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## Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests

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### Abstract

Mixed conifer forests in southern California are exposed to elevated levels of ozone ( $O_3$ ) and atmospheric nitrogen (N) deposition. Growing season 12-h daily average  $O_3$  levels are 0.06–0.09 ppm, and N deposition rates are 5–45 kg N/ha per year. However, N deposition rates have high spatial variability due to the heterogeneous and open-patchy characteristics of these stands. Annual deposition fluxes are greatest to canopy-covered areas with high pollution exposure. The harmful effects of  $O_3$  on sensitive pines are well documented, and selected areas in the San Bernardino and San Gabriel mountains have reached N-saturation as demonstrated by high nitrate ( $NO_3^-$ ) export in streams, and a suite of plant and edaphic indicators. The adverse effects of  $O_3$  culminate at the community level as a result of chronic effects on pine needle structure, retention, and physiology. Alterations in whole-tree biomass occur after several years due to higher carbon retention in the shoot for  $O_3$  detoxification, and lower carbon allocation to roots, as a result of  $O_3$  and N deposition. As a consequence, tree susceptibility to drought, windthrow, and root diseases could be exacerbated. Changes in forest community structure may occur due to the death of  $O_3$ -sensitive pines and fire suppression, and pine replacement by faster-growing,  $O_3$ -tolerant cedar and fir species. The negative impact of atmospheric N deposition occurs at the ecosystem-level as an alteration of biogeochemical nutrient cycling. For trees growing on N-deficient soils, increased supplies of N could moderate harmful  $O_3$  effects on growth for several decades. Over time, levels of soil N rise due to sustained inputs from the atmosphere, and the accelerated production and senescence of N-rich foliage by  $O_3$ . The increase in soil N is expected to favor the proliferation of nitrophilous overstory and understory species relative to pines. At this stage, N-limitation of forest productivity would be partially alleviated, and N emissions from soil and  $NO_3^-$  leaching losses elevated as a result of high soil N availability. In the western San Bernardino Mountains and in low-elevation chaparral watersheds in the San Gabriel Mountains,  $NO_3^-$  levels in streams are as high or higher than in any other undisturbed montane watersheds in North America, and  $NO_3^-$  contamination of domestic water supplies is of near-term concern. The effects of chronic  $O_3$  exposure and N deposition are expected to become more prevalent in the southern Sierra Nevada as human populations and influences in adjacent areas increase in the coming years.

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### 1. Introduction

The harmful effect of photochemical smog on pine trees in southern California has been recognized since the 1950s. The identification of ozone ( $O_3$ ) as the air

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pollutant that caused the chlorotic mottling of needles was achieved through comparison of plant responses in the field to plants exposed to  $O_3$  in controlled fumigation chambers (Miller et al., 1963; Richards et al., 1968). Following these reports, other workers found  $O_3$  injury to pines throughout California, including the central Sierra Nevada (Miller and Millikan, 1971) and the Lake Tahoe Basin (Pedersen, 1989). While controlled studies have shown reductions in growth proportional to the amount of  $O_3$  injury in seedlings (Temple and Miller, 1994), few studies have found radial growth decreases due to ambient  $O_3$  in mature trees (see, e.g. McBride et al., 1975). In the Sierra Nevada,  $O_3$ -caused decreases in ring width have been observed in Jeffrey pine (Peterson et al., 1987); growth during 1960–1988 at exposed sites was less than that at protected sites or from earlier growth periods. In the San Bernardino Mountains, trees from heavily polluted areas exhibited reductions in radial growth, missing rings, or altered ring formation compared to trees at less polluted sites (Miller, 1992). In addition,  $O_3$  injured trees are thought to be more vulnerable to mortality from insect/disease complexes, as high annual counts of trees killed by bark beetles coincide with the presence of  $O_3$  injury (Miller et al., 1997; Miller and McBride, 1999).

Investigations of the effects of atmospheric N in southern California were first conducted in the 1980s. For chaparral watersheds in the San Gabriel Mountains, Riggan et al. (1985) postulated that dry deposition was a major source of N to chaparral vegetation, and may contribute to increased levels of  $NO_3^-$  in stream water and pollution of groundwater. Subsequent studies in the San Gabriel Mountains found that peak diurnal concentrations of ambient  $O_3$  and  $NO_2$  co-occur at Tanbark Flat (Bytnerowicz et al., 1987a), and that rates of dry N deposition exceed values reported in the southeastern U.S. (Bytnerowicz et al., 1987b). In addition, Anderson et al. (1988) found that soil emissions of NO from chaparral watersheds following a prescribed fire were comparable to those from fertilized agricultural areas and persisted for longer periods of time. For soil NO emissions in an unmanaged ecosystem to be similar to that of an agricultural field, N inputs from the atmosphere and other sources are likely to be in considerable excess of plant and microbial needs. With respect to mixed conifer forests, Fenn and Dunn (1989) examined surface litter decom-

position rates along an air pollution gradient in the San Bernardino Mountains. In forests at the more polluted western end of the range, rates of surface litter decomposition were much faster than in forests exposed to moderate or low pollution levels. Exposure to elevated N deposition was postulated to be the major factor contributing to differences in nutrient cycling rates across the San Bernardino Mountains (Fenn, 1991).

In the mountains of southern California, high concentrations of ambient  $O_3$  and  $NO_x$ -derived atmospheric N co-occur in mid-elevation forest areas (Bytnerowicz et al., 1987a). These pollutants, rather than S-containing compounds and heavy metals, are the main atmospheric constituents of concern relative to forest health and nutrient cycling effects in the arid West. While  $NO_2$  is often the dominant N pollutant (Bytnerowicz and Fenn, 1996),  $HNO_3$  vapor may be of greater importance with respect to N deposition to forests because of its high deposition velocity (Hanson and Lindberg, 1991; Lovett, 1994). At heavily polluted sites, summertime 24-h average  $O_3$  levels are 0.07–0.09 ppm, and atmospheric N deposition rates are 20–40 kg N/ha per year. However, at sites 32–48 km downwind, incremental reductions in N deposition are more pronounced than decreases in ambient  $O_3$  due to the higher deposition velocities of  $HNO_3$  vapor and  $NH_3$  gas compared to  $O_3$ . For example, within the San Bernardino Mountains, forests at the highly polluted western end of the range are exposed to 33% higher ambient  $O_3$  concentrations (24-h average) and an 80% higher annual N deposition load than sites 40-km to the east. While selected forest sites on the western end of the range have become N-saturated (Fenn et al., 1998), sites to the east are N-limited (Fenn et al., 1996; Kiefer and Fenn, 1997).

