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Chapter 5

Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada

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Abstract

The greatest air pollution impacts in forests of California are the physiological disturbances imposed on trees as a result of the combined effects of excess N and phytotoxic ozone exposure (Takemoto et al., 2001). In highly-polluted stands in the San Bernardino Mountains in southern California, fine root biomass is greatly reduced and C cycling within the tree and within the ecosystem is also significantly altered. Air pollution effects appear to be more subtle over most of the Sierra Nevada. Individual trees with significant amounts of ozone injury in the southern and western edge of the Sierra have been identified in previous surveys. Additional significant environmental impacts of N deposition in southern California forest and chaparral ecosystems include high NO_3^- concentrations in streamwater and groundwater and increased greenhouse gas emissions from soil. Nitrogen deposition in the Sierra Nevada does not appear to be sufficiently high to cause major physiological impacts or widespread deterioration of water quality, although it is possible that chronic N deposition may be at least partially offsetting the depressive growth effects of ozone in the southern Sierra. However, unusually high nitrate concentrations frequently occur in a chaparral catchment with high N deposition inputs in Sequoia National Park. Preliminary results from N deposition measurements, streamwater analyses for NO_3^-, and soil and plant indicators of N enrichment suggest that N cycling in the mixed conifer forests in the Mountain Home State Park region in the southwestern Sierra Nevada is being altered by N deposition to a greater extent than similar forests in Sequoia National Park. Ozone and N deposition levels are relatively low in high-elevation ecosystems of the Sierra Nevada and do not appear to have severe impacts, although N deposition in the southern Sierra may contribute to the natural peak in nitrate in runoff during early snowmelt. In forests throughout California, periodic droughts and stand densification from long-term fire suppression are major risk factors responsible for reduced tree vigor, greater mortality and predisposition to disease and insect attack; the latter a common ultimate cause of tree mortality. Current land management plans for the Sierra Nevada focus on decreasing overstocking of stands and reducing fuel loads and wildfire risk.

1. Introduction

The most important atmospheric pollutants with potential adverse effects in the Sierra Nevada are ozone and an array of nitrogenous pollutants deposited in both wet and dry forms. The major natural resources at risk include ozone-sensitive tree species such as ponderosa (*Pinus ponderosa* Dougl. Ex Laws.) and Jeffrey pine (*P. jeffreyii* Grev. & Balf.), possibly some understory species (Temple, 1999; Yoshida et al., 2001), and plant and microbial species impacted by increased N fertility (Fenn and Dunn, 1989; Egerton-Warburton and Allen, 2000; Yoshida et al., 2001). These effects on plant species or communities may also result in indirect effects on the biota associated with or dependent upon these plant species. Chronic N inputs to these normally N-limited systems can also increase nitrate leaching in runoff waters of chaparral and forested watershed, thus decreasing water quality.

Ozone is a well known phytotoxicant, while the overall effect of cumulative N deposition is to increase site fertility, which is expected to enhance plant growth. In California forests with a significant ponderosa pine component, the combined effects of ozone and N can result in considerable perturbation of carbon and N cycling. The risk of catastrophic fire is also increased as ozone induces premature foliar senescence and abscission, and N stimulates the production of foliar biomass, the net result of which is greater litterfall and litter accumulation on the forest floor (Arbaugh et al., 1999). These effects in combination with greater forest production due to increased site fertility further increase fuel buildup in stands already at fire risk due to long-term fire suppression. Nitrogen deposition is believed to contribute to this stand densification, thus adding another dimension to the natural stress factors such as drought, insects and diseases that occur in these Mediterranean ecosystems (Ferrell, 1996).

In this chapter air pollution studies are reported from a number of sites in California. Site abbreviations used in this chapter include (see Fig. 1 for site locations): Barton Flats (BF), Camp Paivika (CP), Camp Osceola (CAO),

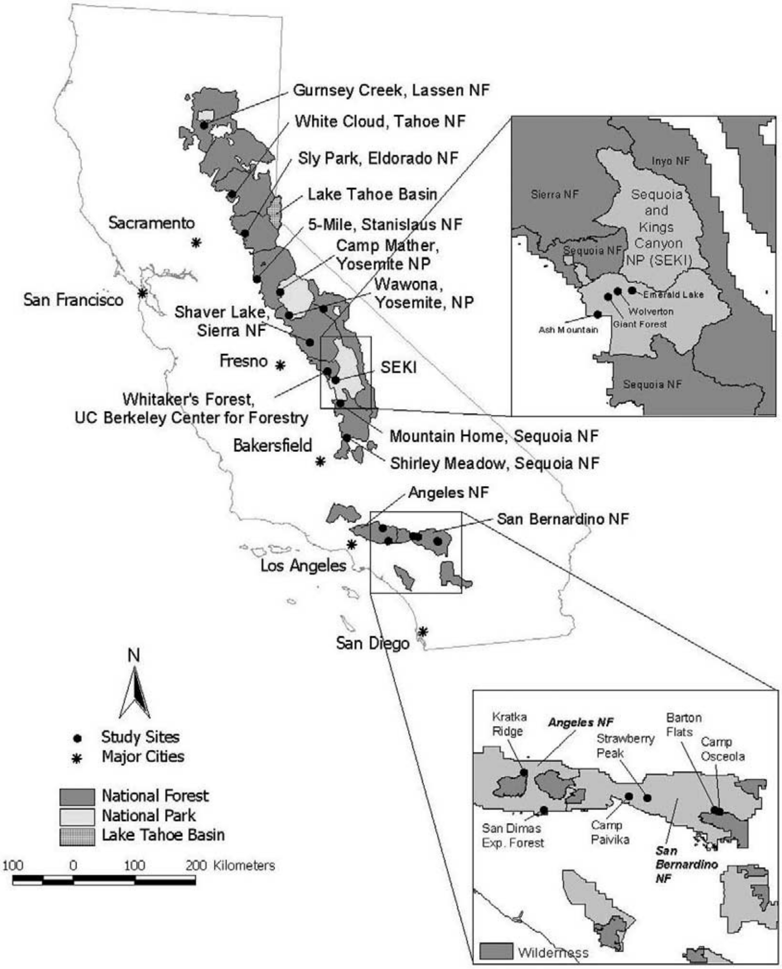

Figure 1. Location of air pollution study sites mentioned in this chapter.

Emerald Lake Watershed (ELW), Mountain Home State Park (MH), Mountain Home Project Forest site 3 (MH-3), San Bernardino Mountains (SBM), San Gorgonio Wilderness (SGW), Chamise Creek (CC), and Sequoia National Park (SNP).

Our knowledge of current impacts of air pollution in forests of the Sierra Nevada comes from limited studies in the Sierra. Our understanding of current and future potential effects of increased pollution is further based on studies across air pollution gradients in the mixed-conifer forest zone of the San Bernardino Mountains (SBM) in the South Coast (Los Angeles) Air Basin. The effects of ozone injury on ponderosa and Jeffrey pine trees in the SBM are a world famous case study of air pollution impacts on a forest ecosystem (Miller and McBride, 1999). The syndrome of ecosystem responses to chronic N deposition is commonly referred to as N saturation, and the occurrence of N saturation has been well documented for forests and chaparral ecosystems in the San Gabriel and San Bernardino Mountains of the Los Angeles Basin. In this chapter we report on the extent to which similar effects have been observed in forests in the Sierra Nevada. The principal objective of this chapter is to summarize the current state of the science in regard to the impacts of ozone and nitrogen pollutants on forests of the Sierra Nevada, within the context of other co-occurring stresses such as drought, disease, insect infestations, fire, fire suppression and stand densification.

2. Spatial gradients of ozone and nitrogen compounds

Ozone exposure data will not be covered in detail in this chapter as it is the focus of other chapters in this volume. Ozone and N compounds are the major pollutants impacting California forests and these two pollutant types usually occur together under the environmental conditions prevalent in California (Table 1). Their co-occurrence is to be expected inasmuch as nitrogen oxides are precursors to ozone formation. However, the decline in N deposition with distance from the source area is three to four times steeper than for ozone in the SBM. Ambient ozone concentrations and dry deposition of inorganic N (measured as NO_3^- and NH_4^+ in branch rinses) were highly correlated at 10 sites across an air pollution gradient in the SBM (Fenn and Bytnerowicz, 1993). The steeper decline in N deposition compared to ozone exposures is thought to be due to the high deposition velocity and reactivity of major N pollutants such as nitric acid vapor and ammonia (Hanson and Lindberg, 1991).

A similar trend of more rapidly declining N deposition than ozone concentrations also occurs in the Sierra Nevada based on bulk throughfall data and ozone monitoring data from nine sites (Fig. 1) along a north/south transect

Table 1. Ozone concentration, N deposition, and forest/watershed effects at a range of montane sites.

