

Air Pollution Impacts in the Mixed Conifer Forests of Southern California¹

Patrick J. Temple, Andrzej Bytnerowicz, Mark E. Fenn, and Mark A. Poth²

Abstract

Air pollution, principally in the form of photochemical ozone and deposition of nitrogen compounds, has significantly affected mixed conifer forests in the mountains of southern California. Foliar injury, premature needle abscission, crown thinning, and reduced growth and vigor have been well documented, particularly for ponderosa (*Pinus ponderosa* Laws.) and Jeffrey (*P. jeffreyi* Grev. and Balf.) pines on the western side of the pollution deposition gradient in the San Bernardino Mountains. Tree mortality of the more ozone-susceptible ponderosa and Jeffrey pines has led to alterations in stand composition, in favor of increased dominance by more ozone-resistant species such as incense cedar (*Calocedrus decurrens* [Torr.] Florin), white fir (*Abies concolor* [Gord. & Glend.] Lindl.), and sugar pine (*P. lambertiana* Doug.). Increased rates of litter deposition, alterations in C/N ratios in litter and soil, and reductions in fine root biomass of trees have also altered the dynamics of biogeochemical processing in stands impacted by ozone and excess N deposition. Research into the effects of atmospheric deposition across the mixed conifer forests of the San Bernardino Mountains continues to provide insights into the complex interactions among anthropogenic and natural stresses in a forest ecosystem.

Key words: air pollution, forest health, nitrogen deposition, ozone, San Bernardino National Forest, water quality

Introduction

For the past 40+ years, mixed conifer forests in the mountains of southern California have been exposed to the highest levels of oxidant air pollution and the highest levels of nitrogen deposition of any ecosystem in North America (Miller and McBride 1999, Takemoto and others 2000). These high concentrations of air pollutants arise as a consequence of a unique set of topographic, climatological, and social factors characteristic of the Los Angeles (LA) air basin. First, the Transverse Ranges, including the Santa Monica, San Gabriel, and San Bernardino Mountains to the north, and the Peninsular Ranges, including the San Jacinto and Santa Rosa Mountains to the east, are barriers to the westward flow of oceanic breezes, particularly during the summer months. The stagnant air masses and strong radiational heating contribute to the formation of a subsidence inversion layer, typically beginning at about 500 m (Edinger 1973). The inversion layer limits vertical mixing, which traps air pollutants at its base, leading to increased pollutant concentrations near ground level. Second, increased industrialization of the region during and after World War II, rapid population growth, and increased reliance on the automobile as the basic and

¹ An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

² Atmospheric Deposition Program, Pacific Southwest Research Station, USDA Forest Service, 4955 Canyon Crest Dr., Riverside, CA 92507 (email: ptemple@fs.fed.us)

necessary form of transportation across the region contributed into the atmosphere massive amounts of precursor pollutants in the form of hydrocarbons from gasoline and oxides of nitrogen from auto exhaust. Photochemical processes converted the precursor molecules to ozone (O_3), peroxyacyl nitrates (PANs), aldehydes, nitric acid, and other highly oxidative compounds (Finlayson-Pitts and Pitts 1986). These photochemical air pollutants, principally O_3 , have had significant adverse effects on the vegetation of the region, from agricultural crops near the coast to the mixed conifer forests of the San Bernardino Mountains.

Historical Trends of Air Quality in the San Bernardino Mountains

Tropospheric O_3 forms by the action of ultraviolet radiation (UV) on oxides of nitrogen, principally NO_2 . The photolysis of NO_2 produces NO and singlet O, which quickly reacts with molecular O_2 to produce O_3 . This reaction is rate-limited by the decomposition of O_3 and its reaction with NO, so that in the absence of other air pollutants, the concentration of O_3 produced by the photolysis of NO_2 is relatively low (Finlayson-Pitts and Pitts 1986). However, in the presence of reactive hydrocarbons, such as those from gasoline and auto exhaust, a series of complex catalytic reactions reduces the concentration of NO, leaving very little NO to react with O_3 and permitting the concentration of O_3 to greatly increase. The amount of surface ozone formed by these reactions depends upon time of day, amounts of precursor pollutants, and meteorological conditions. In the morning, large amounts of precursors are produced by morning rush hour traffic, but the concentration of O_3 is low. Ozone concentrations increase during the day as photochemical reactions continue. Concentrations also increase along a gradient from west to east as onshore breezes transport the polluted air mass eastward. In addition, the height of the inversion layer also increases from west to east as elevations increase from the coastal plain to the mountains and as temperatures increase from the coast to the interior. As a result, the highest O_3 concentrations in the LA Basin are typically found not in the valleys, but in mountain slopes facing LA at 1200 to 1500 m, near the base of the inversion layer. Afternoon heating of the mountain slopes also vents the highly polluted layers up and over the mountain ridgeline by upslope flow (Edinger 1973). The inversion layer may also serve as a reservoir for ozone in the evening. The lack of vertical mixing as the air mass cools and stabilizes reduces contact of ozone with scavenging processes such as deposition to ground surfaces and reaction with NO molecules. As a consequence, high concentrations of O_3 persist in the evening and early morning hours in forested areas of the mountains, while O_3 concentrations in the valleys typically decrease rapidly as the sun sets (Edinger and others 1972). Thus the mixed conifer forests on the western slopes of the San Bernardino Mountains (SBM) have been subjected not only to high concentrations of O_3 during mid to late afternoon but in the early morning as well, when humidity is relatively high and physiological activity of the trees is also at its peak.

Monitoring oxidant concentrations in the SBM began in 1968 with the placement of a Mast ozone meter at Rim Forest/Sky Forest (NRC 1977). Data from this instrument and correlated data from a monitoring station in San Bernardino indicated a continuing upward trend from 1963 in both peak ozone concentrations and in numbers of hours of elevated O_3 in the mountains. These trends culminated in 1974, when maximum hourly O_3 concentrations at Sky Forest exceeded 0.33 parts

per million (ppm) on 46 days. The highest hourly concentrations averaged 0.38 ppm, and the highest hourly concentration ever recorded was 0.60 ppm on June 28, 1974 (NRC 1977). Peak and mean O₃ concentrations in the mountains remained relatively constant throughout the 1970s, with growing season (May to September) means frequently exceeding 0.10 ppm for 10 or more hours daily (Miller and McBride 1975). However, in response to concerted air pollution control activities, O₃ levels have declined steadily since the 1980s (Miller and others 1997). Growing season ozone means in the late 1990s have declined to 0.05 to 0.06 ppm, and recent peak concentrations have rarely exceeded 0.22 ppm in the areas most severely impacted by ozone (CARB 1999).

A network of ozone analyzers located across the SBM was established in the 1970s. Data from these instruments showed that O₃ concentrations decreased along a gradient from west to east and from south to north across the mountain range (Miller and others 1986). Highest concentrations were found at sites facing the LA Basin, such as Crestline, Lake Gregory, and Sky Forest. Ozone concentrations decreased gradually until Barton Flats, and then they more rapidly approached baseline levels at Big Bear, Heart Bar, and Holcomb Valley. A more recent survey of air quality in the SBM indicated that a similar trend continues today, although current O₃ levels are significantly lower than those recorded in the 1970s (Watson and others 1999).

It is more difficult to establish historical trends for nitrogen deposition in the SBM because systematic monitoring for total N deposition has been conducted only relatively recently (Fenn and Poth 1999a). However, NO_x emissions in the south coast (Los Angeles) air basin decreased by 13 percent from 1985 to 1995 and NO₂ concentrations have decreased by 39 percent since 1980 (Alexis and others 1999), suggesting that N deposition has been decreasing since the 1980s. Deposition of reduced N forms (NH_x) in the western SBM is expected to decrease in the next 10 to 15 years as dairy operations in the Chino/Norco area, the major source of reduced N forms in the atmosphere (Luebs and others 1973), move north to central California.