In the following review, the adverse ecological effects of ambient  $O_3$  and atmospheric N deposition on pine trees in California's mixed conifer forests are examined. The ambient air pollution exposures that occur in California forests are distinct from the exposures to elevated levels of S-containing compounds and heavy metals that have caused damage to forests in the eastern U.S. The projected impact of the combined pollutant stress is characterized for three regions where extant impacts occur to varying degrees (Fig. 1): the San Bernardino Mountains, the San Gabriel Mountains, and the Sierra Nevada. In the San Bernardino and San Gabriel mountains, selected forests adjacent

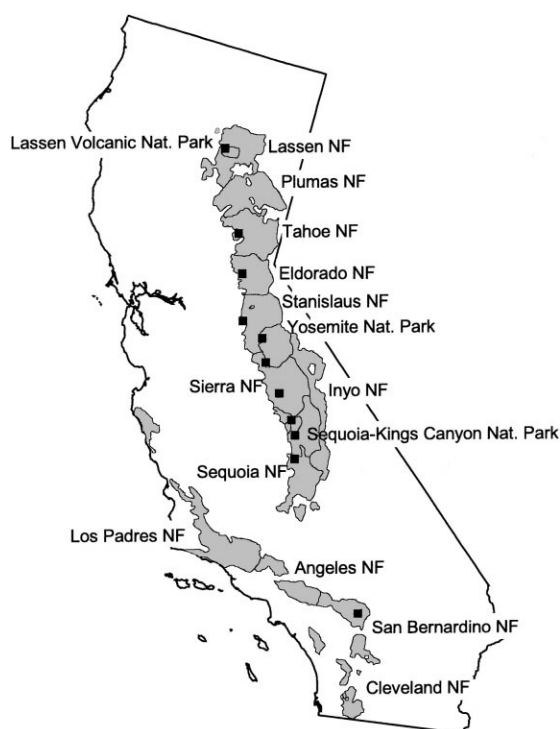


Fig. 1. Selected forest sites in the Sierra Nevada, San Gabriel and San Bernardino mountains in California.

to the Los Angeles Basin experience high  $O_3$  exposures and are N-saturated. Sites downwind from pollution sources experience moderate-to-high  $O_3$  exposures and are N-limited. In the southern Sierra Nevada, forest sites on the western slope experience moderate  $O_3$  exposures and low-to-moderate rates of N deposition.

## 2. Ambient $O_3$ in California's mixed conifer forests

Ozone is the air pollutant of greatest concern relative to forest health in North America (Shriner et al., 1991). Annual average  $O_3$  levels at clean, background sites range from  $\sim 0.015$  to  $0.04$  ppm (Table 1). In comparison, rural forest air quality in the U.S. is subject to  $O_3$  and  $O_3$ -precursor transport from upwind urban centers, and an annual mean concentration of  $0.030$ – $0.045$  ppm is considered to be a representative range for baseline, ambient  $O_3$  (Lefohn et al., 1990). In the Sierra Nevada, growing season (May–October) 12-h daily average  $O_3$  levels range from  $0.05$  to  $0.07$  ppm (Carroll and Dixon, 1993, 1995); 10–100% higher than the rural baseline level for U.S. forests. Similarly, in the San Bernardino Mountains, growing season average  $O_3$  levels at Barton Flats were  $\sim 0.06$  ppm in 1991–1994 (Miller et al., 1996a, b), comparable to levels in the mid-1970s (Miller et al., 1986). Growing season 24-h average  $O_3$  levels of  $\sim 0.09$  ppm may occur at Camp Paivika, near Crestline, on the western end of the San Bernardino Mountains (Grulke et al., 1998). At these levels, ambient  $O_3$  may be inhibiting physiological process rates and/or reducing tree growth. Throughout California, many forest areas currently experience cumulative growing season exposures in excess of 200 ppm-h.

Mixed conifer forests in the Sierra Nevada (Beyers et al., 1992), and in southern California (Bytnerowicz et al., 1989a), are exposed to  $\sim 250$  or  $\sim 350$  ppm-h  $O_3$ , respectively, during the growing season. While these

Table 1

Ambient ozone concentrations at background and rural U.S. forest sites (with special emphasis on California's mixed conifer forests)

Concentration (ppm)	Site	Type of average value	Reference
$\sim 0.015$	American Samoa	Annual, 24-h	Lefohn et al., 1990
$\sim 0.04$	Apache NF, Arizona	Annual, 24-h	Lefohn et al., 1990
$0.03$ – $0.045$	Rural U.S. forests	Growing season, 12-h	Lefohn et al., 1990; Taylor and Hanson, 1992
$0.05$ – $0.06$	Whitaker's Forest, Sierra Nevada	Growing season, 12-h (1988–1990)	Temple et al., 1992
$0.05$ – $0.07$	Mixed conifer forests, Western Sierra Nevada	May–October, 12-h (1991–1994)	Carroll and Dixon, 1993, 1995
$\sim 0.06$	Shirley Meadow, Sierra Nevada	Growing season, 12-h (1989–1990)	Takemoto et al., 1997
$0.07$ – $0.08$	Tanbark Flat, San Gabriel Mountains	April–September, 24-h (1985)	Bytnerowicz et al., 1987b
$\sim 0.06$	Barton Flats, San Bernardino Mountains	May–October, 12-h (1991–1994)	Miller et al., 1996a
$\sim 0.09$	Camp Paivika, San Bernardino Mountains	July–August, 24-h (1993–1994)	Grulke et al., 1998
$0.10$ – $0.11$	Camp Paivika, San Bernardino Mountains	May–October, 12-h (early 1980s)	Miller et al., 1986