Site	Elevation (m)	Ozone-24-hr average (ppbv)	N deposition (kg ha^{-1} yr^{-1})	Ecological effects	Reference
Low- and mid-elevation forests or chaparral					
Camp Paivika (CP), San Bernardino Mountains, CA	1600	80 (Apr. 15–Oct. 15, 1993 & 1994)	31 (1996)[a]	Highly N saturated site; elevated nitrate in runoff and NO emissions	Ozone data from Grulke, 1999; N data from Fenn et al., 2000
Barton Flats (BF), San Bernardino Mountains, CA	1946	70 (Summer 1992–1995)	5–13	N limited site; Low streamwater nitrate levels	Ozone data from Arbaugh et al., 1998; N data from Fenn et al., 2000 and M.E. Fenn, unpublished data
Camp Osceola (CAO), San Bernardino Mountains, CA	2135	62–64 (Apr. 15–Oct. 15, 1993 & 1994)	5–13	N limited site	Ozone data from Grulke, 1999; N data estimated based on proximity to Barton Flats
San Bernardino Mountains (SBM); Simulation modeling for Barton Flats site	1946		Effects seen with N dep. of 20–35 or greater (NuCM model)	Elevated nitrate leaching, decreasing base cations, and increased soil acidity	Arbaugh et al., 1999; Fenn et al., 1996
Giant Forest, Sequoia National Park (SNP), CA	1920	66 (June–Sept. 1992–1994)	6–12 (as throughfall)	N limited site; low streamwater nitrate values (means 0.05–0.36 μeq L^{-1})	Ozone data from Carroll et al., this volume; N data from Chorover et al., 1994 and M.E. Fenn, unpublished data; Streamwater data from Chorover et al., 1994; Stohlgren et al., 1991; Williams and Melack, 1997

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Table 1. (*Continued*)

Site	Elevation (m)	Ozone-24-hr average (ppbv)	N deposition (kg ha^{-1} yr^{-1})	Ecological effects	Reference
Mountain Home State Park (MH), Southern Sierra, CA	1890	71 (June–Sept. 1992–1994)	17	Streamwater nitrate values slightly elevated; 3.7–18.7 μeq L^{-1} in June 1999	Ozone data from Carroll et al., this volume; N deposition estimated from unpublished throughfall data; Streamwater data from this chapter
Chamise Creek (CC), Sequoia National Park (SNP), CA	750	64 (mid May to mid Oct., 1999) at nearby Ash Mt.	15 (as throughfall)	Streamwater nitrate values ranged from 0.0 to 605 μeq L^{-1} from 1983–1998	Ozone data from Bytnerowicz et al., 2002; Throughfall estimated from Ash Mountain, SNP data; Streamwater nitrate data presented in this chapter.
Kratka Ridge, San Gabriel Mountains, CA	2060	N/A	12 (1994) as throughfall	Foliar growth N limited, but soil fertility seems to be increased	N data from Fenn and Kiefer, 1999; Effects data from Kiefer and Fenn, 1997
San Dimas Experimental. Forest, San Gabriel Mountains, CA[b]	800	74 (summer 1987)	23 (1980) as throughfall	Very high nitrate export in streams	Ozone data from Bytnerowicz et al., 1990; N data from Riggan et al., 1985
Fernow Experimental Forest, West Virginia	735–870	38 and 35 (Apr. 1–Oct. 31, 1988 & 1989)	15–20	Severe N saturation; High nitrification rates in soil and high nitrate losses in streamwater	Ozone data from Edwards et al., 1991; N data from Gilliam et al., 1996; Streamwater data from Peterjohn et al., 1996

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Table 1. (*Continued*)

Site	Elevation (m)	Ozone-24-hr average (ppbv)	N deposition (kg ha^{-1} yr^{-1})	Ecological effects	Reference
High-elevation forests or watersheds					
Lake Tahoe Basin	1900 m	45–50 (summer 1999)	4–5	Increased algal growth and decreasing lake clarity; Forest is still highly N limited	Ozone data from Lee, this volume; Wet plus dry N deposition estimated from Tarnay, 2001
San Gorgonio Wilderness (SGW), San Bernardino Mountains, CA (high elevation site)	Ozone at 4 elevations (1885 to 2797 m); Streams sampled at 1380 to 1843 m	56–61 (dry period) 48–56 in wet period; summer 1995	10–15	High nitrate losses in streamwater; Very high peak values with high runoff	Ozone data from Bytnerowicz et al., 1999a; N deposition and streamwater data from Fenn and Poth, 1999a
Emerald Lake Watershed (ELW), Sequoia National Park (high elevation site)	2800	41 (May–Oct. 1999) at Wolverton, Sequoia National Park	2–5 (1985–1998)	Mean nitrate slightly elevated in outflow of lake (4.9 µeq L^{-1})	Ozone data from Bytnerowicz et al., 2002; N deposition and runoff data from Sickman et al., 2001
Colorado Front Range, watersheds	3000–4000		4–7	N saturated; annual minimum nitrate concentrations ca. 10 µeq L^{-1}; diatom communities in lakes impacted	N deposition (estimated) and nitrate trends from Baron and Campbell, 1997 and Williams et al, 1996; impacts on lakes from Baron et al., 2000

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Table 1. (*Continued*)

Site	Elevation (m)	Ozone-24-hr average (ppbv)	N deposition (kg ha^{-1} yr^{-1})	Ecological effects	Reference
Colorado Front Range, Englemann spruce (*Picea engelmannii* Parry ex Engelm.) forest	3000–3500		3–5	Soils and spruce foliage N enriched, but forest not N saturated	Baron et al., 2000

[a] Nitrogen deposition at CP is much higher in years of frequent fog occurrence (Fenn et al., 2000, 2002; M.E. Fenn, unpublished data).

[b] San Dimas Experimental Forest is predominantly chaparral.

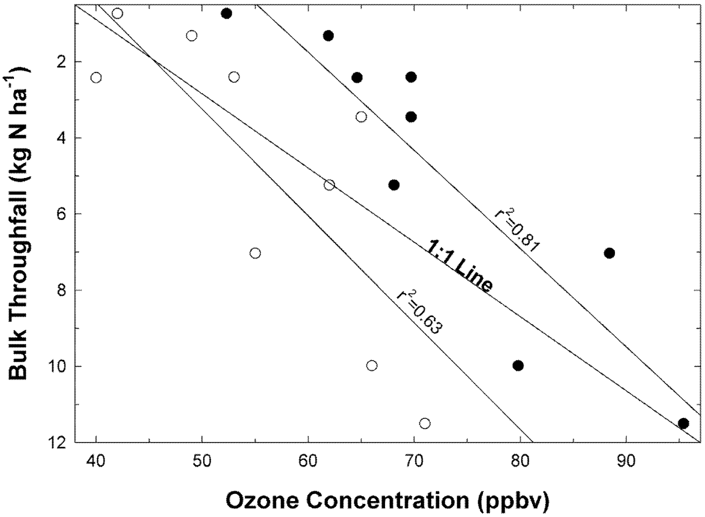

Figure 2. Correlation between mean growing season ozone concentration (June–September, 1992–1994) and N deposition in bulk throughfall under pine canopies at the Project FOREST sites. Nitrogen deposition data are from June to November, 2000. Solid circles represent average daily maximum ozone concentration and open circles are 24-hr ozone mean concentrations. Ozone data are from Carroll et al. (Chapter 2, this volume).

(Figs. 2 and 3). Divergence from the 1 : 1 line in Fig. 2 (plot of throughfall N deposition versus ozone exposure) illustrates the more rapid decrease in N deposition compared to ozone exposure at sites along the Sierran deposition gradient. The ratio of ozone concentration : N deposition in throughfall increased by a factor of 3.6 from MH in the south to Sly Park in the north. If the more rapid decline in N loading with distance from the source area is a general phenomenon in California forests, it suggests that the spatial extent of ozone injury may be more extensive than the impacts from N deposition. However, although high elevation systems are generally more distant from pollution sources and thus less exposed to ozone and N pollutants, the N deposition thresholds for effects in subalpine systems are often much lower than in low- or mid-elevation systems because of the inherently low biotic and abiotic capacity to assimilate additional N inputs (Fenn et al., 1998; Sickman et al., 2003). It has been reported that terrain-effect winds in Sequoia National Park (SNP) are capable of transporting O_3 and particulates to 1800 m elevation during upslope flows, but pollutant transport to elevations at or above 3000 m would be considerably less (Cahill et al., 1989), again suggesting lower deposition inputs at high elevation sites.

