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 factors have been exacerbating forest susceptibility to wildfires over the last century in southern California. Here we report on the significant role that air pollution has on increasing forest susceptibility to wildfires, as unfolded in the San Bernardino Mountains from 1999 to 2003. Air pollution, specifically ozone (O_3), and wet and dry deposition of nitrogenous compounds from fossil fuel combustion, has significantly increased since industrialization of the region after WWII. Ozone and elevated nitrogen deposition cause specific changes in forest tree carbon, nitrogen, and water balance that enhance individual tree susceptibility to drought and bark beetle attack, and these changes contribute to whole ecosystem susceptibility to wildfire. For example, elevated O_3 and N deposition increase leaf turnover rates and leaf and branch litter, and decrease decomposability of litter. Uncharacteristically, deep litter layers develop 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, the latter effect increasing tree susceptibility to drought and beetle attack. Because both foliar and root masses are compromised, carbohydrates are stored in the bole over winter. Elevated O_3 increases drought stress by significantly reducing plant control of water loss. The resulting increase in canopy transpiration, combined with [O_3 + N deposition]-induced decreases

in root mass significantly increase tree susceptibility to drought stress, and when additionally combined with increased bole carbohydrates, perhaps all contribute to success of bark beetle attack. Phenomenological and experimental evidence is presented to support the role of these factors contributing to the susceptibility of forests to wildfire in southern California.

Keywords: Bark beetle, fire suppression, forest densification, N deposition, O_3 exposure.

Introduction

Many factors combine to increase forest susceptibility to wildfire in southern California, and most of these were set in motion decades ago. These factors include a rapid increase in human population and resource use; a shift from timber production to recreational forest use; fire suppression with subsequent forest densification; periodic, extreme drought; and bark beetle outbreaks. The contribution of air pollution to forest susceptibility to wildfire has not been studied extensively. In this paper, we will link air pollution to increasing forest densification, litter build up, drought stress, tree susceptibility to successful bark beetle attack, tree mortality, and increased forest susceptibility to wildfire (Figure 1). A case study will be presented for the San Bernardino Mountain Range in the Transverse Range north and east of Los Angeles, California. We will focus on pollutant effects on ponderosa pine, which dominates the mixed conifer forest in the western part of the range.

In the late 19th century, gold and other valuable minerals were discovered in the San Bernardino Mountains, and the population rapidly increased (Minnich 1988). The forest was logged for buildings, mine shaft support, and for fuel. In 1899, a severe drought occurred, water was limiting, and a premium was placed on reservoir development (Lake Gregory, Arrowhead, Big Bear). As the reservoirs were established, they became magnets for recreation use in the 1920s. With the shift from resource utilization to recreation, incursions of fire from the chaparral into the forest were suppressed, and forest density increased through the 1940s.