ambient exposures are high relative to conditions in other forests (cf. Hogsett et al., 1993), the lack of moisture in summer may lower stomatal conductance and  $O_3$  uptake (Temple and Miller, 1998). Highest monthly flux rates typically occur in May–July, and could account for 60–70% of annual  $O_3$  uptake at Barton Flats in the San Bernardino Mountains (Temple, 1996). In drought years, however,  $O_3$  uptake in July–September is lower than in wet years, and monthly fluxes for this 3-month period may account for <30% of annual  $O_3$  uptake. Ambient  $O_3$  in California is expected to decrease or remain level through 2010, due to proposed hydrocarbon and  $NO_x$  control measures in the California State Implementation Plan for  $O_3$  (ARB, 1994).

### 3. Ozone effects

#### 3.1. Leaf injury

Chamber studies have shown that ponderosa pine seedlings exposed to 0.3–0.5 ppm  $O_3$  exhibited injury to current and 1-year-old needles after 24–108 ppm-h

(Miller, 1969; Miller et al., 1969; Miller and Evans, 1974). In field chamber studies conducted over two or three growing seasons, moderate amounts of  $O_3$  injury were observed in ponderosa pine seedlings grown at Whitaker's Forest (Grant Grove National Park) (Temple et al., 1992), and at Shirley Meadow (Sequoia National Forest) (Takemoto et al., 1997). While the amount of  $O_3$  injury is considerably less following a chronic vs. acute exposure, multi-year exposures to ambient  $O_3$  are a persistent stress to native pines in California (Arbaugh et al., 1998). In the 1990s, tree injury assessments in six National Forests and three National Parks in the Sierra Nevada and San Bernardino Mountains were conducted (Rocchio et al., 1993). Schilling et al. (1995) calculated ozone injury index (OII) (Miller et al., 1996c) values for ponderosa or Jeffrey pine trees growing in the Sierra Nevada and San Bernardino Mountains. During 1991–1994, injury amounts were greater in the southern Sierra Nevada relative to values for trees in the central or northern Sierra Nevada. In the San Bernardino Mountains, a west-to-east gradient of decreasing injury was evident, and average injury amounts were higher than in the Sierra Nevada (Fig. 2). Subsequent analyses found

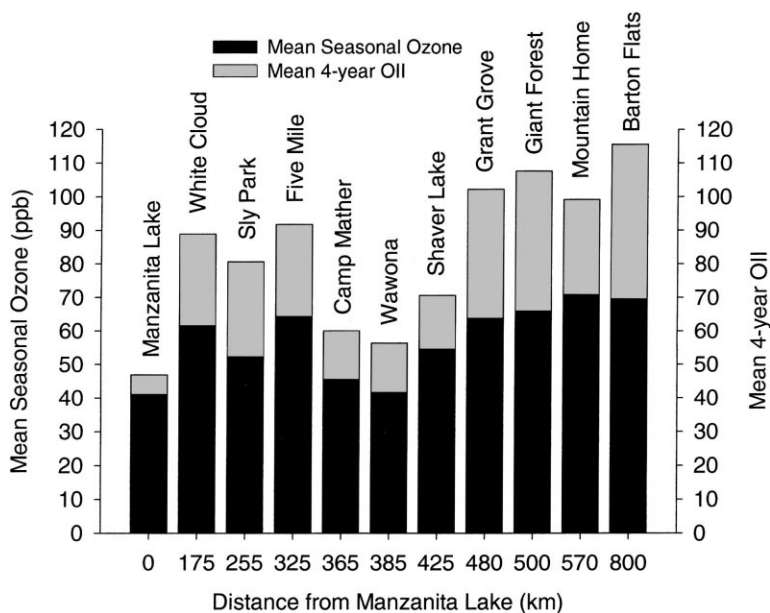


Fig. 2. Average ozone injury index values for pine trees at Project FOREST study sites in the Sierra Nevada and San Bernardino Mountains (from Arbaugh et al., 1998).

Table 2  
Effects of ozone on photosynthesis in Ponderosa pine in California

Response	Ozone exposure	Reference
Decrease	81 ppm-h (0.15 ppm, 9-h/day, 60-days)	Miller et al. (1969)
Decrease	81 ppm-h (0.30 ppm, 9-h/day, 30-days)	Miller et al. (1969)
Lower maximum rate	130–175 ppm-h (0.062–0.08 ppm, 90-days)	Grulke (1999)
No significant effect	140–340 ppm-h (0.06 ppm, 6–7 months)	Bytnerowicz and Takemoto (1989)
Intermittent decreases	~500 ppm-h (0.06 ppm, two growing seasons)	Takemoto et al. (1997)
No significant effect	~600 ppm-h (0.06 ppm, three growing seasons)	Beyers et al. (1992)

that the OII was strongly associated with several other cumulative exposure indexes of summer O<sub>3</sub> (Arbaugh et al., 1998). Using a simple linear model, it was estimated that an average exposure to 365 ppm-h over 4 years is needed to induce a measurable amount of crown injury.