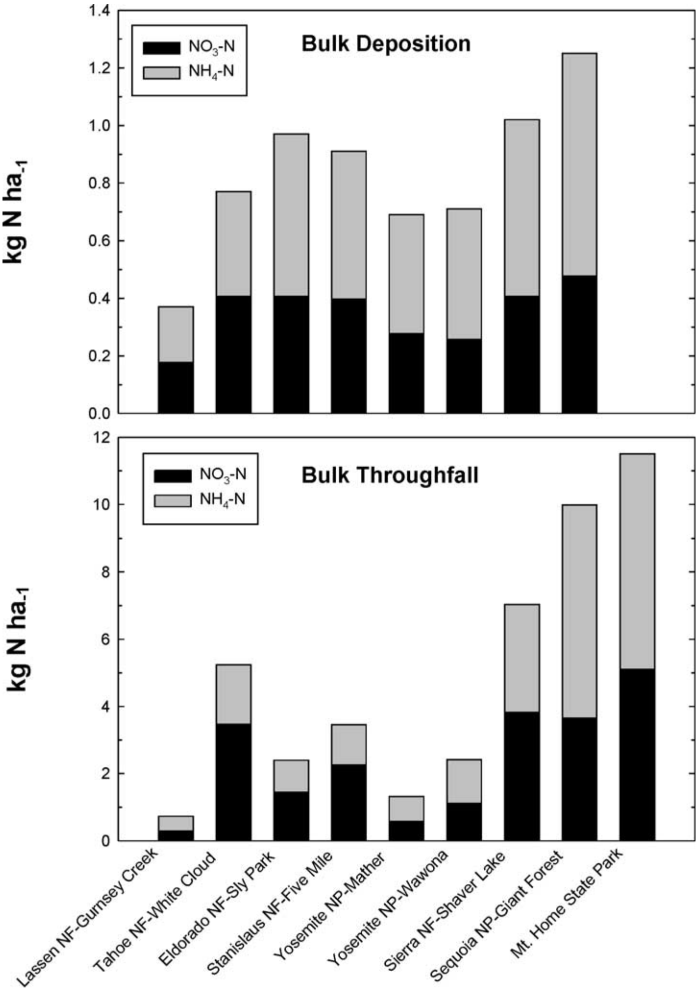

Figure 3. Deposition of NO_3–N and NH_4–N in bulk deposition (open areas) and in bulk throughfall (under pine canopies) at the Project FOREST sites (June–November, 2000). Data are not available for bulk deposition (in open areas) at Mountain Home State Park (MH).

3. Nitrogen deposition in the Sierra Nevada

A primary indication of the spatial extent of air pollution impacts in the Sierra Nevada is the ozone monitoring and injury data from the Project FOREST sites (Lee, Chapter 7; Preisler and Schilling, Chapter 8; Frączek et al., Chapter 9, this volume). Based on the available data, the severity of ozone injury and the impacts of N deposition in the Sierra Nevada are moderate compared to the more exposed forested regions of the Transverse Ranges in the Los Angeles Air Basin (Table 1). Ozone exposures and levels of N deposition in SNP appear to be similar to that reported for Barton Flats in the eastern, low-to-moderate pollution region of the SBM. Mean seasonal (June–September, 1992–1994) 24-hr average ozone concentrations are approximately 80 ppbv (Arbaugh et al., 1998; Carroll et al., Chapter 2, this volume), and N deposition in throughfall was 12–13 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ at both sites in a recent study (M.E. Fenn, unpublished data). At MH, ozone exposure is higher than at BF or SNP (Van Ooy and Carroll, 1995), with a seasonal 24-hr average ozone of 95 ppbv (Carroll et al., Chapter 2, this volume). Ozone injury scores indicate that ponderosa and Jeffrey pine trees at SNP and MH are being affected by ozone. Nitrogen deposition is also slightly greater at MH than in SNP based on the preliminary data shown (Fig. 3). Higher N deposition at MH may be due to its southerly location and higher fog occurrence (Van Ooy and Carroll, 1995; John Pronos, personal commun.). Fog is a major source of N deposition input in the southern Sierra Nevada and in the San Bernardino Mountains (Collett et al., 1990; Fenn et al., 2000). The limited available data suggests that MH is the most polluted forest site in the Sierra studied to date. In addition, several soil and plant indicators of N fertility also indicate that it has been the most affected by N deposition. However, these studies are still in the preliminary stages.

3.1. NH_x vs. NO_x deposition

In much of the Sierra Nevada (Bytnerowicz and Riechers, 1995; Bytnerowicz and Fenn, 1996) and in the western SBM in southern California (Fenn et al., 2000), reduced nitrogenous pollutants (NH_x), mostly from agricultural emissions, make up a large proportion of atmospheric N pollution. The western SBM are exposed to high levels of oxidized N pollutants, mainly from motor vehicle emissions, and simultaneously to high concentrations of reduced N compounds (NH_x) because of the presence of approximately 300,000 dairy cows to the southwest in the Chino/Norco area. Fig. 4 shows the relationship between NO_3^- and NH_4^+ in bulk deposition and in throughfall at the Sierra Nevada Project FOREST sites and at Wolverton in SNP. The ratio of NH_4^+ to NO_3^- in bulk deposition is greater than 1.0 in every case except for the White Cloud, Tahoe NF site. The greater deposition of NO_3^- at White Cloud is believed to be due to NO_x emissions from Sacramento and vehicular traffic along Highway 80 coming from Sacramento. This conclusion is supported by the predominant wind patterns that originate from the San Francisco Bay Area and Sacramento, blowing towards the White Cloud area in spring, summer, and fall (Hayes et al., 1992). In six of ten cases, NH_4^+ deposition in throughfall was also greater than NO_3^- deposition (Fig. 4). The lower incidence of greater

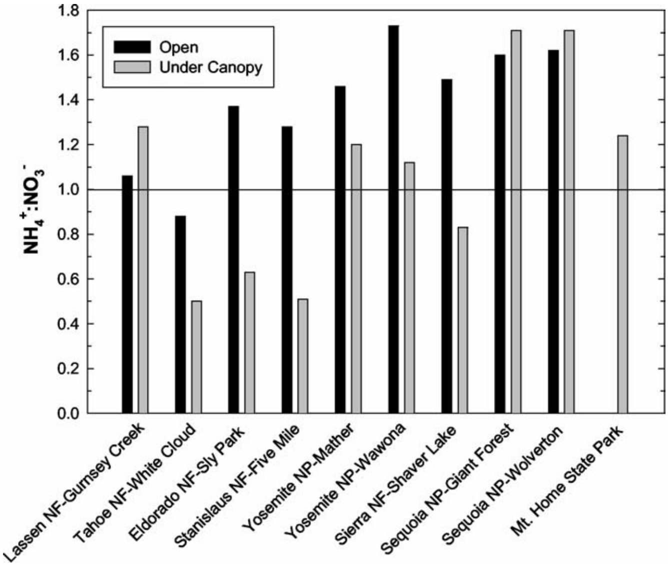

Figure 4. Ratio of $NH_4^+ : NO_3^-$ in bulk deposition (open areas) and in bulk throughfall (under pine canopies) at the Project FOREST sites (June–November, 2000). Data are not available for bulk deposition (in open areas) at Mountain Home State Park. All sites are mixed-conifer (1128–1920 m) except Wolverton (2207 m), which is above the mixed conifer zone.

NH_4^+ to NO_3^- ratios in throughfall is believed to be due to greater canopy retention of reduced N compounds compared to oxidized compounds (Fenn and Leininger, 1995). Concentrations of NH_4^+ in wet deposition and bulk deposition were slightly greater than NO_3^- concentrations (1984–1993) in a previous study in SNP (Williams and Melack, 1997). In a larger study at eleven high elevation sites (Melack et al., 1997), the $NH_4^+ : NO_3^-$ ratio in winter snow, 1.14, was slightly greater than the ratio in non-winter precipitation, 1.03, and may reflect lower NO_x levels during the winter.

3.2. *Nitrogen deposition in throughfall*

Nitrogen deposition in California forests has been reviewed previously (Bytnerowicz and Fenn, 1996), although little data are available on annual N deposition rates in the Sierra Nevada (Melack et al., 1997). Chorover et al. (1994) reported average throughfall deposition in the Giant Forest area of SNP of 6.2 and 10.8 $kg\,ha^{-1}\,yr^{-1}$ (1987–1990) in stands dominated by white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) and giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz), respectively. Recently we began monitoring bulk deposition in open areas and bulk throughfall deposition under ponderosa or Jeffrey pine canopies using ion exchange resin column collectors (Fenn et al., 2002) at Project FOREST sites in the Sierra Nevada. Data from the first exposure period (June–November 2000) are shown in Fig. 3. The monitoring sites are listed along the x-axis from north to south. Except for the Tahoe NF site (White Cloud), the highest N deposition in throughfall was measured in the three most southern sites and the lowest N deposition was in the most northern site, Lassen NF. As mentioned in the previous section, N deposition is presumably high at White Cloud because of its downwind location from Sacramento and proximity to the Highway 80 corridor. Throughfall deposition in this study refers specifically to deposition under the canopies of mature pine trees and thus is higher than deposition levels to the entire stand, which also includes open, canopy-free areas. However, comparing deposition under canopies of similar-sized trees at these nine sites allows for a more accurate comparison of relative deposition inputs with fewer collectors at each site (4 collectors in open areas and 16 under canopy).

Throughfall deposition of N under pine canopies for this 5-month exposure ranged from 7.0 to 11.5 $\mathrm{kg\,ha^{-1}}$ at the three most southern sites (Shaver Lake, Giant Forest in SNP, and MH). Deposition at the Tahoe NF site was 5.2 $\mathrm{kg\,ha^{-1}}$, and the remaining five sites ranged from 0.73 to 3.45 $\mathrm{kg\,ha^{-1}}$ (Fig. 3). Bulk deposition in rainfall is not as effective as throughfall in differentiating among sites, but bulk deposition at Giant Forest and Shaver Lake was higher than in the other sites (Fig. 3). Because of wildlife disturbance to the open collectors, data for bulk deposition were not available for MH.