Measurements of N in throughfall, dry deposition, and fog demonstrate that the gradient of N deposition is steeper than that of O₃ (Fenn and Bytnerowicz 1993). Total N deposition, based on throughfall data, is estimated to average 31 kg ha⁻¹ y⁻¹ in the western SBM and 5 kg ha⁻¹ y⁻¹ at Barton Flats, located at approximately the median of the O₃ gradient (Fenn and others 2000). Spatial variability in N deposition is high due to heterogeneous canopy cover and varying exposure to air pollution. Nitrogen deposition in microsites with high leaf area index is greater than plot-level average values. In the western SBM, it is estimated that total N deposition is greater than 50 kg ha⁻¹ y⁻¹ in sites with complete canopy cover and direct exposure to incoming pollutant masses. Nitrogen deposition in fog is also high in the western SBM, constituting about a third of total annual N deposition (Fenn and others 2000b), due to extremely high concentrations of N compounds in fog and effective fog interception by canopy surfaces. Wet and dry deposition of N pollutants is also much higher than previously expected in the SBM during the winter months (Fenn and Bytnerowicz 1997), the season when, compared to summer, ozone concentrations are extremely low.

Effects of Ozone on the Mixed Conifer Forest

Physiological Responses

Ozone is a gaseous air pollutant with a molecular weight similar to that of carbon dioxide (CO₂), and it follows the same diffusive pathway as CO₂ from the air surrounding a plant to intercellular air spaces. The primary mode of entry of gases into leaves is through the stomata, and the rate at which this gas exchange occurs is known as *stomatal conductance*. All the physiological and environmental factors that control stomatal conductance, such as light intensity, temperature, relative humidity, and soil moisture, also affect the rate at which O₃ enters the leaf (Runeckles 1992). Stomatal conductance is also determined by intrinsic genetic factors often correlated with the rate of growth of the plant. In general, fast growing annual species and agricultural crops have higher rates of stomatal conductance than perennials, shrubs, and trees. Plants with deciduous leaves have higher rates of conductance than those with evergreen foliage. Species adapted for growth under dry conditions have lower rates of stomatal conductance and, in general, are less affected by ozone than those growing under favorable soil moisture conditions. These broad correlations among plant growth rates, stomatal conductance, and ozone response are generally useful in predicting patterns of ozone effects across the landscape, but they cannot be used to predict individual species responses to ozone.

Once inside the leaf, O₃ diffuses through intercellular leaf spaces, following the diffusive pathways of CO₂, to areas of highest cellular physiological activity. The precise intercellular pathways and mechanisms by which O₃ is absorbed into plant cells and the biochemical mechanisms of O₃ toxicity to intercellular components are not well understood (Heath and Taylor 1997). Ozone, or the free radical by-products of its initial reactions at the cell surface, may react with components of the cell membrane, altering active transport of ions such as Ca²⁺ and K⁺ (Castillo and Heath 1990). This change in membrane polarity will also affect the pH gradient across the membrane, leading to a chain of events that include specific enzyme activation and deactivation and altered gene transcription (Heath 1987). If the amount of O₃ absorbed exceeds cellular detoxification and repair mechanisms, membrane function is irrevocably compromised, and normal biochemical activity ceases. One of the first indications of O₃ toxicity at the cellular level is loss of the enzyme responsible for carbon fixation, RUBISCO (ribulose biphosphate carboxylase/oxygenase; Pell and others 1994). This response is reflected at the whole-leaf level by a reduction in the rate of photosynthesis of leaves exposed to O₃. This reduction is reversible at first, but as the length of exposure or O₃ concentrations increase, the loss of photosynthetic capacity, accompanied by a loss of chlorophyll, becomes permanent. The first visible signs of foliar O₃ injury are chlorotic areas on the upper leaf surface, which reflect the permanent loss of photosynthetic capacity in the chloroplasts of the underlying cells. In broad-leaved plants these lesions usually are sharply defined by the network of leaf veins and veinlets, producing a chlorotic stipple over the leaf surface. In conifers, particularly in pines, the injury is more diffuse, producing a characteristic O₃ injury pattern known as *chlorotic mottle*. As O₃ injury accumulates, the leaf appears to age prematurely, leading to accelerated senescence and abscission of older leaves. The reduction in both rate of photosynthesis and amount of photosynthetic tissue in plants exposed to O₃ can lead to significant reductions in total amounts of carbon fixed over the course of the growing season, with concomitant reductions in carbohydrates available for repair, growth, reproduction, and defense (Heath and Taylor 1997).

Ecological Responses

The first indication that air pollution was having an effect on trees in the mixed conifer forest of the SBM was the observation in 1953 of significant needle chlorosis, necrosis, and premature needle abscission on ponderosa pine (*Pinus ponderosa* Laws.) in the vicinity of Crestline-Lake Gregory (Miller and McBride 1975). Possible scale insect or pathogenic disease etiologies were investigated, but observations of similar injury symptoms on grapes growing in the San Gabriel Valley suggested that an air pollutant might have been involved. Laboratory and field exposures of ponderosa pine branches to high concentrations of O₃ elicited injury symptoms similar to those observed in the field, and the chlorophyll content of needles exposed to O₃ was less than that of controls, as was also observed in the field (Miller and McBride 1975). Monitoring of pollutant concentrations in the Crestline area also revealed concentrations of oxidants similar to those that had elicited pine needle injury in the lab, confirming the identification of O₃ as the causal agent. Similar foliar injury symptoms were observed on a variety of plant species in the SBM, including Jeffrey pine (*P. jeffreyi* Grev. & Balf.), California black oak (*Quercus kelloggii* Newb.), sycamore (*Platanus racemosa* Nutt.), big-leaf maple (*Acer macrophyllum* Pursh), and several other trees, shrubs, and perennials (Richards and others 1968). Among conifers native to the SBM, ponderosa and Jeffrey pines were the most susceptible to O₃ injury, followed in order of increasing resistance by Coulter pine (*P. coulteri* D. Don), white fir (*Abies concolor* [G. & G.] Lindl.), big-cone Douglas-fir (*Pseudotsuga macrocarpa* [Vasey] Mayr), knobcone pine (*P. attenuata* Lemmon), incense cedar (*Calocedrus decurrens* [Torr.] Florin), sugar pine (*P. lambertiana* Doug.), lodgepole pine (*P. contorta* ssp. *murrayana* [Grev. & Balf.] Critch.), and limber pine (*P. flexilis* James) (Miller and McBride 1975).

By the late 1960s observations of the extent of oxidant injury to the mixed conifer forest from Crestline to Lake Arrowhead showed that over 46,000 ac of forest had heavy foliar injury, 54,000 ac had moderate amounts of injury, and 61,000 ac had light to no injury (Wert and others 1970). Estimates of tree mortality in the most heavily polluted areas of the forest suggested that over 25 percent of the pines might have died as a result of severe O₃ injury in combination with other causes (Miller and McBride 1975). Pines weakened by O₃ were particularly susceptible to attack by pine bark beetles (*Dendroctonus* spp.). Ozone-injured pines apparently emitted α -pinene, a bark beetle attractant (Stark and others 1968). The weakened pines produced less sap, the primary defense against bark beetle emergence. Tree mortality of ponderosa pines in the heavily damaged areas of the SBM due to increased intensity of bark beetle attacks was estimated to be up to 24 percent during a 3-year period in the late 1960s (Cobb and Stark 1970). Severely O₃-injured pines also did not recover from periods of drought stress as did uninjured trees (Miller and McBride 1975). Thus, pine mortality in the SBM was due to severe O₃ injury acting in combination with other biotic and abiotic stressors.

Historical Trends in Ozone Injury to the Mixed Conifer Forest

In the early 1970s, a series of 18 permanent observation plots were established in the mixed conifer forest of the SBM along the air quality gradient from west to east (fig. 1). At each plot, 50 ponderosa and/or Jeffrey pines >30 cm in diameter were permanently tagged; stem diameter of each was measured, and the amount of O₃

injury on the tree crowns was evaluated. Ozone injury was measured using a scale called the *FPM Score*, which recorded the youngest annual whorl with visible O₃ injury symptoms (FPM=Forest Pest Management; Miller and others 1996). In this scale, low numbers indicate higher O₃ injury. All other trees on the plots >10 cm DBH (diameter at breast height) were also measured and evaluated for O₃ injury (Taylor 1973). Elevation, slope, aspect, precipitation, available soil water, and estimated O₃ dose were also recorded at each plot. Tree condition of pines was measured annually from 1973 until 1978 and at a sub-set of these plots at 4-year intervals from 1978 until 1994. Measurements of crown conditions in 1974 clearly showed a trend for decreased amounts of O₃ injury from plots on the western edge of the forest closest to Los Angeles to those in the northeast. Remeasurements of those same trees in 1988 showed general improvements in crown conditions at all plots except Camp Paivika, the plot with the highest amount of O₃ injury and the highest input of ambient O₃ (Miller and Rechel 1999). Data from remeasurements of a smaller subset of plots in 1994 showed that pines at Camp Paivika showed no improvement in O₃ injury scores over the 20-year period and that the condition of trees at Camp Angeles and Heart Bar had only slightly improved (*fig. 2*). Despite the relatively high O₃ injury scores and high rates of foliar senescence and abscission of ponderosa pines at Camp Paivika, many of these trees have greater relative growth rates and higher standing biomass than ponderosa pines growing in less polluted areas (Grulke and Balduman 2000). The high rates of N deposition at the western end of the gradient appear to compensate for, or indeed override, the adverse effects of O₃ in this area.