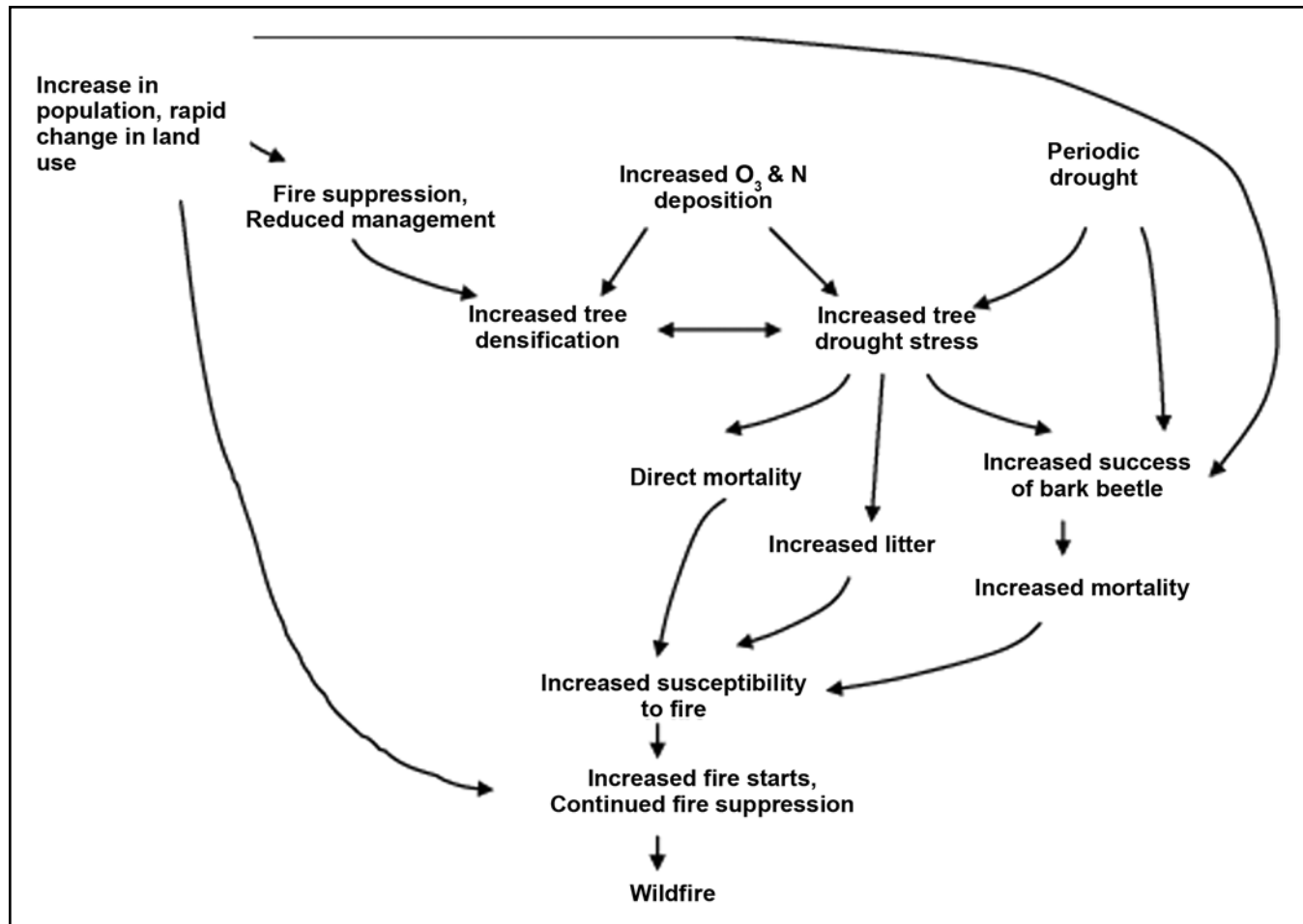


Figure 1—Many factors contributing to forest susceptibility to wildfire were set in motion decades before ignition. However, increased O₃ exposure and nitrogen (N) deposition significantly contribute to forest susceptibility to wildfire by increasing tree drought stress (with subsequent increase in successful bark beetle attack) and promoting formation of deeper, more recalcitrant litter layers.

In the 1950s, the Forest Service made an attempt to thin the forests, but, for aesthetic reasons, the mountain communities strongly opposed both branch trimming and stand thinning. As a consequence, the forest continued to increase in density, and trees grew increasingly closer to structures. In the 1980s, the community councils drew up “Forest Plans” that included branch trimming and thinning of trees within 30 m of valued structures (Asher and Forrest 1982). However, these recommendations were not followed or enforced. The region was, and is, highly susceptible to wildfire.

Air Pollution Effects: O₃ and N Deposition

The primary source of air pollution is fossil fuel combustion from trucks, cars, trains, ships, and industry (South Coast Air Quality Management District 1997). Fossil fuel

combustion emits nitrogen oxides, which are converted to other nitrogen oxides and ozone (O₃) in the presence of high energy UV light. Both nitrogen oxides and O₃ are strong oxidizing agents and cause damage to cells. Ozone is transported long distances. Nitrogen oxides are not transported as far as O₃, but at moderate O₃ levels, dry and wet deposition of nitrogen to plant communities is significant (6 to 9 kg/ha per year) (Fenn and others 1996) and accumulates through time. The effects of O₃, N deposition, and periodic drought are evaluated here as contributing factors to forest susceptibility to wildfires.

Ozone is primarily deposited on surfaces (such as surfaces of leaves, branches, bark, soil, and litter), and there decomposes. Bauer and others (2000) estimated that approximately one-third of the O₃ is taken into the plant

via stomata. When plants take up CO_2 , they also take up O_3 . Once O_3 enters the leaf, it may be decomposed in a thin film of water (apoplastic water) that surrounds cells in the substomatal chamber, or it may pass across the cell membrane to the chloroplast where it degrades photosynthetic pigments. The decomposition of O_3 in the apoplastic water requires the regeneration of oxidized ascorbate with glutathione in the cytosol and energy (De Kok and Tausz 2001). As it passes across membranes, the acidity changes, and membrane permeability is altered such that ions that should be retained by the cell now leak out (K^+), others influx along a chemical gradient (Zhang and others 2001), and other mechanisms of ion transport are blocked (e.g., Ca^{++} channeling) (McAinsh and others 2002). When strong oxides degrade photosynthetic pigments in the chloroplast, the pigments must be reconstructed into functional arrays, which requires energy.

The first measurable effect of O_3 on plants is a decrease in the efficiency of photosynthesis or the carbon-capturing mechanism. Because O_3 damages tissue, there is a metabolic cost in energy and constituent building materials that increases respiration and decreases the total carbon stored by the plant. Carbon-carbon links store energy in plants for later use. Lower total carbon stored and greater requirements for N (to build more photosynthetic pigments) result in retranslocation of materials out of older needles. Older branches are excised in O_3 -exposed trees because the net carbon balance is lower. Presumably, when net carbon balance drops below zero, the branch is excised (Sprugel and others 1991).