Nitrogen deposition in throughfall was also measured at Ash Mountain (504 m) near the headquarters for SNP. The throughfall collectors were placed along three parallel transects following the upper elevations of the drainage of the Middle Fork Kaweah River. Vegetation at the site of throughfall collection is mainly scrub oak with a relatively open canopy. Throughfall was collected over a 15-month period from June 2000 to September 2001 with ion exchange resin column collectors (Fenn et al., 2002). Resin column extracts were analyzed for nitrate and ammonium. Nitrate deposition was 3.4 $\mathrm{kg\,N\,ha^{-1}}$, and ammonium deposition was 9.0 $\mathrm{kg\,N\,ha^{-1}}$ over the 15-month period for a total inorganic N deposition of 12.4 $\mathrm{kg\,ha^{-1}}$. These values represent landscape-level throughfall inputs of N. Because of the sampling design, some collectors were located under oak canopies and others in open areas. Thus, these deposition values are not directly comparable to the data shown in Fig. 3, which represent either throughfall deposition only under mature pine trees or as bulk deposition in open areas. Considering that throughfall underestimates total N deposition due to canopy retention of atmospheric N (Fenn and Bytnerowicz, 1997), we estimate total N deposition at Ash Mountain to be approximately 13 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$.

3.3. Atmospheric concentrations of nitrogenous pollutants

Information on concentrations of N air pollutants in the Sierra Nevada is scarce. Information on concentrations of nitric oxide (NO) is not available except for the Giant Forest location in SNP. In summer 1999, NO hourly maximum concentrations in that location reached 25 ppb, while 24-h averages remained below 5 ppb (Bytnerowicz et al., 2002). Monitoring of nitrogen dioxide (NO_2) has been performed only in a few mountain locations, mainly in the Lake Tahoe Basin. In that area, from 1980 to 1998, maximum NO_2 concentrations ranged between 51 and 150 ppb, while the annual average values were between 10 and 14 ppb. In other unspecified Sierra Nevada locations monitoring was performed only in 1981–1983 when maximum concentrations were between 40 and 60 ppb (California Ambient Air Quality Data, 1999). Concentrations of NO_2 at Shirley Meadow in the Greenhorn Range, southwestern Sierra Nevada, were measured during the summers of 1989 and 1990. Monthly 24-hr average concentrations ranged between 1.0 and 5 ppb, with maximum hourly values between 4 and 13 ppb (Takemoto et al., 1997). At the Giant Forest location in SNP, maximum hourly NO_2 concentrations in summer 1999 were less than 34 ppb and 24-h averages less than 8 ppb (Bytnerowicz et al., 2002). During the same period, average 2-week NO_2 concentrations measured with passive samplers in several locations in SNP were between 0.7 and 2.7 ppb (Bytnerowicz et al., 2002).

More is known about summer-time concentrations of nitric acid (HNO_3) vapor, ammonia (NH_3), and particulate nitrate (NO_3^-) and ammonium (NH_4^+) thanks to several monitoring campaigns performed with denuder/filter pack sampling trains (Fig. 5). The ranges of HNO_3 concentrations in the western Sierra Nevada locations were similar to the values determined at Barton Flats of the SBM, but seasonal averages were lower. At high-elevation sites of SNP and at Mammoth Mountain in the eastern Sierra Nevada, both ranges and average concentrations of HNO_3 were low (Fig. 5A). Concentrations of NH_3 on the western slopes of the Sierra Nevada were higher than at the SBM location, especially at Ash Mountain, a low-elevation site (504 m) close to the major agricultural areas near Visalia in the Central Valley (Fig. 5B). Ranges of particulate NO_3^- on the western slopes of the Sierra Nevada were similar to the concentrations measured in the SBM location, although average seasonal values were two- to fivefold lower (Fig. 5C). Concentrations, ranges, and seasonal averages of particulate NH_4^+, however, were generally higher on the western slopes of the Sierra Nevada than in the SBM location (Fig. 5D).

Direct toxic effects on vegetation are not expected at the concentrations of NO, NO_2, NH_3, and particulate NO_3^- and NH_4^+ recorded in the Sierra Nevada (Bytnerowicz et al., 1998). Nitric oxide (NO) typically does not induce visible injury, and toxic effects have been demonstrated only as reduction of growth

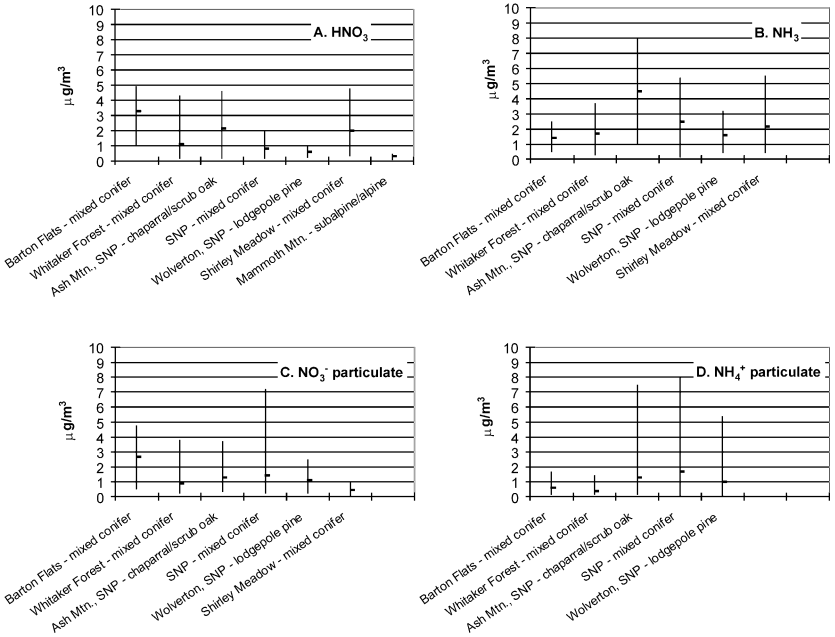

Figure 5. Concentrations of nitrogenous air pollutants in selected Sierra Nevada locations as compared with Barton Flats (BF), a low-to-moderate N deposition site in the San Bernardino Mountains of southern California. Ranges of concentrations are shown by vertical bars, and averages are indicated by the short horizontal line on each bar: (A) HNO_3 vapor, (B) NH_3, (C) NO_3^- in fine particulates, (D) NH_4^+ in fine particulates. “SNP-mixed conifer” represents 3 sites (Crystal Cave, Giant Forest, and Marble Fork). All the data are from annular/denuder systems except for the Mammoth Mountain data, which are passive sampler data collected in a 2-week exposure in August/September 1999 and in August/September 2000. Data from the other sites are summertime 24-hr means. Barton Flats data are from summer 1993; Whitaker Forest data from the summers of 1988–1990; the SNP sites were monitored in summer 1999; and the Shirley Meadow data were collected in the summers of 1989 and 1990.

(Saxe, 1994). Even at elevated concentrations (e.g., 1 ppm NO for 139 days), scorching of leaves was rarely observed in sensitive plants (Saxe and Christensen, 1985). Nitrogen dioxide at concentrations of about 160 ppb, or even at lower concentrations when in combination with SO_2 or O_3, may detrimentally affect foliage (Nihlgard, 1990). At very high concentrations (annual average of about 110 ppb), NH_3 can cause direct damage to vegetation (Temple et al., 1979; Van der Eerden, 1982, Van der Eerden et al., 1992). At normally occurring ambient concentrations of NH_3, direct injury has not been seen. Toxic effects of particulate NO_3^- and NH_4^+ on plants have not been reported to our knowledge, although deposition of these forms of N can contribute to N saturation.

At locations with the highest atmospheric concentrations of HNO_3, phytotoxic effects of this pollutant cannot be excluded. Peak afternoon concentrations of HNO_3 may be much higher than the reported 24-h values, and therefore foliar surfaces of the most sensitive plants could be damaged. California black oak (*Quercus kelloggii* Newb.) and ponderosa pine exposed to elevated levels of HNO_3 (50–100 ppb HNO_3) in short-term (days) controlled exposures developed visible foliar injury symptoms (Krywult et al., 1996; Bytnerowicz et al., 1999b, 2001).

4. Known ecological effects of air pollution in the Sierra Nevada

4.1. Ozone effects

Ozone injury to ponderosa and Jeffrey pine is generally slight in the northern Sierra Nevada, while greater amounts of injury symptoms have frequently been reported from the southern Sierra Nevada forests. Injury is more severe at elevations of 1800 m or less (Carroll et al. Chapter 2, this volume). Temporal trends in ozone injury suggest that symptoms have worsened in the past 25 years. In the southern forests with the highest ozone exposure, ozone injury was not always directly proportional to mean seasonal ambient ozone, presumably due to variability in other environmental factors that affect plant response to ozone exposure (Arbaugh et al., 1998). Peterson et al. (1987) reported an ozone-caused decrease in ring-width of Jeffrey pine at exposed sites in the Sierra Nevada during the 1960–1988 period, but not in ponderosa pine trees showing ozone injury (Peterson and Arbaugh, 1988). Williams and Williams (1986) reported lower radial growth in mature ponderosa pine with ozone injury than in trees without injury. Nitrogen deposition may compensate for ozone-induced growth reductions (Grulke and Balduman, 1999; Fenn and Poth, 2001) by increasing plant-available N (Fenn et al., 1996), although this has not been studied in the Sierra Nevada.