Although the FPM injury score showed only slight improvement over the 20-year period from the 1970s until the 1990s, other measures of tree health indicated that severely injured pines were capable of recovering in response to lower ambient O₃ in recent years (Miller and Rechel 1999). Measurements of the number of annual whorls retained on a sample of over 200 ponderosa pines at Dogwood campground, near Blue Jay, showed that in 1973 most pines held only two to three annual whorls (*fig. 3*). By 1992 many more pines retained four to five annual whorls (*fig. 3*), and 43 percent of all the pines showed improvements in crown condition as indicated by increased needle retention (Miller and Rechel 1999). Increased needle retention has been reflected in increased tree growth in recent years in the same area (Arbaugh and others 1999). Tree ring width data from increment borings of 166 ponderosa pines at Dogwood campground were converted to increments of basal area.

Growth patterns of ponderosa pine from the 1880s to the present can generally be divided into three phases (*fig. 4*). Growth gradually increased from the 1880s until about 1945, but over the next 30 years basal area incremental growth declined, reaching its lowest point in the mid-1970s. After 1975, tree growth increased rapidly, reaching rates similar to those seen before the 30-year growth decline. Although the post-war decline in tree growth and the subsequent recovery roughly corresponded to changes in ambient O₃ air quality over the same time interval, it is likely that long-term patterns of annual precipitation in the forest were the primary factor controlling tree growth. A century of annual precipitation data from Big Bear dam indicates that the period 1925 to 1949 was the wettest on record, 1950 to 1974 the driest, and 1975 to 1991 again was a wet period (Arbaugh and others 1999). However, analysis of tree ring patterns of individual trees suggested that some pines with significant amounts of O₃ injury might have been less able to recover from the drought stress than healthy trees. A similar pattern of growth in response to O₃ and drought stress also has been

observed in bigcone Douglas-fir growing along the O₃ gradient in the SBM (Peterson and others 1995).

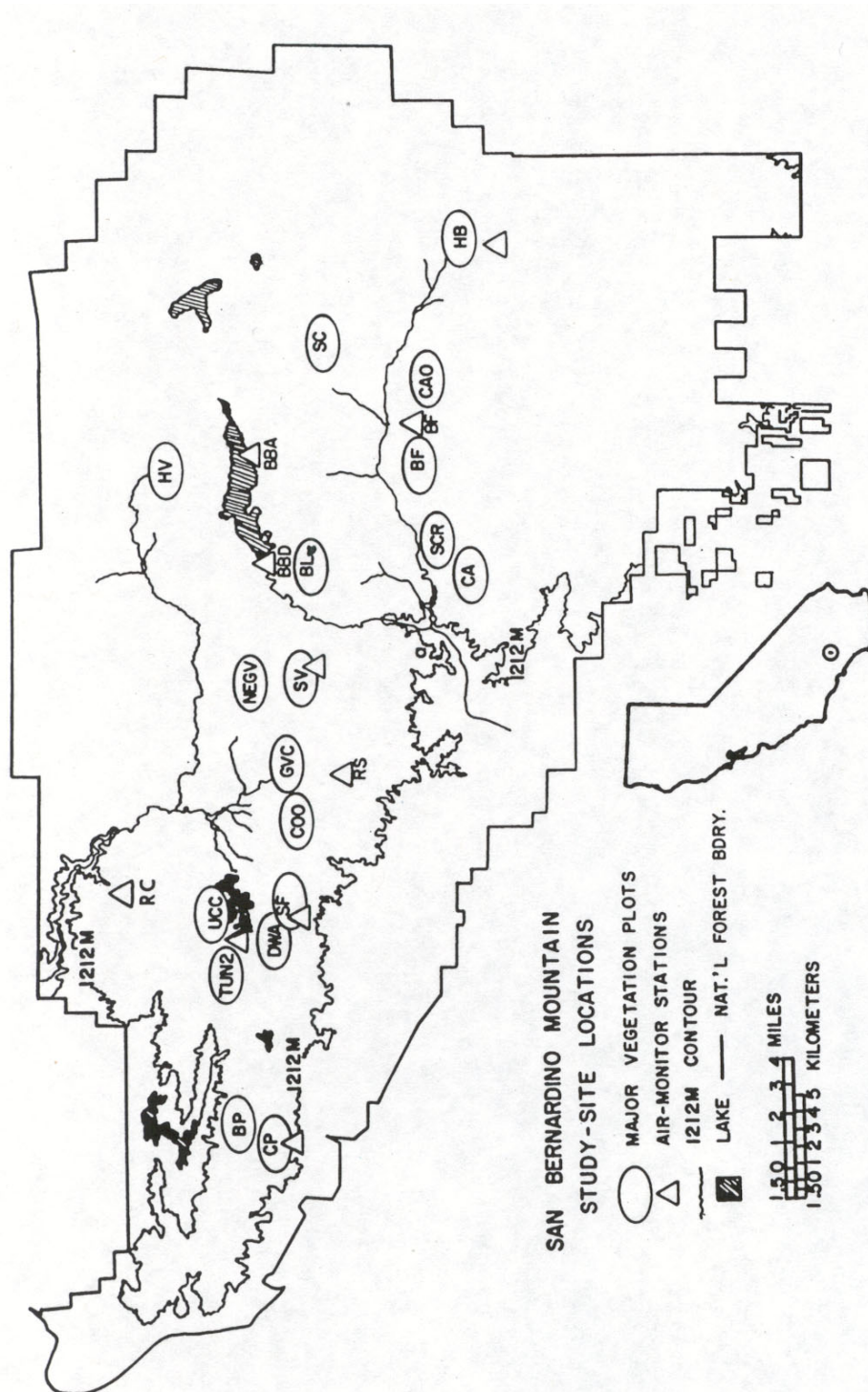


Figure 1—Location of permanent forest plots in the San Bernardino National Forest, established in 1972 to monitor long-term effects of ozone on ponderosa and Jeffrey pines and other dominant tree species in the plots. (Adapted from Miller and Rechel 1999)

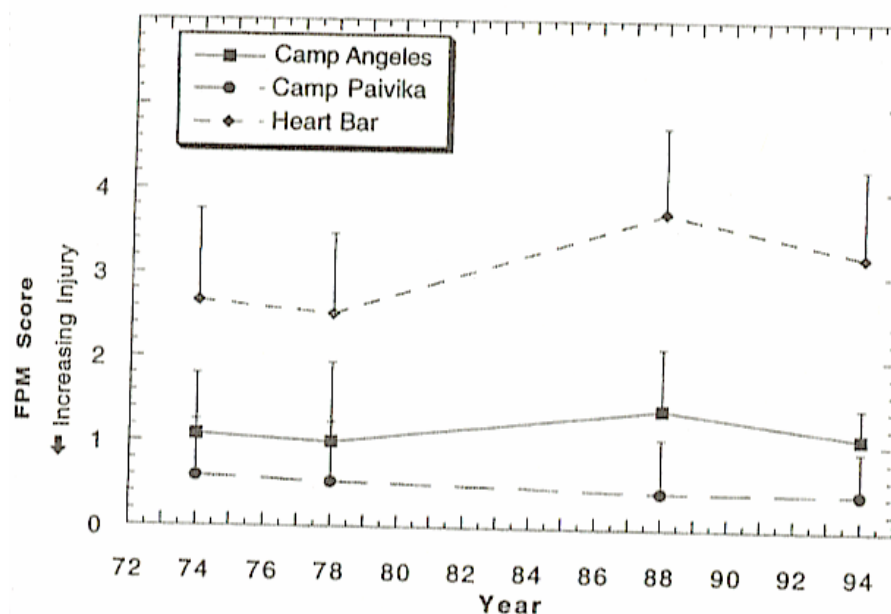


Figure 2—Changes in ozone injury scores from 1974 to 1994 for ponderosa and Jeffrey pines at three plot locations in the San Bernardino Mountains, based on a average of 50 trees per plot. Camp Paivika is in the high ozone area, Heart Bar is a relatively clean site, and Camp Angeles is intermediate. (Adapted from Miller and Rechel 1999)