At the whole plant (tree) level, O_3 exposure results in premature senescence of needles (within-whorl loss of needles, fewer needle-age classes) in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) (Grulke and Balduman 1999) and lower branch abscission (Miller and others 1996b). Greater O_3 exposure and N deposition cause more needle and branch loss. The western end of the San Bernardino Mountains, the part of the mountain range closest to Los Angeles, has the highest N deposition and O_3 exposure (30 to 40 kg N/ha per year, 80 parts per billion (ppb) O_3 per hour, averaged over 24 hours for the 6-month growing season). Premature needle senescence is so extreme that 95

percent of the total canopy biomass in whole-tree harvests is in current year foliage (Grulke and Balduman 1999). At an atmospherically clean site (low N deposition, and 38 ppb O_3 per hour, averaged over 24 hours for the 6-month growing season) near Lassen Volcanic National Park, canopy foliar biomass was evenly distributed across four to five needle-age classes. In response to pollutant deposition, increased needle and branch loss significantly contribute to increased litter inputs to the mixed conifer ecosystem. Needles produced in high O_3 exposure environments have higher lignin content. Greater lignin content reduces decomposability (Fenn and Dunn 1989), further exacerbating litter layer buildup. For example, in the western end of the San Bernardino Mountain Range, where trees are most affected by transported air pollutants, litter depth averaged 25 cm. In the eastern end of the range with significantly lower long-term pollutant exposure, litter depth averaged 0 to 3 cm (N.E. Grulke, field observations). Significant litter buildup in mixed conifer forest was predicted by the simulation model BGC for both high N deposition and O_3 exposure (Arbaugh and others 1999) based on field leaf turnover rates (Miller and others 1996a).

Perhaps because of the increased repair costs for aboveground tissues, less biomass is retained in roots. From the western to the central San Bernardino Mountains, both higher O_3 concentration and greater N deposition contributed to significantly lower fine and medium root mass at 10-, 30-, and 50-cm depths. Root mass at a cleaner site was 6 to 14 times as great as that at a moderate pollution site (6 to 9 kg N/ha per year, and 62 ppb O_3 per hour, averaged over 24 hours for the 6-month growing season) (Grulke and others 1998).

Ponderosa pine had lower leaf mass, lower root mass, and lower carbohydrate content in both leaf and root tissue in areas with higher pollution exposure. In general, over the winter, carbohydrates for spring growth are stored in the roots. However, because of the lower leaf and root mass, overwintering carbohydrate is stored in tree boles (Grulke and others 2001). Although the theory is untested, increased carbohydrate storage in tree boles may enhance fecundity of bark beetles.

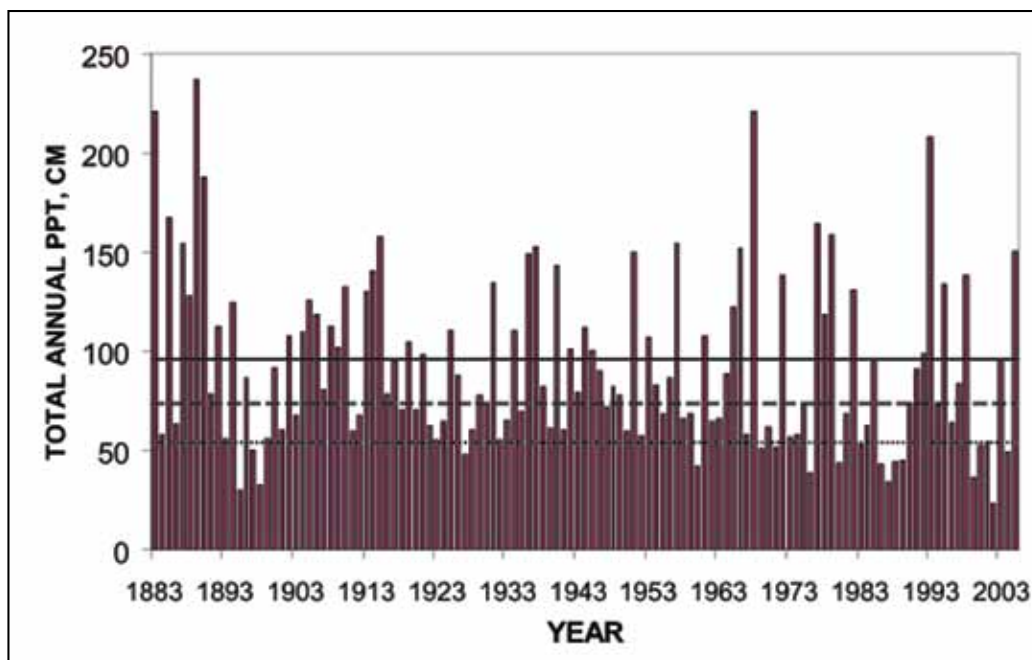


Figure 2—Long-term record of precipitation at Big Bear Dam, California. Total annual precipitation (y-axis in cm) from October 1 to September 30 was accumulated and plotted. The overall average is denoted by a solid line (96 cm), with the 80 percent of average (below which moderate drought stress is incurred) and the 60 percent of average (below which severe drought stress is incurred) denoted by dashed and dotted lines respectively.