Patterson and Rundel (1995) studied the development of ozone injury symptoms and variation in ozone sensitivity in Jeffrey pine stands in SNP. Ninety percent of the trees exhibited some degree of visible ozone injury, 10% were classified as resistant, and 10% were considered highly sensitive. Needles of the most sensitive trees developed chlorotic mottle in their second growing season (1-yr old needles). The mottle became noticeable in July and progressively worsened with summertime ozone exposure. In the following year (third growing season), chlorotic mottle covered on average 20% of their surface area at the beginning of summer, progressing to nearly 40% of the needle surface area covered with mottle in late summer when the needles abscised. In contrast, needle retention in healthy trees is typically 5–6 years. Visible foliar injury was negatively correlated with photosynthetic rate. Premature foliar loss and foliar chlorosis are expected to result in reduced whole plant carbon gain during physiologically active periods and may be the most important factor in ozone-induced reductions in growth (Temple and Miller, 1994; Patterson and Rundel, 1995). Symptomatic and asymptomatic Jeffrey pine trees were commonly observed in close proximity, suggesting a strong genetic determinant of ozone sensitivity in Jeffrey pine populations (Patterson and Rundel, 1995).

Ponderosa pine seedlings were exposed to ambient ozone and 1.5 × ambient ozone for three consecutive growing seasons at Whitaker Forest at an elevation of 1600 m on the western slopes of the Sierra Nevada (36°37′N, 118°51′W). Ambient ozone did not cause statistically significant seedling growth reductions, but 16% of the seedlings abscised most or all foliage formed at least 2 years before (Temple et al., 1993). Seedlings exposed to 1.5 × ambient ozone (a mean seasonal ozone concentration of 88 ppb) for three seasons developed severe foliar injury and reduced radial growth (Temple and Miller, 1994). This study suggested that leaves with 30% or more chlorotic mottle would likely experience significant loss of photosynthetic capacity, and undergo premature senescence and abscission. Trees that lost 2 or more years of foliage showed reduced growth compared to uninjured trees. Furthermore, it was found that in well-watered trees exposed to 1.5 × ambient ozone, nitrogen concentrations in current-year foliage averaged 34% higher than in the charcoal-filtered control chambers (Temple and Riechers, 1995). The increased N content is believed to have facilitated higher photosynthetic rates in current-year foliage of the trees exposed to the high ozone treatments, which helped compensate for the ozone-induced loss of older leaves (Beyers et al., 1992; Temple and Riechers, 1995).

In physiological gas exchange studies in SNP it was reported that foliage of 125-year-old giant sequoia trees was not sensitive to ozone exposure. Branches exposed to up to 3 × ambient ozone for 61 days did not develop visible injury, branch growth was unaffected, and physiological responses were variable (Grulke et al., 1996). It was concluded that individual giant sequoia trees differ in ozone uptake and have different thresholds of response to ozone. Higher stomatal conductance of seedlings compared to saplings and trees resulted in greater ozone concentrations in substomatal cavities and greater intracellular ozone concentrations (Grulke and Miller, 1994). The authors concluded that giant sequoia seedlings are sensitive to atmospheric ozone until they are about 5 years of age. After that, low conductance, high water use efficiency, and compact mesophyll all contribute to a natural ozone tolerance, or defense, or both, in foliage of older trees. Grulke et al. (1996) concluded that highly sensitive sequoia trees will be selected against at a young age; and if ozone concentrations increase, older trees with ozone-sensitive attributes will have reduced net carbon uptake and will be more susceptible to other environmental stresses.

4.2. Estimated thresholds for nitrogen saturation in California forests

Empirical data from sites traversing air pollution gradients in the San Bernardino and San Gabriel Mountains (Transverse Ranges) in southern California and simulation modeling results both suggest that N deposition inputs at which elevated nitrate export from forested or chaparral watersheds occurs (Table 1) are similar to those determined from a wide range of forested watersheds in Europe (Dise and Wright, 1995). Pine forests and chaparral ecosystems in the Los Angeles Basin receiving atmospheric N inputs of approximately 25 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ or more are clearly N saturated, while sites receiving intermediate deposition levels (10–15 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$) only show evidence of the early stages of N saturation (Kiefer and Fenn, 1997).

The Nutrient Cycling Model (NuCM), developed primarily to explore the effects of atmospheric deposition on forest ecosystems, was calibrated for a mixed-conifer forest in the SBM in southern California. Simulation modeling results corresponded well with field studies across air pollution gradients on the levels of N deposition at which significant changes occur in nitrate leaching, percent base saturation, and soil pH. Based on both approaches, annual N deposition inputs between 20–35 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ clearly lead to high levels of nitrate leaching beyond the primary rooting zone, decreasing base cation pools in soil, and increasing soil acidity (Fenn et al., 1996; Arbaugh et al., 1999). However, even in sites receiving 30–40 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ for the past 50 years (Fenn et al., 2000), base saturation of soil is still an order of magnitude higher than high-deposition sites in the eastern US, presumably because of the more advanced chemical weathering and leaching losses of cations in the soils in eastern mesic forests.

Nitrogen deposition thresholds for ecological and environmental effects are likely to be lower in ecosystems with low biological activity compared to more productive ecosystems (Fenn et al., 1998). High-elevation sites along the southern edge of the Class I SGW in the SBM receive estimated N deposition inputs of 10–15 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$. The 3-year average nitrate levels in four of the streams in this area ranged from 10–37 $\mathrm{\mu eq\,L^{-1}}$, and peak concentrations were extremely high, with values as high as 370 $\mathrm{\mu eq\,L^{-1}}$ (Fenn and Poth, 1999a). By comparison, nitrate concentrations in streams along the northern edge of the SGW where deposition is much lower were typical of more pristine N-limited watersheds. Peak nitrate concentrations were generally $\leqslant 10\ \mathrm{\mu eq\,L^{-1}}$, and average values were 0.04 to 0.72 $\mathrm{\mu eq\,L^{-1}}$ (Fenn and Poth, 1999a). These data illustrate that high-elevation systems or ecosystems in California can be impacted by moderate N deposition inputs (Fenn et al., 1998).

These empirical N deposition thresholds are crude guidelines, but seem to be reasonable estimates of N deposition inputs at which these Mediterranean systems are impacted by N deposition (Table 1). The thresholds suggest that

N deposition levels in forests in and near SNP may be approaching the point where incipient signs of N saturation or enrichment are to be expected. Forests in the MH region appear to receive slightly higher N inputs and to be more affected by N deposition than SNP.

4.3. Nitrate leaching

Annual N deposition at Ash Mountain was estimated to be 13 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ in a recent study (M.E. Fenn, unpublished data). Nitrogen deposition at the CC site, although 250 m higher in elevation, may be greater than at Ash Mountain because the leaf area index, and thus the surface area for deposition of nitrogenous pollutants, is expected to be greater in the dense chamise stands compared to the relatively open, oak woodland vegetation at the throughfall collection site at Ash Mountain.

Since CC is an ephemeral stream, sampling is restricted to periods after significant rain events. Over the period of 1986–1998 nitrate concentrations ranged from near the detection limit to 600 $\mu\mathrm{eq\,L^{-1}}$, with most values falling between 10–100 $\mu\mathrm{eq\,L^{-1}}$ (Fig. 6A). Concentrations tended to be greatest during first-flush storms in the autumn following prolonged periods without precipitation; the 1991 nitrate peak was preceded by more than 500 rain-less days. Even during years with abundant rainfall (1993, 1995, and 1998), nitrate concentrations rarely fell below 10 $\mu\mathrm{eq\,L^{-1}}$. Few measurements of organic nitrogen (DON) have been made, but the available data from 1994–1995 indicate that DON concentrations generally exceed nitrate levels.

High nitrate concentrations in CC may be the result of flushing of accumulated dry deposition or nitrification in soils that is stimulated by rewetting events after prolonged rainless periods (Fierer and Schimel, 2002). Nitrifying bacteria are more tolerant of these water-potential shocks and can use the NH_4^+ that is produced when other microbes are killed; rewetting events have been found to kill as much as half of the soil microbial community (Kieft et al., 1987; Schimel et al., 1999). In similar Mediterranean environments nitrate leaching was found to be proportional to the length of antecedent dry periods and was partly a function of surface flowpaths resulting from soil hydrophobicity (Avila et al., 1992; Biron et al., 1999). Consequently, the nitrate pulse in CC may be controlled by the period of asynchrony between nitrogen availability in soil solutions and demand by the chaparral plant community. Further study is needed to determine whether most of the nitrate exported from the catchment is derived directly from stored atmospheric N or is the result of natural biological processes in soils. Riggan et al. (1985) and Davis (1982) concluded that high nitrate concentrations are not characteristic of undisturbed chaparral watersheds, based on data from chaparral watersheds with low N deposition upwind of Los Angeles, California, and in the Mazatzal Mountains in