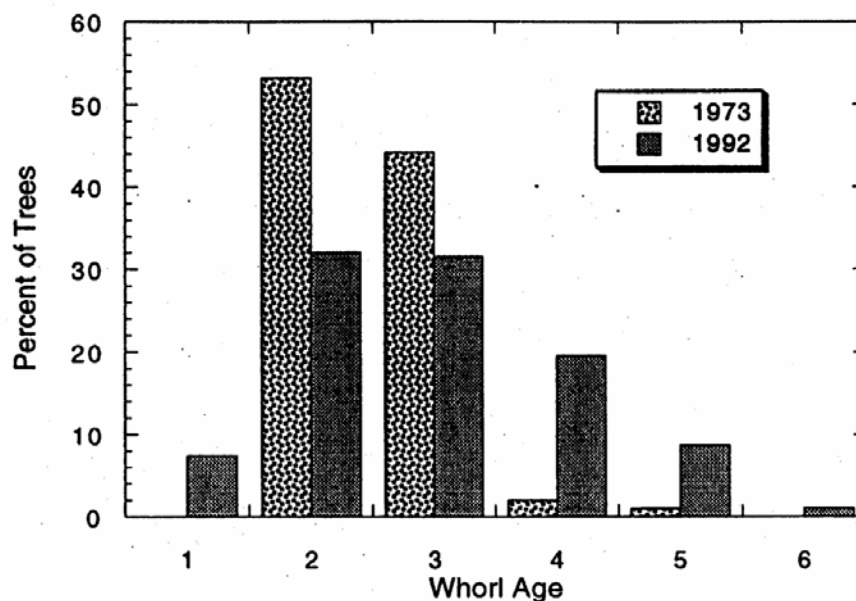


Figure 3—Average number of annual needle whorls retained by ponderosa pines (n=219) in an area of high ambient ozone in 1973 and in 1992. The higher number of annual whorls retained in 1992 is an indication of improved tree health. (From Miller and Rechel 1999)

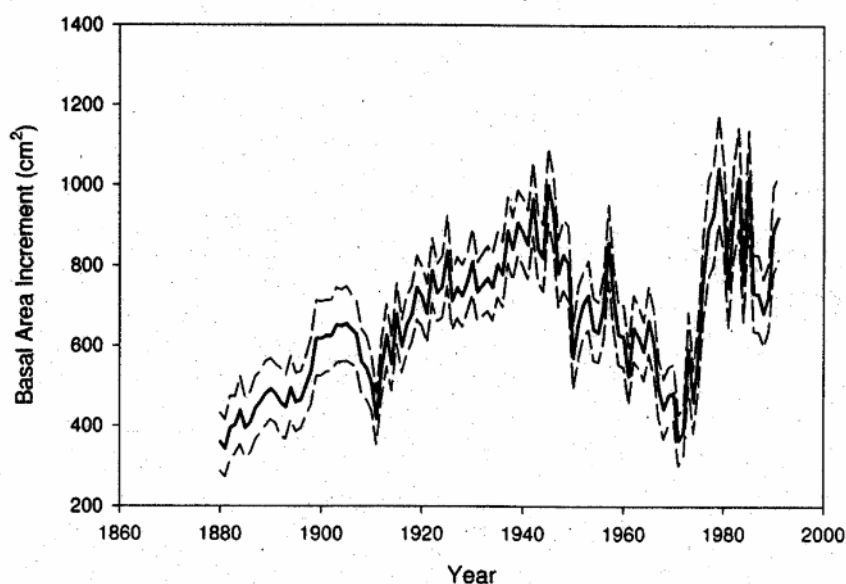


Figure 4—Average annual basal area increments of ponderosa pines ($n=40$ to 166 , based upon tree age) growing near Lake Arrowhead, San Bernardino Mountains. Dashed lines are 95 percent confidence limits. (From Arbaugh and others 1999)

Ozone and Drought

The interaction between O_3 and drought stress is complex and may involve both synergistic and antagonistic reactions (Grulke 1999, Temple and Miller 1998, Temple and others 1993). Trees exposed to O_3 under conditions of drought stress will generally show less O_3 injury than those growing under favorable soil-water conditions because of reduced rates of gas exchange in the drought-stressed trees. This interaction between O_3 and drought has been observed both under experimental conditions (Temple and others 1992, 1993) and in the field (Temple and Miller 1998). However, if the mechanism of stomatal closure is impaired because of O_3 injury (Grulke 1999, Patterson and Rundel 1989, Torsethaugen and others 1999) the trees may be more vulnerable to drought stress because of slow or incomplete stomatal closure. Reduced root biomass in ponderosa pine trees chronically stressed by O_3 may also predispose O_3 -injured trees to increased susceptibility to drought stress (Grulke and others 1998). Severely O_3 -injured pines may also increase rates of stomatal conductance on remaining foliage to compensate for the loss of older annual whorls (Beyers and others 1992, Coyne and Bingham 1982). This increase in the rate of gas exchange may render these needles more susceptible to O_3 injury than needles from uninjured trees. It is also possible that those individual pines that are particularly susceptible to O_3 may have intrinsically higher rates of stomatal conductance than more resistant trees, although the evidence for this is currently tenuous (Coyne and Bingham 1982, Grulke 1999).

Seasonal and annual patterns of precipitation will also alter tree responses to O_3 . In the SBM, where almost all soil water is contributed by winter precipitation, the total amount of available water in the upper soil column at the beginning of summer will control the physiological activity, length of growing season, and thus the total

amount of seasonal O_3 flux for most trees in the mixed conifer forest. Significantly greater amounts of O_3 will be absorbed into leaves following a wet winter than during a dry year, even if ambient O_3 concentrations are the same in both years (fig. 5) (Gulke 1999, Temple and Miller 1998). As an additional complication, the morphology and physiology of pine needles are altered by the environmental conditions under which they develop. Leaves developing during periods of favorable moisture conditions tend to be larger, longer, and have greater intrinsic rates of stomatal conductance than those produced during drought years. Those larger needles will develop greater amounts of O_3 injury than the smaller ones, even when exposed to similar ambient O_3 concentrations (Temple and Miller 1998). Ponderosa and Jeffrey pines will retain greater numbers of annual whorls of needles during periods of drought. But in the first wet year following a drought, the great increase in the amount of O_3 injury on older pine foliage leads to accelerated senescence and premature abscission of older age classes of needles. As a consequence, litter accumulation in the high O_3 areas of the mixed conifer forest increases greatly in the year following a drought (Temple and Miller 1998).