### 3.2. Photosynthesis

While significant decreases in photosynthetic rates have been observed following acute O<sub>3</sub> exposures (Table 2), adverse effects following exposure to ambient O<sub>3</sub> are usually observed only after two or more years. In three field chamber studies, the effect of ambient O<sub>3</sub> on photosynthesis in ponderosa pine seedlings was investigated. No significant effects were reported after exposure to 140–340 ppm-h O<sub>3</sub> at Tanbark Flat (Bytnerowicz et al., 1989b), or after 200–600 ppm-h O<sub>3</sub> at Whitaker's Forest (Beyers et al., 1992). In comparison, rates in 1-year-old needles were inhibited on selected dates after exposure to ~500 ppm-h O<sub>3</sub> at Shirley Meadow in the southern Sierra Nevada (Takemoto et al., 1997). In most instances, the depression of photosynthesis in ponderosa or Jeffrey pine by ambient O<sub>3</sub> has not been strongly correlated with stomatal closure (Grulke, 1999). In terms of whole-tree photosynthesis, rates in O<sub>3</sub>-stressed trees would be further reduced by decreased levels of foliar chlorophyll and higher rates of needle senescence (Coyne and Bingham, 1981; Grulke and Balduman, 1999). Assuming that trees in central and southern California receive growing-season O<sub>3</sub> exposures of 150–250 ppm-h per year, a cumulative exposure of 600–1000 ppm-h would be achieved within 4-years. Upon reaching this level of O<sub>3</sub> accumulation, adverse effects on photosynthesis may become evident in 3- and 4-year-old needles,

possibly due to the loss of normal stomatal function (Grulke, 1999).

### 3.3. Carbon allocation (C-allocation)

Carbon skeletons produced by photosynthesis are distributed within plants to sustain growth, homeostasis, defense, and repair processes (McLaughlin and Shriner, 1980). In their review of O<sub>3</sub> effects on C-allocation and C-partitioning, Cooley and Manning (1987) reported that while O<sub>3</sub> often reduces whole-plant dry-matter content, in most cases, the amount of carbon reserves is most affected by ambient O<sub>3</sub>. In ponderosa pine seedlings, exposure to O<sub>3</sub> reduced root biomass and C-allocation to associated mycorrhizal symbionts (Andersen and Rygielwicz, 1995). Subsequent studies found that O<sub>3</sub>-caused reductions in photosynthate availability, coupled with decreases in the starch content of stems, coarse roots and fine roots, contributed to lower new root growth in the following year (Andersen et al., 1997). In a gradient study conducted in the San Bernardino Mountains, peak root biomass in trees at Camp Osceola, the least O<sub>3</sub>-polluted site, was 6–14 times greater than at Camp Paivika, the most polluted site (Grulke et al., 1998). Significant decreases in fine and medium root biomass were observed in the upper 40-cm of mineral soil between sites. Sustained reductions in C-allocation to roots may adversely affect water and nutrient acquisition, which is especially important in Mediterranean climates where summer droughts are long and severe. With respect to aboveground biomass, Grulke and Balduman (1999) found marked differences in needle and stem biomass allocation in trees growing at Camp Paivika and Camp Osceola. At Camp Osceola, foliar biomass was evenly distributed in three of the five needle age classes retained. In comparison, ~95% of

the foliar biomass was present in the current-year needle age class in trees at Camp Paivika, suggestive of the biomass allocation pattern for leaves in deciduous trees.

### 3.4. Tree growth

Pye (1988) reviewed the responses of 43 tree species to  $O_3$ , and postulated that reductions in seedling growth may be occurring throughout the U.S., including ponderosa and Jeffrey pine in the West. While the negative impacts of  $O_3$  alone on tree growth are well documented, the degree of  $O_3$  inhibition of growth may be moderated at sites where high rates of atmospheric N deposition have contributed to N-saturation. In the Sierra Nevada, pine tree growth in mixed conifer forests is N-limited, and air pollution-caused reductions in growth are most likely due to ambient  $O_3$ . However, in the mountains of southern California, decrements in tree growth during the 1950–1970s are postulated to result from  $O_3$  alone (McBride et al., 1975), but responses to  $O_3$  may have been altered in the 1980–1990s due to N-saturation at selected sites (e.g. Camp Paivika in the San Bernardino Mountains) (Grulke and Balduman, 1999). Relative to the 1950s, substantial reductions in ambient  $O_3$  have also occurred, which could have enabled the trees that survived the  $O_3$ /bark beetle/drought complex to grow more rapidly on N-rich soils. The growth-inhibiting impacts of ambient  $O_3$  may have been balanced, or possibly overcome, by the growth-enhancing inputs of N to soil that accumulated after 20–30 years of atmospheric deposition.

Studies conducted in Sequoia National Forest showed that radial growth in mature ponderosa pine trees, which exhibited  $O_3$  injury, was lower than in trees without injury (Williams and Williams, 1986). In subsequent studies, Peterson et al. (1987) observed a similar level of growth inhibition in injured Jeffrey pine trees (11% lower than uninjured trees), which tended to be more pronounced in larger, older trees. However, these workers did not find significant growth reductions in ponderosa pine, which exhibited chlorotic mottle and premature needle senescence (Peterson and Arbaugh, 1988). At Whitaker's Forest, Temple et al. (1993) found that well-watered ponderosa pine seedlings exposed to  $O_3$  (~900 ppm-h) exhibited 70% and 48% decreases in 2 and 1-year-old needle bio-

mass, respectively. While the mass of current year needles was not reduced, significant decreases were observed in stem diameter (6%) and coarse root dry weight (14%). Total plant dry weight was 14% lower in  $O_3$ -exposed plants relative to plants grown in charcoal-filtered air. Temple and Miller (1994) later reported that the reduction in radial growth was correlated with foliar injury in well-watered trees; needles with >30% injury tended to abscise before the end of the next growing season.

In the San Bernardino Mountains, radial growth responses in ponderosa pine varied over the period from 1925 to 1991 (Arbaugh et al., 1999). From 1925 to 1949, radial growth rates exhibited an increasing trend, and a decreasing trend from 1950 to 1974 due, in part, to the combined effects of drought and ambient  $O_3$ . From 1975 to 1991, radial growth responses appear to have recovered to levels similar to those in the 1930s, which coincides with an increase in precipitation amount, but only slight declines in ambient  $O_3$ . The accumulation of N from atmospheric deposition could have enhanced growth during this 16-year period of modest air-quality improvement. Despite the poor air quality at Camp Paivika, the average total mass of 20–60-year-old trees was greater than at Strawberry Peak or Camp Osceola (Grulke and Balduman, 1999). Moreover, at Camp Paivika, the highest proportion of whole-tree biomass was allocated to stems and branches, and the least to roots.