At the scale of the stand, both N deposition and moderately high to high O₃ concentrations increased stand density (Arbaugh and others 1999, Miller and others 1989), especially on north-facing slopes and in microsites with more water availability or lower evapotranspiration (topographic lows). Individual tree growth further increased after O₃ concentrations had been decreased in the early 1990s because of heightened regulatory controls (see Tingey and others 2004). Across seven sites varying in both O₃ exposure and N deposition, three of the four sites with the highest pollutant load (Cedar Pines Park, Dogwood Campground, and Camp Angeles) had the highest tree mortality rate (primarily ponderosa pine) (Arbaugh and others 1999).

Effects of Periodic Drought

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. We have used the longest record of precipitation for the range, collected over the last 120 years at Big Bear Dam

(San Bernardino Water Management District), to identify the level of drought stress experienced by ponderosa pine from year to year. Moderate drought stress is defined physiologically as reduced cell turgor that generally results in reduced stomatal conductance (reduced water loss from the leaf), and lower cellular water potential, which allows the tissue to hold onto the water that is in the leaf more tenaciously (Levitt 1980). In 1994, a year of 80 percent of the average precipitation (preceded by an above-average precipitation year), ponderosa pine experienced moderate drought stress from mid-July through the end of the growing season (Grulke 1999). Severe drought stress is also accompanied by reduced cell turgor, reduced stomatal conductance, and reduced cell-water potential. The water potential is lowered sufficiently that cell solutes are concentrated enough to disrupt enzymatic function, and cell turgor is reduced enough and for a long enough duration that cell elongation growth is limited. Needles produced in years of severe drought stress are shorter. In 1996, a year of 60 percent of the average precipitation (preceded by an above-average precipitation year), ponderosa pine experienced

severe drought stress from the end of June through the end of the growing season (Grulke 1999). Over the period of the long-term precipitation record, roughly 15 percent of the years had low enough total annual precipitation to result in moderate drought stress; 30 percent of the years had low enough total annual precipitation to result in severe drought stress. Using this rough index of the level of physiological stress, ponderosa pine experienced drought stress 45 percent of the years since 1883 when precipitation records were initiated (Figure 2).

Where O_3 exposure and nitrogen deposition reduce root biomass, trees are predisposed to drought stress. In general, low to moderate O_3 exposures (<60 ppb hourly O_3 , averaged over 24 hours for the 6-month growing season) reduce water loss from trees. Ozone reduces photosynthetic rates, less CO_2 is required, and stomatal apertures are reduced to conserve water. However, under concentrations that are moderately high or higher, O_3 exposure modifies stomatal behavior in ways that increase drought stress.

For example, sugar maple (*Acer saccharum* Marsh.) was exposed to O_3 concentrations of 70 ppb during daylight hours (Tjoelker and others 1995). Early in the growing season and experiment, neither the net photosynthetic rate nor stomatal conductance was affected by the treatment. By midseason, 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 had control seedlings grown in charcoal-filtered air. By late season, both net photosynthesis and stomatal conductance were suppressed in plants grown in chronic O_3 exposure. In a field study of sensitive and tolerant genotypes of Jeffrey pine (*Pinus jeffreyi*; Grev. & Balf.) exposed to the same ambient O_3 levels (~68 ppb O_3 averaged over 24 hours, for the 6-month growing season in Sequoia National Park), sensitive genotypes had lower water loss under moist, favorable conditions and higher water loss under dry, unfavorable conditions (Patterson and Rundel 1989). Under favorable conditions, Jeffrey pine had less water loss, but because the stomatal apertures were smaller, there was also less photosynthetic carbon gain. Under unfavorable conditions (most of the day in the Sierra Nevada), sensitive

Jeffrey pine had higher water loss, which would result in greater desiccation.

Although physiologists often report plant response under steady state (stable) conditions, the light environment in the forest is often dynamic. Understanding stomatal responses under rapidly changing environmental conditions with concurrent O_3 exposure can perhaps better 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 receives flecky light two-thirds of the time (Grulke 2000). For example, the cutleaf coneflower (*Rudbeckia laciniata* L. var. *digitata* Mill. Fiori) is one of the most sensitive native plants to ambient O_3 concentrations in Great Smoky Mountains National Park. It persists in forest gaps and on forest-meadow margins, both with flecky light environments. Tolerant plants of cutleaf coneflower had normal responses to experimentally manipulated change in light from low to high and back down to low levels. However, O_3 -sensitive plants had either no stomatal response or a muted stomatal response to changes in light level. The level of water loss from leaves with no or muted response to changing light level was high—they did not conserve water when light was low, and this failure to conserve water would contribute to desiccation. When humidity was lowered slowly, O_3 -sensitive plants closed their stomata at much lower relative humidities than did O_3 -tolerant plants, and this also contributed to greater desiccation (Grulke and others 2007a). In a similar experiment with California black oak saplings (*Quercus kelloggii* Newb.) exposed to anthropogenic high O_3 in a natural stand, stomatal closure in response to abruptly reduced light level was slower in plants without additional N amendment, and N amendment partially mitigated the desiccating effects of high O_3 exposure (Grulke and others 2005).