Effects of Ozone on Species Composition

The mixed conifer forest of today in the SBM differs greatly from the forest found by the original European settlers. The original forests were subjected to frequent low-intensity fires that burned grasses, shrubs, and competing understory trees. The forest landscape was dominated by large-diameter pines and other fire-resistant species in open, irregularly distributed stands. Following a century of intense logging of old-

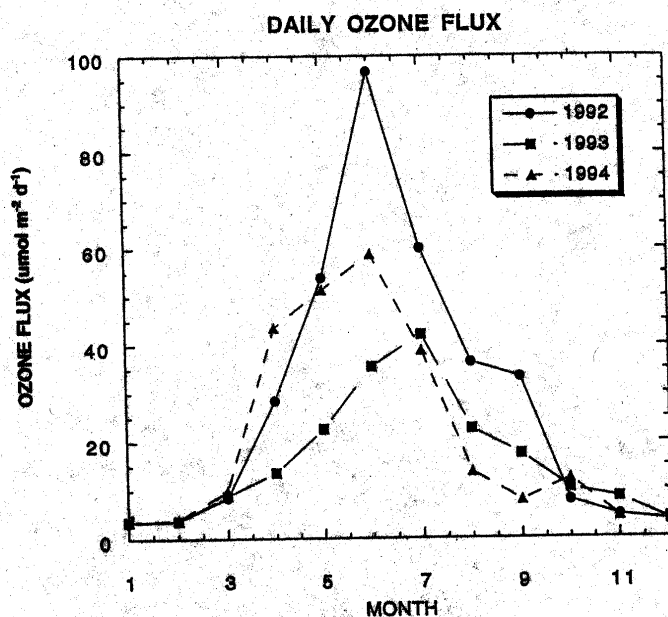


Figure 5—Mean daily ozone flux to 1-year-old needles of mature ponderosa and Jeffrey pines growing at Barton Flats, San Bernardino Mountains, from 1992 to 1994. Higher fluxes in 1992 reflected improved growing conditions in 1991-1992, following several previous years of drought. (Adapted from Temple and Miller 1998)

growth trees, stand-replacement fires, bark beetle infestations, salvage logging, strict fire suppression tactics, O₃ damage, and nitrogen deposition, the forest has been transformed. In the western, more mesic areas of SBM, the open growth, fire-resistant pine-dominated forest has become a closed-canopy forest dominated by dense stands of incense cedar and white fir (Minnich 1999). While fire-suppression policies have played a major role in this transformation, the impacts of air pollution should not be minimized. Ponderosa and Jeffrey pines are significantly more susceptible to O₃ than are incense cedar and white fir (Miller and McBride 1978), and they suffered far greater damage due to O₃. Salvage logging removed over 25 percent of mature pines damaged by combinations of O₃ and bark beetle infestations in the 1970s (Miller and McBride 1975). Measurements of basal diameter growth of all trees >30 cm in diameter in plots along the O₃ gradient from west to east showed that in high O₃ areas ponderosa pine basal area growth was reduced relative to incense cedar and white fir (Miller and others 1997). Measurements of tree seedling mortality and establishment also showed increased success of incense cedar and white fir seedlings and saplings, relative to that of pines (McBride and Laven 1999). Ozone injury to pines also greatly increased the amount of leaf litter on the forest floor in high O₃ areas of the forest, because of accelerated senescence and abscission of O₃-injured pine needles (Arkley and others 1980). Rates of leaf litter accumulation and decomposition may also be significantly increased by the higher rates of N deposition at these plots on the western side of the SBM (Fenn 1991). The thick litter layer discourages the establishment of pine seedlings, which is an additional factor in the transformation of the mixed conifer forest from open-growth pine stands to a closed canopy, dense incense cedar/white fir-dominated forest.

The effects of O₃ in altering species composition and community dynamics of forest understory species are less well known. Ozone injury symptoms have been noted since the 1950s on understory species such as blue elderberry (*Sambucus mexicana* C. Presl.), wild grape (*Vitis girdiana* Munson), and several woody species of riparian areas such as sycamore (*Platanus racemosa* Nutt.) and big-leaf maple (*Acer macrophyllum* Pursh) (Richards and others 1968). Foliar O₃ injury symptoms also have been observed on a variety of annual and perennial herbaceous plants in the mixed conifer forest (Temple 1999). However, unlike the systematic study of O₃ effects on injury and growth of overstory trees, no careful chronological sequence measurements of understory species frequency or density have been conducted along the air pollution gradient in the SBM. Shrub and herbaceous plant cover was measured once along the pollution gradient in 1973 (Taylor 1973), but these observations were not sufficient to establish a causal relationship between ambient O₃ concentrations and changes in community structure or composition. The same species of herbaceous annuals and perennials and woody shrubs recorded in plots in high O₃ areas in 1972 were also present in 1996 (Temple 1999). Some of these species, such as blue elderberry and mugwort (*Artemisia douglasiana* Besser) are also highly susceptible to O₃ (Temple 1999). These observations, while hardly definitive, suggest that O₃ may have had only minor direct effects on understory plant community composition in the SBM in comparison with other factors, such as habitat alteration, fire suppression, invasion by weedy plants, and N deposition (see below).

Most of the rare, threatened, endangered or endemic plant species in the SBM are found to the north and east of high O₃ areas, primarily in the Bear Valley and on the limestone deposits on the north slope of the mountains. However, at least 23 species or subspecies of rare or threatened plants are found in western areas of the forest (Skinner and Pavlik 1994). Scattered observations on some of these species did

not reveal any foliar O₃ injury in recent years (Temple 1999). However, no systematic surveys of O₃ injury have been conducted on these plants, so no conclusions can be drawn regarding the impacts of O₃ on threatened and endangered plant species in the SBM. Epiphytic lichen communities in the San Bernardino Mountains have been dramatically reduced both in species diversity and in numbers both historically and relative to comparable habitats with little air pollution (Nash and Sigal 1999). However, the role of O₃ in this reduction, relative to other factors such as N deposition or other pollutants, has not been determined.

Nitrogen Deposition in the Mixed Conifer Forest

Nitrogen Cycling in Forest Ecosystems

Nitrogen is the mineral nutrient most limiting to growth of forest trees. Most N in forest ecosystems is stored in the soil in the form of organic N, not readily assimilable by plant roots. Mineralization of organic N and nitrification convert N to forms readily available to plants. Because mineral N is generally present in limiting amounts in forest ecosystems, these systems have evolved tightly-coupled processes to conserve N through the cycle of litter decomposition, mineralization, bacterial and fungal associations, and internal N cycling (Chapin 1980). Conifers in particular are adapted to nutrient-poor soils, and they have evolved efficient mycorrhizal associations for nutrient uptake from the soil and internal retranslocation of N from senescent foliage prior to abscission (Chapin 1980). Because of this tight coupling of N deposition, mineralization, and uptake, cycling of N through forest ecosystems is generally highly efficient, and in a healthy ecosystem leaching of mineral N is low (Johnson 1992). Mixed conifer forests of California are no exception, and trees respond with increased growth to added N (Kiefer and Fenn 1997). Thus, increased rates of deposition of atmospheric N may actually increase tree growth if other nutrients and particularly water are not also limiting. However, if N deposition from atmospheric sources is in excess, normally conservative processes of N cycling and N retention within the ecosystem can be disrupted, producing a condition referred to as N saturation (Aber and others 1995).

Nitrogen Deposition in the San Bernardino Mountains

Recent studies in the mixed conifer forest in the SBM have suggested that western sections of the forest are currently experiencing N-saturated conditions (Fenn and Poth 1999a). Rates of N deposition, primarily in the form of dry deposited nitrate, ammonium, and nitric acid and N deposition in fog, can exceed 30 kg ha⁻¹ y⁻¹ as an average near Crestline/Lake Gregory and points west (Fenn and Bytnerowicz 1993). As mentioned earlier, total N deposition is estimated to be as high as 50 kg ha⁻¹ y⁻¹ in sites with complete canopy cover and direct exposure to polluted air masses (Fenn and others 2000). In contrast, total N deposition on the eastern side of the SBM is generally <5 kg ha⁻¹ y⁻¹. Evidence for N-saturation in areas of high N deposition includes increased nitrate concentrations in stream water from contaminated watersheds, elevated nitrate concentrations in soil solution and soil leachate, increased volatilization of N from the soil, decreased C:N ratios in soil and foliage, increased N concentrations and N:P ratios in foliage, nitrate accumulation in foliage of understory and overstory plants, and altered rates of litter decomposition (Fenn and others 1996, Fenn and Poth 1999a, 1999b).