### 4. N deposition to California's mixed conifer forests

In California, the majority of the state experiences a Mediterranean climate, in which ~80% of annual precipitation is deposited in October–March. In April–September, thunderstorms occur sporadically in the mountain and coastal areas. Additionally, fog/cloud intercepts occur in fall/spring, but few data are available to develop reliable estimates of N inputs from fog/cloud across the state. Statewide, regional estimates by Blanchard and Michaels (1994) did not consider inputs from fog/cloud, which may be important at selected mountain sites (Waldman et al., 1985; Collett et al., 1989; Muir and Böhm, 1989). Wet N deposition ( $NO_3^- + NH_4^+$ ) was 3 kg N/ha per year or

Table 3

Total N deposition rates to forests in California

Site	Total N deposition (kg N/ha/year)	Reference
Eastern Brook Lake (3150 m) — Eastern Sierra Nevada	~1.0	Bytnerowicz et al., 1992; Blanchard and Michaels, 1994
Emerald Lake (2800 m) — western Sierra Nevada	~1.5	Bytnerowicz et al., 1991; Blanchard and Michaels, 1994
Northern California Forests	2–4	Blanchard and Michaels, 1994
Shirley Meadow (1950 m) — western Sierra Nevada	2–4	Takemoto et al., 1997; Blanchard and Michaels, 1994
Barton Flats (1900 m) — San Bernardino Mountains	5–9	Bytnerowicz et al., 1996
Kratka Ridge (2060 m) — San Gabriel Mountains	6–11	Fenn and Kiefer, 1999
Sequoia National Park (2100 m) — western Sierra Nevada	8–13	Chorover et al., 1994
Tanbark Flat (800 m) — San Gabriel Mountains	20–35	Bytnerowicz and Fenn, 1996
Camp Paivika (1600 m) — San Bernardino Mountains	35–45	Fenn and Bytnerowicz, 1997

less, and dry N deposition was estimated to range from <1 to 28 kg N/ha per year across the state. Overall, urban sites exhibited the highest total N deposition amounts (15–30 kg N/ha per year), and forests in northern and central California had the lowest values (2–4 kg N/ha per year) (Table 3). These analyses indicate that differences in total N deposition across the state are primarily due to the amount of dry N deposition. In ponderosa pine, foliar uptake of N-containing air pollutants occurs through stomata and by transcuticular transport (Bytnerowicz et al., 1999). Under controlled conditions,  $\text{HNO}_3$  vapor entry into exposed needles is largely due to stomatal uptake (Krywult et al., 1996), and only a small portion remains in the epicuticular wax layer.

Bytnerowicz and Fenn (1996) surveyed the literature concerning N deposition to forests in California. At Shirley Meadow, total N deposition was projected to be 2–4 kg N/ha per year, in consideration of N-containing dry-particle and gas measurements at the site (Takemoto et al., 1997) and multi-year average precipitation data at Lake Isabella (Blanchard and Michaels, 1994). In the Giant Forest area in Sequoia National Park (elevation 2100–2200 m), Chorover et al. (1994) measured throughfall N deposition and estimated dry N deposition to range from 6 to 11 kg N/ha per year in mixed fir and giant sequoia stands. At higher elevations, rates of dry N deposition were measured at Emerald Lake Watershed (elevation 2800 m) in Sequoia National Park (Bytnerowicz et al., 1991). Mean deposition rates for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were 0.45 and 0.41  $\mu\text{eq}/(\text{m}^2 \text{ h})$ , respectively, which yields an annual dry N deposition rate of ~0.5 kg N/ha per year. Assuming a wet N deposition

rate of ~1 kg N/ha per year for alpine sites on the western slope of the Sierra Nevada (Melack et al., 1995), total N deposition would be ~1.5 kg N/ha per year. Total N deposition at Eastern Brook Lake Watershed (elevation 3150 m) on the eastern slope of the Sierra Nevada was estimated to be ~1 kg N/ha per year (cf. Bytnerowicz et al., 1992).

In comparison to northern California, forests in southern California experience higher total N deposition levels. Rates of total N deposition to chaparral ecosystems in the San Gabriel Mountains are >20 kg N/ha per year (Riggan et al., 1985). At Tanbark Flat (elevation 800 m), Bytnerowicz and Fenn (1996) estimated that total N deposition ranges from 20 to 35 kg N/ha per year, consistent with the earlier estimates of Riggan et al. (1985). Detailed analyses indicate that the major dry N species at Tanbark Flat are  $\text{HNO}_3$  vapor, peroxyacetyl nitrate (PAN), and peroxypropionyl nitrate (Grosjean and Bytnerowicz, 1993). At three Jeffrey pine sites in the San Gabriel Mountains, near Kratka Ridge (elevation 2060 m), with varying degrees of exposure to prevailing winds, total N in throughfall ranged from 6 to 11 kg N/ha per year (Fenn and Kiefer, 1999). These values are 45–80% less than deposition rates in the chaparral vegetation zone (elevation 800 m).

Elevated N deposition has also been reported for sites in the San Bernardino Mountains. At Camp Paivika, on the western end of the mixed conifer zone, total N deposition is estimated to be 20–53 kg N/ha per year (Fenn and Poth, unpublished). Wet deposition provides 20%, fog/cloud 35%, and dry deposition 45% of the total N deposition. At Barton Flats, ~42 km southeast of Camp Paivika, total N deposition was

estimated to be 5–9 kg N/ha per year (Fenn and Bytnerowicz, 1997). Wet deposition provides 30%, and fog/cloud and dry deposition account for the remainder. Between Camp Paivika and Barton Flats, total N deposition decreases by 85%, possibly due to rapid  $\text{HNO}_3$  vapor and gaseous  $\text{NH}_3$  deposition to foliage, and to edge effects (Fenn and Kiefer, 1999). At the stand-level, rates of N deposition in the San Bernardino Mountains are highly variable due, in part, to the open nature of western mixed conifer forests. For example, stand cover was estimated to be ~67% at Barton Flats (Fenn and Bytnerowicz, 1997), and slightly higher at Camp Paivika. Patchy stand structure results in high spatial variability in N deposition. While gaps in open stands reduce landscape-level deposition fluxes, nutrient deposition to trees at forest edges are higher than to trees away from the edge due to higher leaf area indexes and greater wind turbulence at the edge (Beier and Gundersen, 1989). Variations in N deposition rates are likely to occur when gap or edge effects are predominant within a stand (Weathers et al., 1999).