Moderate to high O_3 exposure can also cause stomata to remain partially open at night. In experimental O_3 exposures, this was first observed in Norway spruce (*Picea abies* (L.) Karst), (Weiser and Havranek 1993) and in birch (*Betula pendula* Roth), (Matyssek and others 1995). Nighttime water loss rates were 25 percent as great as

Table 1—Historical record of drought years and bark beetle epidemics in the San Bernardino Mountains

Drought years	Aver. percent ppt	Beetle epidemic?
1898-1900	50	Not known
1923-1925	66	Not known
1927-1930	70	Not known
1948-1951	79	Yes ¹
1959-1961	63	Yes ¹
1970-1972	59	no
1976-1977	61	Yes ¹
1988-1990	45	Yes ¹
1999-2002	45	Yes ²

Note: Shown are the years of moderate or severe drought, the average percentage of total average annual precipitation (based on the 120-year record), and whether a bark beetle epidemic occurred after the sequence of drought years.

¹ California Pest Reports, 1949 to present.

² N. Grulke, personal observation.

full daytime rates for Norway spruce, and 50 percent as great for birch. This was corroborated in ponderosa pine across the San Bernardino Mountain pollution gradient, with both higher O₃ and NO₂ and HNO₃ exposure. In the San Bernardino Mountains, nighttime water losses were 10 percent of full daytime rates (Grulke and others 2005). Because these studies were largely phenomenological, a new gas exchange system was designed and built to directly test known O₃ concentrations on single leaves. Chronic, moderate O₃ exposure (70 ppb O₃ for 8 hours per day for 1 month) significantly increased nighttime foliar water loss in California black oak and blue oak (*Quercus douglasii* Hook. & Arn.) (Grulke and others 2007b). Nighttime water losses were attributable directly to O₃ exposure and were 30 percent and 20 percent, respectively, of daytime rates in these species. Moderately high (or higher) O₃ exposure increases foliar water loss and increases tree susceptibility to drought stress.

Susceptibility to Successful Bark Beetle Attack

Air pollution exposure (O₃ and N deposition) increases tree susceptibility to drought stress, and drought stress increases tree susceptibility to successful beetle attack. Dunning

(1928) was one of the first to report a relationship between drought conditions and increased levels of tree mortality caused by western bark beetles. In the west, bark beetles reach epidemic proportions after 2 to 3 years of drought. The correlation between beetle attacks and climate can be diffuse because bark beetles may delay or prolong the exact time of tree mortality. However, mortality tends to increase in multiyear droughts, particularly in highly dense stands or those with pre-existing damage or stress. Figure 2 indicates that sequences of 2 to 3 years of drought have occurred nine times (Table 1) in the last 120 years. We can document five bark beetle epidemics associated with those sequences.

Beetles are opportunists that attack trees in a weakened state. With only a few exceptions, either the host tree is killed by the colonizing bark beetles or the host resistance of the tree kills the attacking adults. To kill a tree, large numbers of bark beetles must successfully colonize it in a relatively short period of time (Paine and others 1984, 1997). However, fewer beetles may be sufficient to kill a compromised tree (Paine and others 1984). The bark beetles most commonly responsible for tree mortality in the western San Bernardino Mountains are western pine beetle (*Dendroctonus brevicomis*) and mountain pine beetle (*D. ponderosae*). Western pine beetle can produce up to four generations in a year in southern California, where the Mediterranean climate is conducive to rapid population expansion when an abundance of susceptible host material is available for colonization.

Eggs are laid in the inner bark and the larvae excavate galleries. Pupation occurs in either the inner or outer bark, depending on the species of beetle. Adults emerge from the larval host tree and search for susceptible hosts. Healthy pines and firs respond by exuding pitch, which either pitches out the adults or blocks their progress. Resin production impedes bark beetle attack both physically and chemically. Oleoresin pressure, caused by turgidity of cells lining the resin ducts, forces preformed resin to the site of injury or invasion and results in a flushing action. The cell turgidity is derived from the transpirational stream, so if the tree is under moisture stress, the cells become increasingly flaccid, the resin pressure is reduced, and the effectiveness

of the preformed resistance is compromised (Vite 1961). In weak trees with reduced resin pressure, the adults are able to initiate colonization and produce specific pheromones that attract other colonizing adults. Pheromone production ceases when the host tree ceases resin flow (i.e., when the tree dies) (Raffa and Berryman 1983).

Severe drought and other stresses also 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 (Paine and Stephen 1987a, 1987b). Drought-stressed trees are also known to have elevated levels of free, translocatable proteins (Lei and others 2006), which are produced to generally increase cell osmoticum. We conjecture that increased bole carbohydrate content as a result of O₃ exposure + N deposition + drought and elevation of protein levels in response to drought enhance beetle fecundity. Pollutant-exposed trees may thus be primed for successful bark beetle attack.