Effects of Excess N Deposition

The direct and indirect effects of excess N deposition on the mixed conifer forest are under investigation. Deposition of nitric acid on plant foliage can alter surface wax structure and chemical composition (Bytnerowicz and others 1998b). In addition, nitric acid deposited on plant leaves may be a source for plant N, both through a transcuticular pathway (Hanson and Garten 1992) and stomatal uptake (Bytnerowicz and others 1998a). Concentrations of N in plant foliage from contaminated areas of the forest are significantly higher than those from areas of low N deposition (Fenn and others 1996). As a result of the combined effects of ozone stress (enhanced foliar senescence and abscission) and nitrogen (greater foliar and branch growth), litter production is increased in the western SBM. Litter with high N concentrations frequently exhibits higher decomposition rates in the short term (Fenn 1991, Fenn and Dunn 1989), but numerous studies show greatly reduced decomposition rates and greater humus accumulation in the later stages of decomposition when litter N content is high (Berg 2000, Fog 1988). Thus, N enrichment as a result of chronic N deposition favors litter accumulation on the forest floor by stimulating litter production and simultaneously causing long-term reductions in litter decomposition rates. The available evidence also suggests that C sequestration also may be greater in these forests influenced by the combined effects of ozone and N, with greater amounts of C stored in the forest floor and in woody biomass.

As noted earlier, the thick litter layer in the western SBM can retard germination of pine seeds, contributing to the change in species composition of the forest. It has not been clearly established whether higher rates of N deposition have increased growth of pines or other trees in the mixed conifer forest, but growth rates are higher in the western high pollution sites than in the less polluted sites to the east, notwithstanding the high O₃ concentrations that co-occur with N deposition (Arbaugh and others 1999, Grulke and Balduman 1999, M.E. Fenn and M.A. Poth, unpublished data). However, other environmental factors such as elevation, precipitation, temperature, and soil characteristics also vary across this gradient, making it difficult to determine the most important factors causing higher growth rates in the high pollution sites. Interactions between O₃, which can inhibit tree growth, and N, which can enhance growth, are complex, particularly as both interact with seasonal and annual variations in soil water availability. However, the higher growth rates in the western SBM suggest that elevated N deposition in areas such as Camp Paivika has acted to ameliorate the adverse effects of O₃ on the growth of ponderosa pine in this area of the forest. The effects of excess N on N-fixation, mycorrhizal associations, N mineralization, insect and disease infestations, and other ecosystem processes need further investigation (Fenn and Poth 1999a).

Nitrogen enrichment of the mixed conifer forest may also play a role in altering species composition and competitive interactions among species (Takemoto and others 2000). Because most native forest species have adapted to an N-limited environment, they may be at a competitive disadvantage to species able to utilize the extra N from atmospheric deposition to enhance growth and reproductive potential. The latter may be particularly true for alien weedy species of grasses that have invaded the mixed conifer forest in recent years. Excess atmospheric deposition of N may have contributed to the recent rapid conversion of coastal sage shrub habitats to annual grasslands dominated by weedy annual species of Mediterranean origin (Allen and others 1998). However, there is as yet no direct evidence that excess N has

contributed to the invasion of the mixed conifer forest in the SBM by weedy species or has altered competitive interactions among native species of annuals, perennials, or woody plants. Bracken fern (*Pteridium aquilinum* [L.] Kuhn), a nitrophilous species with a known capacity to accumulate nitrate in foliage (Fenn and others 1996), is a dominant, vigorously growing understory species at Camp Paivika, an N-saturated site in the SBM. However, it is not known whether long-term N deposition has favored bracken fern or whether bracken fern was already the dominant understory species prior to the occurrence of elevated N deposition.

The clearest response of the mixed conifer forest in the SBM to excess N deposition is the greatly increased concentrations of nitrate in stream water draining areas with high N deposition. Elevated nitrate loss is observable at the watershed scale and is the classic symptom of an N-saturated ecosystem (Fenn and others 1996). Surprisingly, and notwithstanding the N enrichment of soil and foliage in the western SBM, the bole diameter growth of ponderosa pine and California black oak trees at Camp Paivika increased significantly after three years of N fertilization at 50 or 150 kg ha⁻¹ yr⁻¹. It is not yet clear how the forest can export large quantities of excess N in stream water and as gaseous N emissions from soil and yet the production of woody biomass is still N-limited. Earlier studies indicated that foliar biomass production in ponderosa pine was not N-limited at Camp Paivika, but it was N-limited in low pollution sites in the SBM and San Gabriel Mountains (Kiefer and Fenn 1997). Further studies are underway to address this phenomenon. The interactive effects of high N deposition and ozone on conifer growth and carbon allocation are also under active investigation. Early results indicate that O₃ injury and N deposition can interact to increase rates of foliage loss and reduce fine root growth of ponderosa pine (Grulke and Balduman 2000). The consequences of this interaction in relation to drought stress and seasonal patterns of soil water availability are currently under investigation.

In a 3-year study of 19 streams across the SBM, a strong relationship was found between N deposition rates and nitrate concentrations in stream water (Fenn and Poth 1999b). Stream nitrate concentrations generally peaked in mid-winter, in response to large volume winter storms, although extremely high peak summertime concentrations also occurred following summer thundershowers in some streams draining the San Geronio Wilderness. Asynchronies between periods of maximum availability of mineralized N and biological demand contribute to increased leakage of N from the system (Fenn and Poth 1999a, 1999b). This temporal asynchrony is a function of the Mediterranean climate, characterized by major runoff periods in the winter, while plant N demand is expected to be greatest in the warm, dry spring and summer seasons. Another critical factor contributing to the highly open N cycling nature of these N saturated systems is the high nitrifying potential of the soil. Laboratory and field studies of N mineralization and nitrification show that ammonium is rapidly and completely nitrified in soil. This means that all the mineralized N is rapidly converted to nitrate, a highly mobile form of N, for which there are no effective retention mechanisms in soil except for microbial and plant uptake. The possibility that high concentrations of nitrate in stream water may be toxic to aquatic organisms during sensitive periods in their reproductive cycle will be investigated in future studies (Fenn and others 2000a).

Nitrate concentrations in streams of the SBM and San Gabriel Mountains are the highest reported for wildland ecosystems in North America. Peak concentrations approaching 400 µEq L⁻¹ (fig.6; Fenn and Poth 1999b, Riggan and others 1985) are

not unusual during high runoff periods. In the more severely N saturated watersheds in the SBM, nitrate levels in streams and springs remain elevated ($>70 \mu\text{Eq L}^{-1}$) year-round. By comparison, in relatively undisturbed forested watersheds, peak nitrate levels are typically $5\text{--}10 \mu\text{Eq L}^{-1}$ or lower, and baseline values are beyond detectable limits.