## 5. N-saturated forests in California

Nitrogen is the mineral nutrient that plants require in the greatest quantity, and that most frequently limits growth in both, agricultural and natural systems (Chapin et al., 1987). The N-limitation of western conifer growth has been demonstrated in studies in which trees in plantations and natural stands, supplied with N-fertilizer, grew larger than unfertilized, control trees (Powers and Jackson, 1978; Powers et al., 1988). As forest tree species have adapted to growing on N-poor soils, when N is available in excess of nutritional requirements, trees may assimilate intemperate quantities of N, which could be detrimental to their long-term health (Nihlgård, 1985).

Nitrogen saturation is broadly defined as the availability of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in excess of total combined plant and microbial nutritional demand, excluding the use of  $\text{NO}_3^-$  as a substrate for denitrification (Aber et al., 1989). Fertilization of ponderosa or Jeffrey pine trees growing in the San Gabriel and San Bernardino mountains has shown that selected sites are N-limited while others are clearly N-saturated. In the San Gabriel Mountains, needle growth and foliar N concentra-

tions in Jeffrey pine were significantly higher at Kratka Ridge, Vista, and Rock Creek following N-fertilization (500 kg N/ha). In the San Bernardino Mountains, needle growth responses to N-fertilization indicated that ponderosa pine trees were not N-limited at Camp Paivika, but trees at Camp Osceola, near Barton Flats, were N-limited (Kiefer and Fenn, 1997). However, in ponderosa pine and California black oak at Camp Paivika, positive bole growth responses have been observed following N-fertilization for three consecutive growing seasons (Fenn and Poth, unpublished data).

In N-saturated ecosystems, N losses occur due to  $\text{NO}_3^-$  leaching from soil,  $\text{NO}_3^-$  removal in stream water, increased emissions of  $\text{NO}/\text{N}_2\text{O}$ , and large reductions in fine root biomass. Of these loss processes, leaching from soil is usually the most important, although gaseous N losses at Camp Paivika may be of similar magnitude to N losses from leaching (Fenn and Poth, 1998). Because  $\text{NO}_3^-$  is poorly adsorbed to most soils, nitrification in excess of plant/microbial uptake in aerobic soils leads to  $\text{NO}_3^-$  leaching (Johnson, 1992). Evidence of N leaching in the San Bernardino Mountains was reported by Fenn et al. (1996) who measured soil solution  $\text{NO}_3^-$  concentrations of 3000–4000  $\mu\text{mol/l}$  at Camp Paivika and 500–800  $\mu\text{mol/l}$  at Barton Flats. Post-fire  $\text{NO}_3^-$  concentrations in soil solution ranged from 100 to 1000  $\mu\text{mol/l}$  at Giant Forest in Sequoia National Park, which were up to 300-times higher than the pre-fire levels (Chorover et al., 1994).

At two N-saturated sites in southern California, total inorganic N outputs in stream water ranged from 0.04 to 11.6 kg N/ha per year (Riggan et al., 1985; Fenn and Poth, 1999). Riggan et al. (1985) found  $\text{NO}_3^-$  concentrations in streams draining chaparral watersheds in the San Gabriel Mountains to range from 140 to 500  $\mu\text{mol/l}$  (mean=260  $\mu\text{mol/l}$ ). These values were 1–2 orders of magnitude higher than mean values measured in the Santa Ana (15.0  $\mu\text{mol/l}$ ), Santa Monica (4.3  $\mu\text{mol/l}$ ), and Palomar-Black (3.6  $\mu\text{mol/l}$ ) mountains in southern California. Subsequent studies found that annual  $\text{NO}_3^-$  losses from severely burned watersheds may be 40-times greater than from unburned watersheds (Riggan et al., 1994). Three-year average  $\text{NO}_3^-$  concentrations in streams draining Devil Canyon, at the western end of the San Bernardino Mountains, immediately downslope of Camp



Paivika, ranged from 10 to 150  $\mu\text{mol/l}$ . These values were markedly higher than in streams along southern (5–40  $\mu\text{mol/l}$ ) or northern (<2  $\mu\text{mol/l}$ ) transects in the San Geronio Wilderness, where N deposition rates are lower (Fenn and Poth, 1999). The peak  $\text{NO}_3^-$  concentration in the primary stream draining Devil Canyon was 350  $\mu\text{mol/l}$  in December 1997, and is one of the highest values reported for undisturbed forest or shrub-land watersheds in North America. In the Sierra Nevada, Chorover et al. (1994) measured mean  $\text{NO}_3^-$  concentrations of 0.36  $\mu\text{mol/l}$  in Log Creek and 0.05  $\mu\text{mol/l}$  in Tharp's Creek in the vicinity of Giant Forest (Sequoia National Park) prior to prescribed fire. In the East,  $\text{NO}_3^-$  concentrations in streams draining undisturbed watersheds in the Catskill Mountains (New York) ranged from 2 to 36  $\mu\text{mol/l}$  (Lovett et al., 1999), and from 35 to 85  $\mu\text{mol/l}$  in the Fernow Experimental Forest (West Virginia) (Gilliam et al., 1996).