The forest had been recently thinned early in the late 19th century by commercial logging, so we would not expect to observe an epidemic beetle infestation in immature, low-density stands despite the drought stress experienced in the late 1920s (Minnich and others 1995). Human population in the Los Angeles Basin significantly increased after World War II, but air pollution levels were not quantified (or reconstructable) until 1963. From 1963 through 1980, peak 1-hour O₃ concentrations averaged 250 to 425 ppb (Lee and others 2003). From 1980 on, peak 1-hour O₃ concentrations were still high (>250 ppb), but cumulative O₃ exposures over the growing season began to decline. Through strong regulatory controls, O₃ concentrations declined further to tens of occurrences to only isolated occurrences of hourly concentrations exceeding 95 ppb from the mid-1990s to present in the mountains. Throughout this time, N deposition continued to accumulate, and drought stress was exacerbated by chronic, if not acute, O₃ exposure.

The most extreme drought recorded in 250 years was experienced in the hydrologic year 2002 (10/1/01 through 09/30/02) after 3 years of chronic drought. Results of 3 years of chronic drought (1999–2001) and extreme drought

(2002) are shown in a sequence of imagery taken at 5 km above the forest canopy at the most polluted site in the western San Bernardino Mountains (Figure 3). After the chronic drought, bark beetles attacked, and there were clusters of tree mortality. However, the average stand tree mortality rate was near 0 percent. After the chronic and severe drought, tree mortality (primarily ponderosa pine) from both bark beetle and drought increased to approximately 5 percent at the stand level. In the spring following the wet winter, bark beetle populations reached epidemic proportions, and 42 percent of the stand had died (ponderosa pine, white fir [*Abies concolor* (Gord. & Glend.) ex Hildebr.], and sugar pine). The stand was at high risk for an intense fire with high litter layers, high numbers of standing dead trees, and exacerbated drought stress. In autumn of that year, the Old Fire swept through the stand. Interestingly, not all of the red trees (standing dead trees 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+ year-old trees—the effects of O₃ exposure, N deposition, and drought had promoted lower branch abscission (Miller and others 1996b), so that the lowest branches were attached at heights of 60 ft or greater. Trees are still dying from bark beetle at this site (as of 7/06), but the rate of change is now statistically undetectable.

Conclusions

The role of air pollutants in increasing tree susceptibility to drought, successful bark beetle attack, tree mortality, and the susceptibility of forests to wildfire have not been formally supported. 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 bark beetle attack. The combination of chronic drought in 1999–2001 and acute drought in 2002 resulted in a bark beetle epidemic in the western San Bernardino Mountains. We contend that the severity of tree mortality in the western San Bernardino Mountains was significantly exacerbated by the higher air pollutant deposition in this region.