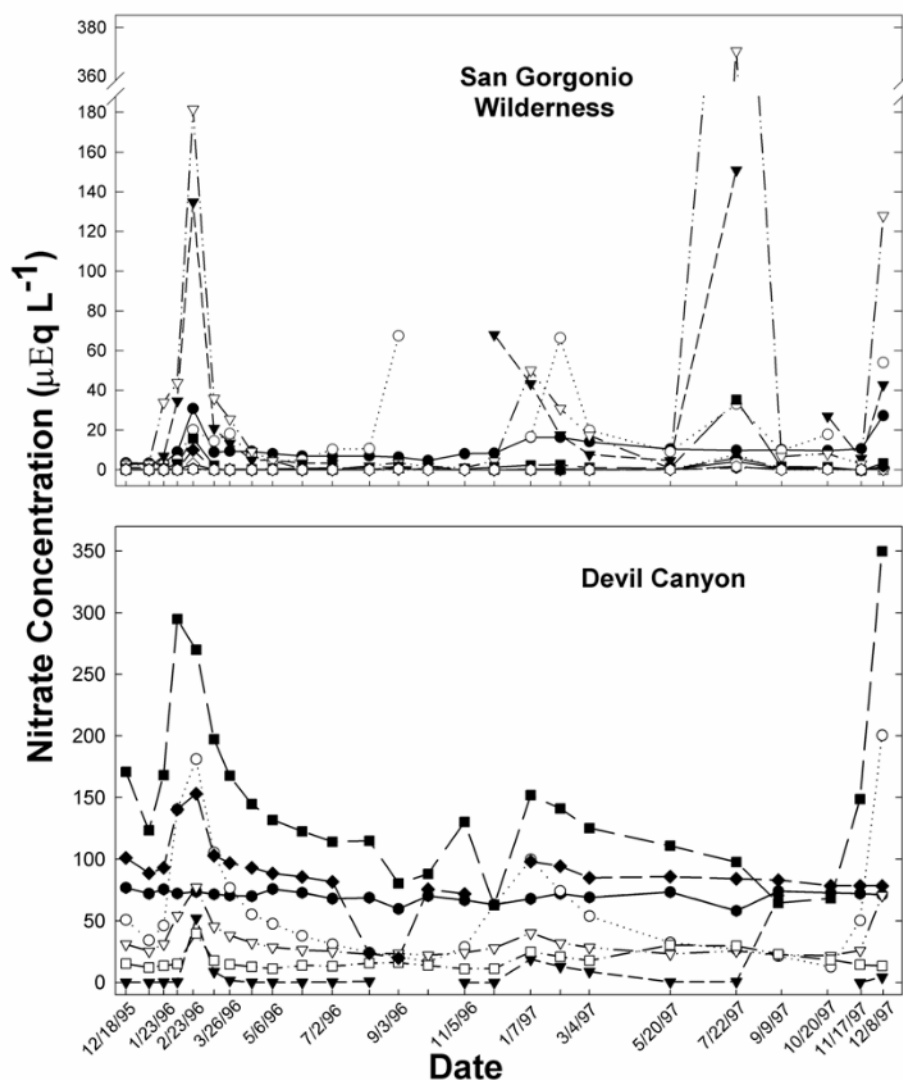


Figure 6—Nitrate concentrations in streamwater draining from areas of high nitrogen deposition (Devil Canyon) and low to moderate deposition (San Gorgonio Wilderness) in the San Bernardino Mountains, 1995 to 1997. (Adapted from Fenn and Poth 1999)

Summary

Montane forests in southern California have been subjected to high levels of ozone air pollution and deposition of nitrogen compounds for several decades. Severe O_3 injury to ponderosa and Jeffrey pines and other forest tree species was observed

beginning in the late 1950s. By the early 1970s, over 25 percent of the pines growing on the west side of the San Bernardino Mountains had died because of O₃ damage in combination with bark beetles, drought, and other natural stressors. The selective removal of pines in association with fire-suppression policies has contributed to the change in species composition of the mixed conifer forest, from open, pine-dominated stands to dense, closed stands dominated by incense cedar and white fir. Ambient O₃ concentrations in the mountain forests are now significantly lower than in previous decades, and crown conditions and growth rates of pines have improved in recent years. However, O₃ injury to pines and other species of native annuals, perennials, and woody plants of the mixed conifer forest continues to be observed on slopes and ridge-tops facing Los Angeles, and O₃ continues to have significant adverse impacts on these forests.

The effects of excess N deposition on the mixed conifer forest have only recently been investigated. Evidence has accumulated that the westernmost areas in the SBM are N-saturated, with consequences for biogeochemical cycling of N, tree growth, C sequestration, and export of N from the forest ecosystem. Both N deposition and ozone toxicity interact with seasonal and annual variations in precipitation and in soil water availability. The effects of excess N deposition in the mixed conifer forest on productivity, biogeochemical cycling, and soil and stream water hydrology are areas of continuing investigation.

Acknowledgments

The authors would like to acknowledge the extraordinary contributions of Dr. Paul R. Miller to the research on ecosystem effects of atmospheric deposition in the San Bernardino Mountains.

References

- Aber, J.D.; Magill, A.; McNulty, S.G.; Boone, R.D.; Nadelhoffer, K.J.; Downs, M.; Hallett, R. 1995. **Forest biogeochemistry and primary production altered by nitrogen saturation**. *Water, Air, and Soil Pollution* 85: 1665-1670.
- Alexis, A.; Gaffney, P.; Garcia, R.C.; Nystrom, M.; Rood R. 1999. **The 1999 California almanac of emissions and air quality**. Sacramento, CA: California Environmental Protection Agency, Air Resources Board.
- Allen, E.B.; Padgett, P.E.; Bytnerowicz, A.; Minnich, R. 1998. **Nitrogen deposition effects on coastal sage vegetation of southern California**. In: Bytnerowicz, Andrzej; Arbaugh, Michael J.; Schilling, Susan L., technical coordinators. *Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems*. Gen. Tech. Rep. PSW-GTR-166. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 131-139.
- Arbaugh, M.J.; Peterson, D.L.; Miller, P.R. 1999. **Air pollution effects on growth of ponderosa pine, Jeffrey pine, and bigcone Douglas-fir**. In: Miller, Paul R.; McBride, Joe R., editors. *Oxidant air pollutant impacts in the montane forests of southern California*. *Ecological Studies* No. 134. New York: Springer; 179-207.
- Arkley, R.J.; Glauser, R. 1980. **Effects of photochemical air pollution on pine litter fall and the forest floor**. In: Miller, Paul R., technical coordinator. *Proceedings of the symposium on effects of air pollutants on Mediterranean and temperate forest ecosystems*. Gen. Tech. Rep. PSW-GTR-43. Berkeley, CA: Pacific Southwest Range and Experiment Station, Forest Service, U.S. Department of Agriculture; 225.

- Berg, B. 2000. **Litter decomposition and organic matter turnover in northern forest soils.** Forest Ecology and Management 133: 13-22.
- Beyers, J.L.; Riechers, G.H.; Temple, P.J. 1992. **Effects of long-term ozone exposure and drought on the photosynthetic capacity of ponderosa pine (*Pinus ponderosa* Laws.).** New Phytologist 122: 81-90.
- Bytnerowicz, A.; Padgett, P.; Percy, K.; Krywult, M.; Riechers, G.; Hom, J. 1998a. **Direct effects of nitric acid on forest trees.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 270-287.
- Bytnerowicz, A.; Percy, K.; Riechers, G.; Padgett, P.; Krywult, M. 1998b. **Nitric acid vapor effects on forest trees – deposition and cuticular changes.** Chemosphere 36: 697-702.
- California Air Resources Board (CARB). 1999. **Annual report, 1998.** Sacramento, CA: California Air Resources Board.
- Castillo, F.J.; Heath, R.L. 1990. **Ca²⁺ transport in membrane vesicles from pinto bean leaves and its alteration after ozone exposure.** Plant Physiology 94: 788-795.
- Chapin, F.S. 1980. **The mineral nutrition of wild plants.** Annual Review of Ecology and Systematics 11: 233-260.
- Cobb, F.W., Jr.; Stark, R.W. 1970. **Decline and mortality of smog-injured ponderosa pine.** Journal of Forestry 68: 147-149.
- Coyne, P.I.; Bingham, G.E. 1982. **Variation in photosynthesis and stomatal conductance in an ozone-stressed ponderosa pine stand: Light response.** Forest Science 28: 257-273.
- Edinger, J.G. 1973. **Vertical distribution of photochemical smog in Los Angeles basin.** Environmental Science and Technology 7: 247-252.
- Edinger, J.G.; McCutchan, M.H.; Miller, P.R.; Ryan, B.C.; Schroeder, M.J.; Behar, J.V. 1972. **Penetration and duration of oxidant air pollution in the south coast air basin of California.** Journal of the Air Pollution Control Association 22: 882-886.
- Fenn, M.E. 1991. **Increased site fertility and litter decomposition rate in high-pollution sites in the San Bernardino Mountains.** Forest Science 37: 1163-1181.
- Fenn, M.E.; Bytnerowicz, A. 1993. **Dry deposition of nitrogen and sulfur to ponderosa and Jeffrey pine in the San Bernardino National Forest in southern California.** Environmental Pollution 81: 277-285.
- Fenn, M.E.; Bytnerowicz, A. 1997. **Summer throughfall and winter deposition in the San Bernardino Mountains in southern California.** Atmospheric Environment 31: 673-683.
- 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. 1999a. **Nitrogen deposition and cycling in Mediterranean forests: The new paradigm of nitrogen excess.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 288-314.
- Fenn, M.E.; Poth, M.A. 1999b. **Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California.** Journal of Environmental Quality 28: 822-836.
- 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.