Firestone and Davidson (1989) reviewed the microbiological basis of NO and  $\text{N}_2\text{O}$  emissions from soil. The production of NO via nitrification occurs by the oxidation of  $\text{NH}_4\text{OH}$  or the reduction of  $\text{NO}_2^-$ . In microbial denitrification, NO may be an intermediate, or may be formed by chemical denitrification of  $\text{HNO}_2$ . In the San Gabriel Mountains, NO fluxes from unburned dry and wet soils were 9.7 and 21.4 ng N/( $\text{m}^2 \text{ s}$ ), respectively (Anderson et al., 1988). Similar values were obtained by Fenn et al. (1996) at Camp Paivika in the San Bernardino Mountains (i.e. on dry and wet soils, mean values were 8.1 and 21.6 ng N/( $\text{m}^2 \text{ s}$ ), respectively). These workers estimated from monthly measurements that gaseous NO emissions at Camp Paivika resulted in a loss of 4.5 kg N/ha per year (Fenn and Poth, 1999). Gaseous N losses at Camp Paivika were of magnitudes similar to the reported values of  $\text{NO}_3^-$ -N losses in stream water (3.6–11.6 kg N/ha per year). In comparison, rates at Camp Osceola, ~42 km east of Camp Paivika, were calculated to be 0.25 kg N/ha per year.

The open nature of N processing, temporal asynchrony between hydrologic fluxes of  $\text{NO}_3^-$  in soil and plant/microbial demand, and presence of soils with high base saturation are key factors conceptualizing the developmental stages of N-saturation in western conifer forests (Fenn et al., 1998). Rates of nitrification,  $\text{NO}_3^-$  leaching, and NO emissions from soil are high in western conifer forests exposed to chronic N

deposition. While similar responses occur during the late stages of N-saturation in eastern forests (Aber et al., 1989), widespread forest decline due to the depletion of base cations is not expected to occur in the West, given their abundance in native forest soils. However, forest decline could occur if excess N predisposes western conifers to damage from  $\text{O}_3$  or other stressors (e.g. insects or drought).

## 6. Combined effects of $\text{O}_3$ and atmospheric N on mixed conifer forests

Ozone-caused foliar injury and acceleration of leaf senescence reduce the total amount of photosynthetic leaf area of pines in mixed conifer forests in southern California. With less photosynthetically active leaf tissue, decreases in photosynthate production may result, which could limit tree growth. As net carbon retention in the shoot tends to be greater in  $\text{O}_3$ -stressed vs. unstressed trees, air pollution-caused reductions in ponderosa pine root biomass at Camp Paivika have been documented, which could render these trees more susceptible to other stressors (e.g. root diseases, drought, and windthrow) (Gulke et al., 1998). In a subsequent study, ponderosa pines growing at Camp Paivika and Strawberry Peak were found to exhibit increased resource allocations to stems and branches after a multi-decade period of exposure to  $\text{O}_3$  and atmospheric N (Gulke and Balduman, 1999). In these trees, biomass allocation to stems and branches was 77–80 vs. 59% at Camp Osceola, 42 km east of Camp Paivika. While percent allocations to root and leaf biomass were lower at Camp Paivika and Strawberry Peak than at Camp Osceola, the distribution of leaf biomass among age classes was skewed toward current-year needles at the two western sites. It was postulated that the combined pollution exposure to  $\text{O}_3$  and atmospheric N is causing a shift in pine tree biomass allocation favoring the retention of only 1–2 over-wintering needle age classes.

Elevated atmospheric N inputs may be a factor in mitigating  $\text{O}_3$ -induced reductions in tree growth, but they are ineffective insofar as they moderate the development of  $\text{O}_3$  injury to needles. The phenology of needle growth at Camp Paivika, a highly polluted site, is quite distinct from that of trees growing at less polluted sites where as many as 6–7 years of needles

may be retained. At Camp Paivika and Strawberry Peak (7 km east), 95 and 75% of the total physiologically active leaf biomass is present as current-year needles. Grulke and Balduman (1999) suggested that this type of growth habit, in which only one needle age class is retained over winter, more closely approaches the biomass allocation pattern of a deciduous tree than a pine. As a consequence of retaining only 1–2 needle age classes, large amounts of litter accumulate on the forest floor, which has long-term implications with respect to pine seedling establishment, carbon sequestration, and fire sensitivity. Litter is a barrier to the germination of some pine species that require a mineral seedbed and thin litter layer for germination and survival. When the litter layer is too deep, pine rootlets are unable to reach the mineral soil before they dehydrate (Kozłowski et al., 1991). At Camp Paivika, there is virtually no regeneration of ponderosa pine. In short-term studies, N-rich litter decomposed faster than litter with a lower N concentration (Fenn and Dunn, 1989). However, over the long term, decomposition rates are slower for N-rich litter, enabling carbon to accumulate on the forest floor (Fog, 1988).

For California's mixed conifer forests, exposure to  $O_3$  and the deposition of N-containing compounds are the airborne constituents of greatest concern. As potential modifiers of long-term forest health,  $O_3$  is a stressor and N deposition is an enhancer of ponderosa/Jeffrey pine physiology and growth (Grulke and Balduman, 1999). The progression toward a deciduous growth habit, higher shoot:root biomass ratios, increasing depths of litter, tree densification, and elevated  $NO_3^-$  concentrations in soil and soil solution, all point to the replacement of pine species with nitrophilous, shade and  $O_3$ -tolerant tree species, such as fir and cedar (Minnich et al., 1995; Minnich, 1999).

## 7. Current and future impacts of air pollution in three montane regions

California spans over 100 million acres of which ~9.3 million acres are covered by mixed conifer forests (CDF, 1988) (Fig. 3). In Sections 7.1–7.3, expected near-term impacts to three mixed conifer forest regions are described. Presently, forests in the San Bernardino and San Gabriel Mountains are at the

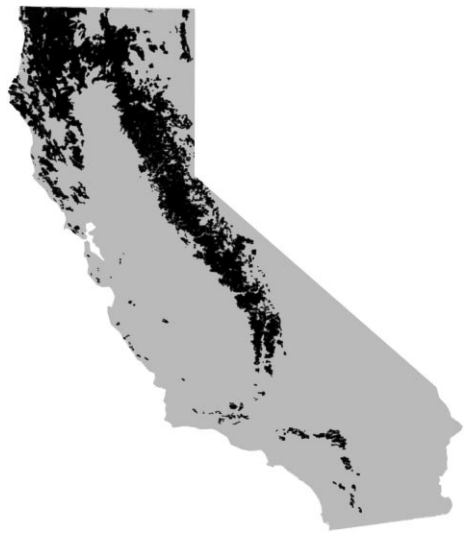


Fig. 3. Distribution of mixed conifer forests in California.

greatest risk, with trees exhibiting severe  $O_3$  injury and N-saturation, in some cases. The risk to forests on the western slope of the Sierra Nevada is moderate.