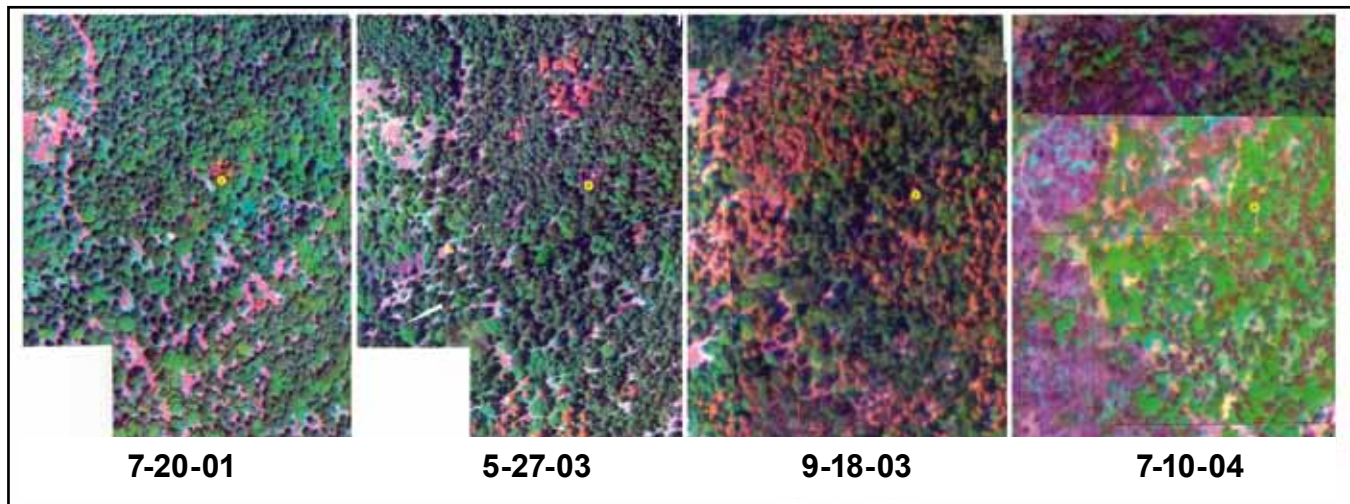


Figure 3—Remote imagery of Cedar Pines Park, San Bernardino National Forest, CA. This forest stand is the most affected by air pollution deposition in the USA and is only second (to forests surrounding Mexico City) to the worst deposition in North America (Miller and McBride 1999). The sequence of remote imagery 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 are indicated in fuchsia. On 7-20-01, 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 5-27-03, after 3 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 9-18-03, after the drought years plus the wet year (2003), tree mortality continued to accelerate, primarily in ponderosa pine, white fir, and some sugar pine. On 7-10-04, tree mortality was further increased (purple and fuchsia-colored areas) after the Old Fire swept through the area on 10-12-03. At the stand level, the tree mortality for the first three dates, respectively, was 0 percent, 5 percent, and 42 percent. Observed mortality (estimated from proportion of pixels) declined to 32 percent in the 7-10-04 image from needle loss on standing dead trees.

Literature Cited

- Arbaugh, M.; Bytnerowicz, A.; Grulke, N.E. [and others]. 2003.** Photochemical smog effects in mixed conifer forests along a natural gradient of ozone and nitrogen deposition in the San Bernardino Mountains. *Environment International*. 29: 401–406.
- Arbaugh, M.J.; Johnson, D.W.; Pulliam, W.M. 1999.** Simulated effects of N deposition, ozone injury, and climate change on a forest stand in the San Bernardino Mountains. In: Miller, P.R.; 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. New York: Springer-Verlag: 353–372.
- Asher, J.E.; Forrest, D.W. 1982.** Lake Arrowhead communities forest management plan's "State of the Forest" report. Lake Arrowhead, CA: Lake Arrowhead Property Owners Association. [Not paged].
- Bauer, M.R.; Hultman, N.E.; Panek, J.A.; Goldstein, A.H. 2000.** Ozone deposition to a ponderosa pine plantation in the Sierra Nevada Mountains (CA): a comparison of two different climatic years. *Journal of Geophysical Research*. 105: 123–136.
- California Pest Reports. (annual).** State and Private Forestry, USDA Forest Service, 1323 Club Drive, Vallejo, CA 94592.
- De Kok, L.J.; Tausz, M. 2001.** The role of glutathione in plant reaction and adaptation to air pollutants. In: Grill, D.; Tausz, M.; De Kok, L.J., eds. *Significance of glutathione to plant adaptation to the environment*. Dordrecht: Kluwer Academic Publishers: 185–205.
- Dunning, D. 1928.** A tree classification system for selection forests of the Sierra Nevada. *Journal of Agricultural Research*. 36: 755–771.

- Fenn, M.E.; Dunn, P.H. 1989.** Litter decomposition across an air-pollution gradient in the San Bernardino Mountains. *Soil Science Society of America Journal*. 53: 1560–1567.
- Fenn, M.E.; Poth, M.A.; Johnson, D.W. 1996.** Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *Forest Ecology and Management*. 82: 211–230.
- Grulke, N.E. 1999.** Physiological responses of ponderosa pine to gradients of environmental stressors. In: Miller, P.R.; McBride, J., eds. *Oxidant air pollution impacts in the montane forests of southern California: the San Bernardino Mountain case study, ecological studies*. New York: Springer-Verlag: 126–163.
- Grulke, N.E. 2000.** An analysis of short-, medium-, and long-term O₃ exposure in influencing stomatal conductance of ponderosa pine. In: *Proceedings, IUFRO Working Group 7.04. Air Pollution Effects, April 2000*. Houghton, MI: Michigan Technical University: 6.
- Grulke, N.E.; Andersen, C.P.; Fenn, M.P.; Miller, P.R. 1998.** Ozone exposure and N deposition reduces root biomass in ponderosa pine across the San Bernardino Mountains, California. *Environmental Pollution*. 103: 63–73.
- Grulke, N.E.; Andersen, C.P.; Hogsett, W.E. 2001.** Seasonal changes in carbohydrate pools of ponderosa pine in stands under differing environmental stress. *Tree Physiology*. 21: 173–184.
- Grulke, N.E.; Balduman, L. 1999.** Deciduous conifers: high nitrogen deposition and ozone exposure effects on ponderosa pine. *Water, Soil, Air Pollution*. 116: 235–248.
- Grulke, N.E.; Dobrowolski, W.L.; Mingus, P.; Fenn, M.E. 2005.** California black oak response to N-amendment at an N-saturated site. *Environmental Pollution*. 137: 536–545.
- Grulke, N.E.; Neufeld, H.S.; Davison, A.W.; Chappelka, A. 2007a.** Stomatal behavior of ozone-sensitive and -insensitive coneflowers (*Rudbeckia laciniata* var. *digitata*) Great Smokey Mountains National Park. *New Phytologist*. 173(1): 100–109.
- Grulke, N.E.; Paoletti, E.; Heath, R.L. 2007b.** Chronic vs. short-term acute ozone exposure effects on nocturnal transpiration in two Californian oaks. *TheScientificWorldJOURNAL*. 7(SI): 134–140.
- Lee, E.H.; Tingey, D.T.; Hogsett, W.E.; Laurence, J.A. 2003.** History of tropospheric ozone for the San Bernardino Mountains of Southern California, 1963–1999. *Atmospheric Environment*. 37: 2705–2717.
- Lei, Y.; Yin, C.; Li, C. 2006.** Differences in some morphological, physiological, and biochemical responses to drought stress in two contracting populations of *Populus przewalskii*. *Physiologia Plantarum*. 127: 182–191.
- Levitt, J. 1980.** Responses of plant to environmental stresses. London: Academic Press. 297 p.
- Matyssek, R.; Günthardt-Goerg, M.S.; Mauer, S.; Keller, T. 1995.** Nighttime exposure to ozone reduces whole-plant production in *Betula pendula*. *Tree physiology*. 15: 159–165.
- McAinsh, M.R.; Evans, N.H.; Montgomery, L.T.; North, K.A. 2002.** Calcium signalling in stomatal responses to pollutants. *New Phytologist*. 153: 441–447.
- Miller, P.R.; Chow, J.; Watson, J.G., eds. 1996a.** Assessment of acidic deposition and ozone effects on conifer forest in the San Bernardino Mountains. Final Report to California Air Resources Board A032-180. Sacramento, CA: California Environmental Protection Agency. [Not paged].
- Miller, P.R.; McBride, J.R., eds. 1999.** Oxidant air pollution impacts in the montane forests of southern California: a case study of the San Bernardino Mountains. *Ecological Studies* 134. New York: Springer-Verlag.