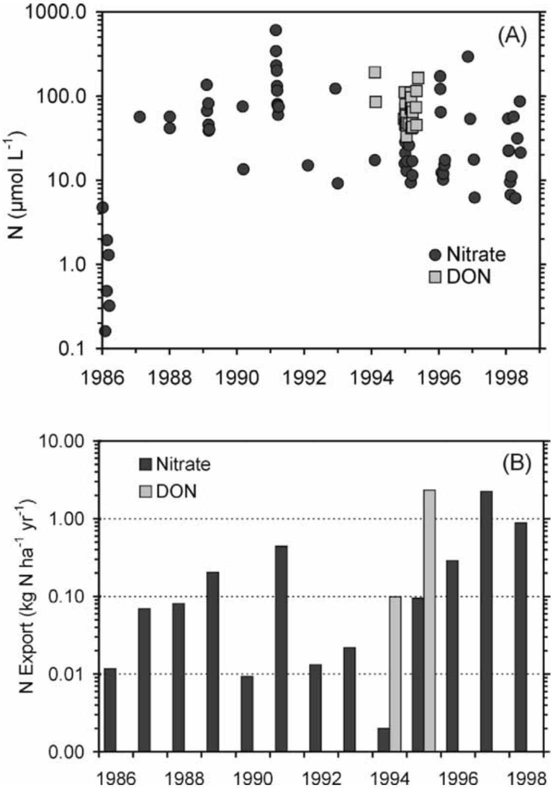

Figure 6. (A) Nitrate and dissolved organic nitrogen (DON) in Chamise Creek (CC), and (B) annual outflow loss of nitrate and DON from the Chamise Creek watershed from 1986 through 1998. Nitrate concentrations and export are displayed on a logarithmic axis.

central Arizona. If this generalization is true for the western Sierra Nevada as well, it supports the hypothesis that N deposition is a driving factor leading to high nitrate concentrations in CC, either as a result of leaching of N deposition accumulated in the soil and on plant surfaces or indirectly through stimulation of nitrification (Johnson, 1992), or both mechanisms may be important.

In relation to atmospheric deposition ($\sim 15\ \mathrm{kg\,ha^{-1}\,yr^{-1}}$), export of nitrate from the CC watershed is small and is limited by the amount of runoff. In dry years only a small fraction ($< 1\%$) of the deposited nitrate is lost and even in infrequent wet years, N export (inorganic + organic nitrogen) comprises less than 15% of atmospheric nitrate deposition (Fig. 6B). Thus, despite the fact that high nitrate concentrations are observed in CC, the chaparral ecosystem within the watershed is still consuming most of the atmospheric N-deposition.

In a survey of six streams sampled in the MH area in June 1999, nitrate concentrations ranged from 3.7–18.7 µeq L^{-1} with a mean concentration of 11.0 µeq L^{-1}. These values are much greater than those measured during the growing season in streams in the BF area over a 3-year period, where summertime values were usually near detection limits (< 0.2 µeq L^{-1}), and are also much greater than in Giant Forest in SNP. In Giant Forest volume-weighted average nitrate concentrations in two streams (Log Creek and Tharp's Creek) from 1984–1987 were generally less than 0.1 µeq L^{-1} (Stohlgren et al., 1991) with peak concentrations $\leqslant 1.0$ µeq L^{-1} (Williams and Melack, 1997). In another study at these same two sites, volume-weighted streamwater NO_3^- concentrations for 1987–1990 were 0.05 and 0.36 µeq L^{-1} (Chorover et al., 1994). These low streamwater nitrate concentrations in SNP suggest that these forests still may be at Stage 0 of the Aber N saturation model (Aber et al., 1989). In contrast, the nitrate values reported from the MH area suggest that N deposition is contributing to N losses from these watersheds (i.e., Stage 1 of the N saturation model), and that N deposition at MH is having a greater impact on N cycling than at BF. However, the volume-weighted mean nitrate concentration at CC (1986–1998) was 24 µeq L^{-1}, with annual means as high as 180 µeq L^{-1}, suggesting that chaparral ecosystems are, currently, the most impacted by atmospheric N deposition in the Sierra Nevada.

4.4. *C : N ratio and nitrogen mineralization/nitrification*

The C : N ratio of soil (0–15 cm depth) and litter (F layer) were compared under ponderosa pine trees in 11 mixed conifer sites in the Sierra Nevada and in the SBM. C : N ratios in soil were fairly high at all the Sierran sites (21.0–25.5) except at MH where soil C : N was 17.2 (Fig. 7). By comparison, at the highly N saturated site, CP in the SBM, soil C : N was 17.5. Litter C : N was lowest at CP (24.2), compared to values of 28.9–39.7 in the Sierran sites. Litter C : N was 31.8 or greater at all the Sierran sites except for Kings River. Litter C : N at MH was 31.9. It is not clear why litter C : N at MH had the median value for all the sites, yet in soil, MH had the lowest C : N value of all 11 sites. Soil and litter C : N ratios at CAO were among the highest of the sites, suggesting the low N fertility of this site. CAO is on the eastern, low-pollution end of the N deposition gradient in the SBM (Fenn and Bytnerowicz, 1993; Fenn et al., 2000).

Potential net N mineralization and net nitrification rates were determined from laboratory incubations of moistened soil and litter sampled under ponderosa pine trees at two sites near Mountain Home State Park (MH and MH-3), and at CP (N saturated site) and CAO (low N deposition) in the SBM. Subsamples were taken weekly, extracted with 2N KCl, and analyzed for NH_4^+ and NO_3^-. In soil from all the sites, NH_4^+ concentrations were relatively low

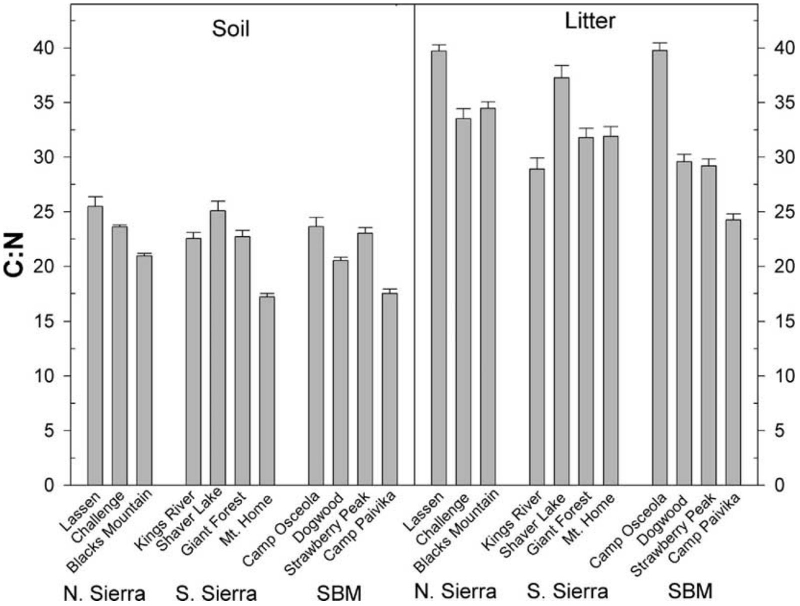

Figure 7. Carbon to nitrogen ratio of soil (0–15 cm depth) and litter (F layer) under ponderosa pine trees in 11 mixed conifer sites in the northern and southern Sierra Nevada and in the San Bernardino Mountains (SBM). Camp Osceola (CAO) is a low pollution site, while the other three SBM sites are high pollution sites, although N deposition is highest at Camp Paivika (CP).

throughout the incubation period. Nitrate concentrations in soil were highest at CP, until the last two sampling dates when NO_3^- was higher from MH-3 (Fig. 8). Nitrate levels were intermediate at the MH plot and were lowest in soil from CAO. In the litter incubations, extractable NH_4^+ was generally highest at CP, but levels were also relatively high at CAO during the latter half of the incubation. Ammonium levels in litter extracts at the MH sites were fairly low with little change throughout the incubation. Nitrate production in litter was highest at CP early on, but after 2–3 weeks of incubation NO_3^- levels were similar at CP and the two Mountain Home sites (MH and MH-3). Nitrate production was slowest to respond and levels were lowest at CAO (Fig. 8). In summary, these potential N mineralization experiments with soil and litter strongly suggest that nitrification potential is greatest at CP, a severely N-saturated site in the SBM, but that nitrification potential at the MH sites is only slightly less than at CP. Potential nitrification in soil and litter at the CAO site in the SBM is the lowest of the four sites. These nitrification assays and soil C : N data support the hypothesis that N deposition is having an impact in increasing N fertility and N cycling rates in the MH area in the Sierra Nevada.