### 7.1. San Bernardino Mountains

Mixed conifer forests at Camp Paivika are exposed to high levels of  $O_3$  (summertime 24-h average  $\sim 0.09$  ppm) and N deposition (35–45 kg N/ha per year). Throughout much of the San Bernardino Mountains, many of the most  $O_3$ -sensitive trees have died as a result of the combined effects of ambient  $O_3$ , drought, and insect attack since the 1950s, and have been removed in salvage logging operations (Dale, 1996). Forests in the vicinity of Camp Paivika are clearly N-saturated, based on a suite of indicator responses (Fenn et al., 1996) including year-round export of high levels of  $NO_3^-$  in stream water (Fenn and Poth, 1999). As stream water from the San Bernardino Mountains recharges underground aquifers and wells used by the cities of San Bernardino and Riverside,  $NO_3^-$  pollution of drinking water and associated effects on human health are of near-term concern. If combined exposures to  $O_3$  and atmospheric N continue at extant levels, forests to the east of Camp Paivika may show signs of N-saturation in future decades.

## 7.2. San Gabriel Mountains

While mixed conifer forests are primarily found at elevations of 1200 m or higher in the Angeles National Forest, little data are available to characterize in situ pollution exposures. However, considerable data have been collected at an elevation of ~800 m in the San Dimas Experimental Forest to document air pollution levels in the chaparral watersheds near Tanbark Flat (Bytnerowicz et al., 1987b). At this site, growing-season 12-h average O<sub>3</sub> levels are 0.07–0.08 ppm (Bytnerowicz et al., 1989b), and summertime exposures are estimated to be 300–350 ppm-h. Total N deposition is calculated to be 20–35 kg N/ha per year at this elevation (Bytnerowicz and Fenn, 1996). Clearly, air pollutants are present at phytotoxic levels and N deposition leads to severe stream water NO<sub>3</sub><sup>-</sup> pollution (Riggan et al., 1985, 1994). At higher elevation (2060 m), Kiefer and Fenn (1997) estimated that throughfall N deposition at mixed conifer sites near Kratka Ridge was 6–11 kg N/ha per year. At these sites, fertilizer experiments demonstrated that atmospheric N had not alleviated conditions of N deficiency in Jeffrey pine. Widespread air pollution damage to forests in the San Gabriel Mountains has not been reported, possibly because chaparral vegetation dominates the lower elevations at which pollution exposures are the greatest.

## 7.3. Sierra Nevada

Most of California's mixed conifer forest acreage exists on the western slope of the Sierra Nevada (CDF, 1988). The sources of air pollution to these sites include upwind urban centers and agricultural areas throughout the Central Valley and San Francisco Bay Area. Cahill et al. (1989) reported that terrain-effect winds were capable of transporting O<sub>3</sub> and particulates to 1800 m elevation during upslope flows, but pollutant transport to elevations at or above 3000 m would be considerably less. During the growing season, 24-h average O<sub>3</sub> levels on the western slope of the Sierra Nevada are 0.05–0.07 ppm (Carroll and Dixon, 1993, 1995). These average O<sub>3</sub> values are comparable to levels measured at Barton Flats in the San Bernardino Mountains, 40 km east of Camp Paivika. Nitrogen deposition was reported to be 2–3 kg N/ha per year at an elevation of 1200–1800 m (Bytnerowicz and

Fenn, 1996), but rates of 8–13 kg N/ha per year may occur at more exposed locations (Chorover et al., 1994). Currently, the risk posed by O<sub>3</sub> and atmospheric N in the Sierra Nevada is far less than in the San Bernardino or San Gabriel Mountains. However, rates of population growth in the San Joaquin Valley and Sierra Foothills are among the highest in California, and pollutant exposures are expected to rise in the years ahead (ARB, 1993). Ozone injury to trees has occurred in a number of Sierran forests, but decreases in growth have not been severe (possibly due to the alleviation of N-deficiency by atmospheric N). Issues relating to N-saturation have largely been unexplored in the Sierras, but deposition and N effects studies are underway at Blodgett Forest (Jeanne Panek, personal communication), Mountain Home State Forest and Sequoia National Park (Mark Fenn, unpublished data).

## 8. Regulatory issues and future effects

Critical or target loads, are the means by which decision-makers identify what amount of pollution is harmful to sensitive ecosystems or is achievable, respectively (Bull, 1991). Critical loads for European forests ranging from 3 to 48 kg N/ha per year have been reported (Schulze et al., 1989), and these values were chosen to prevent permanent, adverse damage to the most sensitive resource to which the load applies (Nilsson, 1988). Currently in California, uncertainties, insofar as the relationship between field and laboratory tree response data and issues of scaling including whole-tree pollutant uptake and leaf area indexes, need to be addressed before regulatory action can be considered. As a first step, a clearer understanding of the relationship between emissions of N-containing pollutants and their deposition to forest sites in southern California is needed. This would allow for estimating how much of a reduction in ambient O<sub>3</sub> and N deposition may result from the measures in the California State Implementation Plan for O<sub>3</sub> (ARB, 1994). This information is fundamental to determining whether future control measures will/will-not provide long-term protection from ambient O<sub>3</sub> and N deposition in southern California, based on current knowledge. Clearly, extant exposures have already caused N-saturation to selected forest and chaparral

watersheds in the region, but the prevalence of N-saturated forests in southern California and in the southern Sierra Nevada may increase if emission reductions are insufficient to protect other sensitive sites.

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