- Fenn, M.E.; Poth, M.A; Meixner, T. 2000a. **Atmospheric nitrogen deposition and habitat alteration in terrestrial and aquatic ecosystems in southern California: Implications for threatened and endangered species.** Poster. Presented at the symposium on planning for biodiversity: Bringing research and management together; 2000 Feb. 29-Mar. 2; California Polytechnic University, Pomona, CA. (extended abstract in this volume)
- Fenn, M.E.; Poth, M.A; Schilling, S.L.; Grainger, D.B. 2000b. **Throughfall and fog deposition of nitrogen and sulfur at an N-limited and N-saturated site in the San Bernardino Mountains, southern California.** Canadian Journal of Forest Research 30(9): 1476-1488.
- Finlayson-Pitts, B.J.; Pitts, J.N., Jr. 1986. **Atmospheric chemistry: Fundamentals and experimental techniques.** New York: John Wiley and Sons.
- Fog, K. 1988. **The effect of added nitrogen on the rate of decomposition of organic matter.** Biological Review 63: 433-462.
- Gulke, N.E. 1999. **Physiological responses of ponderosa pine to gradients of environmental stressors.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 126-163.
- Gulke, N.E.; Balduman, L. 2000. **Deciduous conifers: high N deposition and ozone exposure effects on growth and biomass allocation in ponderosa pine.** Water, Air, and Soil Pollution 116: 235-248.
- Gulke, N.E.; Anderson, C.P.; Fenn, M.E.; Miller, P.R. 1998. **Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California.** Environmental Pollution 103: 63-73.
- Hanson, P.J.; Garten, C.T. 1992. **Deposition of H¹⁵NO to white oak, red maple and loblolly pine foliage: Experimental observations and generalized model.** New Phytologist 22: 329-337.
- Heath, R.L. 1987. **The biochemistry of ozone attack on the plasma membrane of plant cells.** Advances in Phytochemistry 21: 29-54.
- Heath, R.L.; Taylor, G.E., Jr. 1997. **Physiological processes and plant responses to ozone exposure.** In: Sander mann, H.; Wellburn, A.R.; Heath, R.L., editors. Forest decline and ozone. Ecological Studies No. 127, Berlin: Springer. 317-368.
- Johnson, D.W. 1992. **Nitrogen retention in forest soils.** Journal of Environmental Quality 21: 1-12.
- Kiefer, J.W.; Fenn, M.E. 1997. **Using vector analysis to assess nitrogen status of ponderosa and Jeffrey pine along depositional gradients in forests of southern California.** Forest Ecology and Management 94: 47-59.
- Luebs, R.E., Davis, K.R.; Laag, A.E. 1973. **Enrichment of the atmosphere with nitrogen compounds volatilized from a large dairy area.** Journal of Environmental Quality 2: 137-141.
- McBride, J.R.; Lavin, R.D. 1999. **Impact of oxidant air pollutants on forest succession in the mixed conifer forests of the San Bernardino Mountains.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 288-314.
- Miller, P.R.; Arbaugh, M.J.; Temple, P.J. 1997. **Ozone and its known and potential effects on forests in western United States.** In: Sander mann, H.; Wellburn, A.R.; Heath, R.L., editors. Forest decline and ozone. Ecological Studies No. 127. Berlin: Springer; 39-67.

- Miller, P.R.; McBride, J.R. 1975. **Effects of air pollutants on forests.** In: Mudd, J.B.; Kozlowski, T.T., editors. Responses of plants to air pollutants. New York: Academic Press, 195-235.
- Miller, P.R.; McBride, J.R., editors. 1999. **Oxidant air pollution impacts in the montane forests of southern California.** Ecological Studies No. 134. New York: Springer; 424 p.
- Miller, P.R.; Rechel, J. 1999. **Temporal changes in crown condition indices, needle litterfall, and collateral needle injuries of ponderosa and Jeffrey pines.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 164-178.
- Miller, P.R.; Stolte, K.W.; Duriscoe, D.M.; Pronos, J. 1996. **Evaluating ozone air pollution effects on pines in the western United States.** Gen. Tech. Rep. PSW-GTR-155. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Miller, P.R.; Taylor, O.C.; Poe, M.P. 1986. **Spatial variation of summer ozone concentrations in the San Bernardino Mountains.** Preprint 86-39.2. Annual Meeting, Air Pollution Control Association, Pittsburgh, PA.
- Minnich, R.A. 1999. **Vegetation, fire regimes, and forest dynamics.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 44-78.
- Nash, T.H.; Sigal, L.I. 1999. **Epiphytic lichens in the San Bernardino Mountains in relation to oxidant gradients.** In: Miller, Paul R.; McBride, Joe R., editors. Oxidant air pollutant impacts in the montane forests of southern California. Ecological Studies No. 134. New York: Springer; 223-234.
- National Research Council. 1977. **Ozone and other photochemical oxidants.** Washington, DC: National Academy of Sciences; 719 p.
- 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.S. editors. Effects of air pollution on western forests. APCA Transactions Series No. 16. Pittsburgh, PA: Air and Waste Management Association; 419-428.
- Pell, E.J.; Eckardt, N.; Glick, R.E. 1994. **Biochemical and molecular basis for impairment of photochemical potential.** Photosynthetic Research 39: 453-462.
- Peterson, D.L.; Silsbee, D.G.; Poth, M.A.; Arbaugh, M.J.; Biles, F.E. 1995. **Growth responses of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) to long-term ozone exposure in southern California.** Journal of the Air and Waste Management Association 45: 36-45.
- Richards, B.L., Sr.; Taylor, O.C.; Edmunds, F.G., Jr. 1968. **Ozone needle mottle of pines in southern California.** Journal of the Air Pollution Control Association 18:73-77.
- Riggan, P.J.; Lockwood, R.N.; Lopez, E.N. 1985. **Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California.** Environmental Science and Technology 19: 781-789.
- Runeckles, V.C. 1992. **Uptake of ozone by vegetation.** In: Lefohn, A.S., editor. Surface level ozone exposures and their effects on vegetation. Chelsea, MI: Lewis Publishers; 157-188.
- Skinner, M.W.; Pavlik, B.M. 1994. **CNPS inventory of rare and endangered vascular plants of California.** Sacramento, CA: The California Native Plant Society.

- Stark, R.W.; Miller, P.R.; Cobb, F.W.; Wood, D.L.; Parmenter, J.R. 1968. **Photochemical oxidant injury and bark beetle (Coleoptera: Scolytidae) infestation of ponderosa pine. I. Incidence of bark beetle infestation in injured trees.** *Hilgardia* 39: 121-126.
- Takemoto, B.K.; Bytnerowicz, A.; Fenn, M.E. 2001. **Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests.** *Forest Ecology and Management* 144: 159-173.
- Taylor, O.C. 1973. **Oxidant air pollution effects on a western coniferous forest ecosystem. Task B Report.** Riverside, CA: Air Pollution Research Center, University of California, Riverside; 231 p.
- Temple, P.J. 1999. **Effects of ozone on understory vegetation in the mixed conifer forest.** In: Miller, Paul R.; McBride, Joe R., editors. *Oxidant air pollutant impacts in the montane forests of southern California.* Ecological Studies No. 134. New York: Springer; 208-222.
- Temple, P.J.; Miller, P.R. 1998. **Seasonal influences on ozone uptake and foliar injury to ponderosa and Jeffrey pines at a southern California site.** In: Bynerowicz, Andrzej; Arbaugh, Michael J.; Schilling, Susan L., technical coordinators. *Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems.* Gen. Tech. Rep. PSW-GTR-166. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 221-228.
- Temple, P.J.; Riechers, G.H.; Miller, P.R. 1992. **Foliar injury responses of ponderosa pine seedlings to ozone, wet and dry deposition, and drought.** *Environmental and Experimental Botany* 32: 101-113.
- Temple, P.J.; Riechers, G.H.; Miller, P.R.; Lennox, R.W. 1993. **Growth responses of ponderosa pine to long-term exposure to ozone, wet and dry acidic deposition, and drought.** *Canadian Journal of Forest Research* 23: 59-66.
- Torsethaugen, G.; Pell, E.J.; Assmann, S.M. 1999. **Ozone inhibits guard cell K(+) channels implicated in stomatal opening.** *Proceedings National Academy of Sciences* 96(23): 13577-13582.
- Watson, J.G.; Chow, J.C.; Frazier, C.A.; Hinsvark, B; Green, M. 1999. **Ambient air quality at Barton Flats and other California forests.** In: Miller, Paul R.; McBride, Joe R., editors. *Oxidant air pollutant impacts in the montane forests of southern California.* Ecological Studies No. 134. New York: Springer; 81-105.
- Wert, S.L.; Miller, P.R.; Larsh, R.N. 1970. **Color photos detect smog injury to forest trees.** *Journal of Forestry* 68: 536-539.