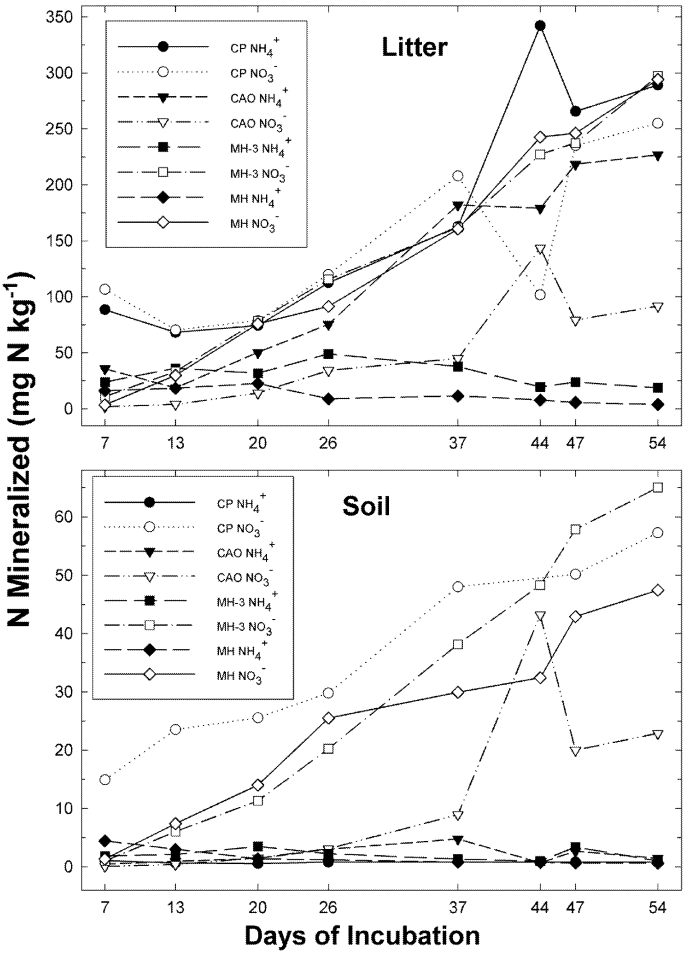

Figure 8. Nitrogen mineralization and nitrification rates in soil and litter in laboratory incubations. Samples were collected from Camp Paivika (CP) and Camp Osceola (CAO) in the San Bernardino Mountains (SBM) and two sites near Mountain Home State Park in the southern Sierra Nevada (MH and MH-3).

4.5. *Bracken fern nitrogen status*

Bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) foliage was collected from sites in SNP, MH, and in the SBM in early June 1999 and analyzed for total N and extractable nitrate as indicators of site N fertility (Table 2). Based on the concentration of N in foliage, the C : N ratio of foliage, and the

Table 2. Percent N, C : N ratio, and extractable nitrate concentrations in bracken fern foliage collected from mixed-conifer sites in the Sierra Nevada and San Bernardino Mountains. Values followed by different letters are significantly different.

Site	% Nitrogen	C : N	Extractable NO_3^- ($mg\,kg^{-1}$)
San Bernardino Mountains sites			
Camp Paivika	3.96 a	11.3 a	1422 a
Strawberry Peak	2.89 b	15.3 b	62 b
Barton Flats	2.18 c	20.3 d	–
Sierra Nevada sites			
Mountain Home	2.94 b	16.0 bc	103 b
S-52 Mountain Home	3.65 a	12.3 a	10 e
Marble Fork-SNP	2.47 b	18.0 c	18 d
Stony Creek-SNP	2.10 c	22.1 d	28 c

concentration of extractable nitrate from dried bracken foliage, it is clear that CP is the most N enriched site. Ferns at Strawberry Peak, a site located ca. 10 km to the east of CP in the SBM, were less N enriched. Values for fern from the BF site, a relatively low N deposition site compared to CP, suggest that this site is more N deficient than MH, but similar to the SNP sites. The results from samples collected in the two MH sites, suggest that this area is N enriched, as indicated by the low foliar C : N ratios from the S-52 site and the moderately-high NO_3^- levels in fern foliage at the MH site (Table 2). These findings support the streamwater NO_3^-, soil C : N, and N mineralization results discussed above, in suggesting that the MH area is more N enriched than SNP and BF in the eastern SBM.

4.6. Nitrogen deposition effects in high elevation sites

Although the focus of this chapter and this volume is on terrestrial effects, the impacts of N deposition on ionic solute fluxes in high elevation catchments will be briefly summarized here. The ELW in SNP is the most intensively studied site. Total atmospheric N deposition loading at ELW ranged from 2.0–4.9 $kg\,ha^{-1}\,yr^{-1}$ from 1985–1998 (Sickman et al., 2001). Annual total N export was 0.4–3.2 $kg\,ha^{-1}\,yr^{-1}$ (including inorganic and organic N) during this same period. At ELW about half of the exported N was as dissolved inorganic N, mainly as nitrate. Similarly, in six other high-elevation lakes in the Sierra, organic N export was similar to or greater than inorganic N export and was generally a function of the amount of soil cover in the watershed; low-soil sites exported proportionally more nitrate, while at catchments with greater soils, organic nitrogen was the dominant N loss mechanism (Sickman et al., 2001). A relatively high proportion of organic N to inorganic N in runoff is commonly reported in N-limited watersheds with low N deposition (Hedin et al., 1995; Campbell et al., 2000a; Sickman et al., 2001).

Climatic forcing (e.g., consecutive drought years) also affected NO_3^- export from these Sierran catchments, suggesting a negative feedback between ongoing trends toward earlier snowmelt (Dettinger and Cayan, 1995; Johnson, 1998) and nitrate levels in streams (Sickman and Melack, 1998; Sickman et al., 2001). The extended drought from 1987–1992, with early and compressed snowmelt seasons, may have driven the declining NO_3^- concentrations in snowmelt runoff from ELW after 1988. In several studies a decline in streamwater NO_3^- was reported during this time period in mixed-conifer watersheds in SNP (Williams and Melack, 1997; Sickman and Melack, 1998; Meixner and Bales, 2002). However, at Emerald Lake, declining levels of nitrate during growing seasons in the late 1990s were likely the result of increasing atmospheric deposition of phosphorus (Sickman, 2001) which increased the incidence of N-limitation of lake phytoplankton during the growing season. These P inputs have caused mild eutrophication in the lake and may be the cause of increasing total P and declining nitrate levels in lakes throughout the Sierra Nevada (Sickman, 2001). Explanations for increased P supply to high-elevation lakes include changes in the rates of mineral weathering of P-bearing minerals in response to climate change, increased regeneration of P from lake sediments, and aeolian transport of P from the Central Valley (Sickman, 2001).

Unusually high NO_3^- concentrations (as high as 175 $\mu eq\,L^{-1}$) occurred in Topaz Lake in some years during late summer through the onset of snowmelt, although this pattern is rare for Sierra Nevada lakes (Sickman and Melack, 1998). These high concentrations were not associated with NO_3-rich precipitation events or snowmelt and were likely the result of transfers of N from microbial pools to surface waters due to vegetation senescence brought on by freezing or low water potential in extensive meadow soils that altered the balance between microbial mineralization/nitrification and plant uptake (Sickman et al., 2003). In contrast, peak snowmelt NO_3^- concentrations at ELW were between 6–14 $\mu eq\,L^{-1}$ (1984–1999) and less than 2.0 $\mu eq\,L^{-1}$ in Lost, Topaz, and Crystal Lakes, which have a higher percentage of soil cover within their watersheds (Sickman et al., 2002). The volume-weighted mean NO_3^- concentration in the outflow of ELW was 4.9 $\mu eq\,L^{-1}$ during 1985–1998 (Sickman et al., 2001). Similarly, in two small catchments near ELW, peak streamwater NO_3^- concentrations were generally $\leqslant 4 \mu eq\,L^{-1}$ (Meixner et al., 1998). However, in an earlier study (1985–1987), peak NO_3^- concentrations in inflow streams were approximately 20 $\mu eq\,L^{-1}$ during the first part of snowmelt runoff (Williams et al, 1995). Isotopic studies of nitrate in the ELW suggest that 30–50% of the nitrate exported during snowmelt is derived directly from the snowpack with the balance coming from microbial nitrification (Sickman et al., 2003). Thus, the combination of a snowmelt nitrate pulse, coupled with a short growing season, and limited soils and vegetation results in temporal asynchrony between N availability and N demand, suggesting that high-elevation ecosystems in the Sierra Nevada will respond quickly to increased N deposition.

This hypothesis is supported by the Sierra Episodes Study in which ten extreme elevation lakes in the Sierra were studied to investigate the effects of large volumes of relatively dilute snow on poorly buffered lakes with little or no soil or vegetation cover (Stoddard, 1995). All of the lakes exhibited increases in NO_3^- concentrations during early snowmelt. In High Lake (John Muir Wilderness in the Inyo National Forest), peak NO_3^- concentrations during snowmelt were greater than 40 $\mu eq\,L^{-1}$. Atmospheric inorganic N deposition is not well characterized in these sites, but is reportedly near 1 $kg\,ha^{-1}\,yr^{-1}$ in wet deposition (Sickman et al., 2002). Mass balances at the High Lake watershed show that annual N export exceeded atmospheric N inputs during the 2 years of study, and along with several of the Sierra Episodes watersheds, are at stage 2 or 3 of the N-saturation model (Sickman et al., 2002). However, Sickman et al. (2002) question whether the classic N-saturation scheme should be applied to these watersheds, since they are severely lacking in recognizable soils and vegetation and have such short growing seasons that they may be naturally N saturated.

In summary, high-elevation watersheds in the Sierra Nevada appear to export NO_3^- during early snowmelt, even with relatively low atmospheric N deposition inputs. The impact of N deposition on NO_3^- export in the high Sierra is not entirely clear, but current levels of N deposition do not appear to have as severe an impact on lake and streamwater chemistry in catchments with appreciable soil as those reported for high-elevation systems in the Colorado Front Range (Campbell et al., 2000b; Sickman et al., 2002). Differing responses between these two regions may be caused by higher N deposition in the Rockies or by the effects of climatic and environmental differences on N cycling and retention Sickman et al., 2001, 2002). For example, the greater extent of soil freezing in the Rockies may reduce the N retention capacity of these watersheds (Sickman et al., 2002). Nitrogen saturation may be a natural condition in Sierran catchments with little or no soil and at elevational extremes.