- Miller, P.R.; McBride, J.R.; Schilling, S.L.; Gomez, A.P. 1989.** Trends of ozone damage to conifer forests between 1974 and 1988 in the San Bernardino Mountains of southern California. In: Olson, R.K.; Lefohn, A.S., eds. Effects of air pollution on western forests. Transactions. Pittsburgh, PA: Air and Water Management Association: 309–324.
- Miller, P.R.; Stolte, K.W.; Duriscoe, D.; Pronos, J. 1996b.** Evaluating ozone air pollution effects on pines in the Western United States. Gen. Tech. Rep. PSW-GTR-155. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 79 p.
- Minnich, R.A. 1988.** The biogeography of fire in the San Bernardino Mountains of California: a historical survey. University of California Publication in Geography 28. 128 p.
- Minnich, R.A.; Barbour, N.G.; Burk, J.H.; Fernau, R.F. 1995.** Sixty years of change in California conifer forest of the San Bernardino Mountains. Conservation Biology. 9: 902–914.
- Paine, T.D.; Raffa, K.F.; Harrington, T.C. 1997.** Interactions among *Scolytid* bark beetles, their associated fungi and live host conifers. Annual Review of Entomology. 42: 179–206.
- Paine, T.D.; Stephen, F.M. 1987a.** Influence of tree stress and site quality on the induced defense system of loblolly pine. Canadian Journal of Forest Research. 17: 569–571.
- Paine, T.D.; Stephen, F.M. 1987b.** The relationship of tree height and crown class to the induced plant defenses of loblolly pine. Canadian Journal of Botany. 65: 2090–2092.
- Paine, T.D.; Stephen, F.M.; Taha, H.A. 1984.** Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. Environmental Entomology. 13: 619–624.
- Patterson, M.T.; Rundel, P.W. 1989.** Seasonal physiological responses of ozone-stressed Jeffrey pine in Sequoia National Park, California. In: Olson, R.K.; Lefohn, A., eds. Effects of air pollution on western forests. Pittsburgh, PA: Air and Waste Management Association: 419–427.
- Raffa, K.F.; Berryman, A.A. 1983.** The role of plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs. 53: 27–49.
- South Coast Air Quality Management District. 1997.** The Southland's war on smog: 50 years of progress toward clean air. <http://www.aqmd.gov/news1/Archives/History/marchcov.html> [Date accessed unknown].
- Sprugel, D.G.; Hinckley, T.M.; Schaap, W. 1991.** The theory and practice of branch autonomy. Annual Review of Ecology and Systematics. 22: 309–334.
- Tingey, D.T.; Hogsett, W.E.; Lee, E.H. 2004.** Stricter ozone ambient air quality standard has beneficial effect on ponderosa pine in California. Environmental Management. 34: 397–405.
- Tjoelker, M.G.; Volin, J.C.; Oleksyn, J.; Reich, P.B. 1995.** Interaction of ozone pollution and light effects on photosynthesis in a forest canopy experiment. Plant, Cell and Environment. 18: 895–905.
- Vite, J.P. 1961.** The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. Contributions of the Boyce Thompson Institute. 21: 37–66.
- Wieser, G.; 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.
- Zhang, X.; Zhang, L.; Dong, F. [and others]. 2001.** Hydrogen peroxide is involved in abscisic acid-induced stomatal closure in *Vicia faba*. Plant Physiology. 126: 1438–1448.