4.7. Nitrogen deposition effects on Lake Tahoe

Lake Tahoe, situated on the California–Nevada border, is one of the largest, deepest, and clearest mountain lakes in the world and is renowned for its scenic beauty. The history of human impacts and the list of major ecological issues of concern to forests in the Lake Tahoe Basin appear to be the same as those impacting the rest of the Sierra Nevada (Elliott-Fisk et al., 1997). These issues in common include stand densification as a result of previous logging history and fire suppression, drought, pest infestations, catastrophic wildfire risk, and air pollution (Murphy, 2000). As a result, high levels of standing dead timber are found in the Basin (Elliott-Fisk et al., 1997). Since the mid-1970s, land managers at Lake Tahoe recognized the value of prescribed burning. However, greater understanding is needed of the ecological effects of fuels treatments, such as thinning, salvage logging, prescribed burning or other silvicultural options.

The primary single measure of human impacts in the Tahoe Basin, and the issue of greatest focus, is the trend in lake clarity. Clarity of the lake has been declining for at least the past 30 years, while algal growth has increased during this same period (Jassby et al., 2001). Lake Tahoe functions as a nutrient sink with a fluctuating but generally increasing store of nutrients. In years with extensive vertical mixing, this enriched supply of nutrients stored mainly in the deeper waters can increase algal production in the more productive surface layer (Jassby et al., 1992).

Jassby et al. (1995) argue that the following factors make Lake Tahoe a prime candidate for atmospheric influences: low catchment to lake area ratio (1.6), the predominance of granitic rock type in the basin, 85% forest cover in the watershed, and strong sources of atmospheric N. The first three factors are known to generally contribute to low nutrient runoff from terrestrial watersheds. Evidence suggests that atmospheric deposition of N has been a factor in the declining clarity of the lake. Studies over the past 30 years suggest that phytoplankton communities in the lake have changed from co-limitation by N and P to P limitation (Goldman et al., 1993), presumably because of atmospheric N deposition (Jassby et al., 1994). Some evidence suggests that the lake still may be close to the boundary separating N limitation from predominantly P limitation (Reuter and Miller, 2000), and it is likely that the trophic status of the lake is affected by alterations in P supply as well (cf. Sickman, 2001). Of the estimated 418 metric tons of N loaded to the lake during a representative year, more than half comes from atmospheric deposition (Reuter and Miller, 2000). Gaseous NO_x in the Basin is mainly of local origin from motor vehicles, while particulate ammonium nitrate deposition in the spring, summer, and fall comes predominantly from upwind urban sources (the San Francisco Bay Area and Sacramento valley) and from the Sierran foothills (Cliff and Cahill, 2000). Preliminary studies suggest that nitric acid vapor (HNO_3) may be a major source of atmospheric N deposition in the Basin (Tarnay et al., 2001). However, it is still unclear what proportion of atmospheric deposition in the Basin is from local sources and how much is transported from upwind sources. Tarnay (2001) estimated that 23% and 28% of the N deposition to the lake and terrestrial watershed, respectively, were of local origin.

Although the current nutrient budget reflects the overall importance of atmospheric deposition of N, the watershed is still an important contributor (Reuter and Miller, 2000). In a study of 10 streams in the Tahoe Basin, organic N yield in runoff averaged 1.05 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ over 10 years (Coats and Goldman, 2001). Biological availability of organic N inputs is not well understood. The importance of this organic N runoff on the decline in lake clarity depends on the potential of this N source to increase the growth of bacteria and algae. A review of the literature suggests that bacteria and phytoplankton utilize dissolved organic N as well as inorganic N (Antia et al., 1991). The watersheds surrounding Lake Tahoe are not considered N saturated as evidenced by low streamwater $\mathrm{NO_3^-}$ concentrations (peak values $< 8\ \mu\mathrm{eq\,L^{-1}}$) and low annual runoff yield of $\mathrm{NO_3^-}$ (0.081 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$). Low nitrate runoff is expected from these watersheds, considering the relatively low N deposition inputs in the Tahoe Basin (approximately 4 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$; Tarnay, 2001). Organic N concentrations in runoff were typically ten times that of inorganic N (Coats and Goldman, 2001)). Dominance of organic N over inorganic N in streamwater is typical of pristine watersheds with low N deposition (Hedin et al., 1995; Campbell et al., 2000a; Perakis and Hedin, 2002). Key questions remain as to whether this organic N flux to the lake is biologically available, contributing to greater algal productivity and decreased lake clarity, and whether atmospheric N deposition contributes to the export of organic N to the lake. Also, a greater understanding of the rates and impact of P-loading are needed to predict how the lake will respond to increasing levels of N-loading. For example, will concurrent increases in both N and P will produce a greater trophic-effect in the lake than inputs of N alone (Sickman and Melack, 1992)?

4.8. Summary and future projections of air pollution effects in the Sierra

Future trends in ozone exposures and N deposition in the Sierra Nevada and their corresponding effects on forests and watersheds will depend largely on the net effects on emissions of rapidly increasing populations, trends in agricultural activity (particularly dairy and livestock operations), and stricter regulatory controls on emissions. The sites most at risk of ozone injury to sensitive species such as ponderosa and Jeffrey pine are in the southern and western regions of the Sierra Nevada. Of the sites studied, the available evidence suggests that MH and CC are the sites most affected by atmospheric N deposition. Chaparral ecosystems in the Sierra Nevada are poorly studied, but may be closest to N saturation due to high rates of N deposition and as evidenced by very high concentrations of nitrate in outflow streams. It seems likely that ozone injury will increase in severity and geographic extent only if ozone exposures become more severe. If this scenario occurs, it may be that greater pine mortality would occur due to greater susceptibility to bark beetle attacks as has been documented in the SBM where high ozone exposures are prevalent (Pronos et al., 1999).

Symptoms of N saturation (Aber et al., 1989) may worsen in the region near CC and MH, especially if N deposition increases, as N continues to accumulate in these ecosystems. Long-term fire suppression probably facilitates this process of N accumulation, since fire is the major mechanism of N loss from these fire prone systems (Johnson and Susfalk, 1997). However, we do not have sufficient understanding of the mechanisms controlling N retention and N saturation in forest ecosystems in general, and in Mediterranean systems in particular, to be able to predict future responses to N deposition in the Sierra Nevada. Empirical evidence from montane ecosystems in southern California does suggest, however, that strong symptoms of N saturation are evident, based on very high nitrate export in streamwater, when N deposition reaches levels of approximately 20–25 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ (Table 1). For this to occur at the mixed conifer site at MH, we estimate that N deposition would have to increase by 30–50%. We caution, however, that these are very rough estimates given only as our best perspective at this time. At CC, a chaparral site, elevated nitrate export is already occurring, suggesting that increases in N deposition will lead to further increases in N storage and nitrate export. Data from high elevation ecosystems suggest there will be a direct ecosystem-response to higher N-deposition since large amounts of atmospheric N escape biological cycling in these systems.

5. Potential ecological effects of air pollution in the Sierra Nevada: Studies in the SBM

In California forests with high ozone exposure, elevated N deposition is almost certain to occur as well. Some of the effects caused by air pollution make it difficult to know which pollutant or pollutants are contributing to the observed response. One exception to this is the classic visible injury symptoms in ponderosa and Jeffrey pine trees caused by ozone (e.g., chlorotic mottle and premature needle abscission). However, controlled seedling studies and field studies suggest that N may partially ameliorate some of the detrimental effects of ozone (Pääkkönen and Holopainen, 1995; Grulke and Balduman, 1999), although the reported effects of N on ozone impacts vary depending on plant species and environmental conditions (Karnosky et al., 1992). Thus, pollution interactions are an important consideration in understanding air pollution effects on forests in the Sierra Nevada. Long-term N fertilization studies are underway in the SBM and in SNP in order to better understand the relative importance of ozone and N pollutants in impacting forest ecosystem processes.

Much of our knowledge of the impacts of ozone and N pollutants on mixed-conifer forests in California is based on studies along the air pollution gradient in the SBM. Some of the effects observed in the SBM have not been well studied in the Sierra Nevada; thus, the extent to which similar effects may be occurring in the most exposed areas is as yet unknown. In this section, we will summarize air pollution impacts in the SBM, and we discuss the possible implications of this for the Sierra Nevada.

5.1. Nitrogen deposition effects

Excess nitrogen in these naturally N-limited ecosystems is a major ecological disturbance leading to more rapid N turnover in soil and in vegetation, disruption of plant physiological processes, alteration of carbon storage in woody biomass and soil, and it may contribute to vegetation type conversion and invasion of exotic plant species in some areas (e.g., coastal sage ecosystems in southern California).

Because of the high nitrification activity of the soils in California (Fenn et al., 1998; Fenn and Poth, 2001) chronic N deposition inputs to these systems results in even greater nitrate production and large leachate losses of nitrate in streamwater and groundwater and elevated fluxes of nitric oxide gas from soil (Fenn et al., 1998; Fenn and Poth, 1999a, 1999b). As a result of the high nitrate concentrations in streams and groundwater from N saturated forests, drinking water quality from these forested watersheds is also affected (Fenn and Poth, 1999a).

Atmospheric N deposition likely causes a fertilizer effect, increasing N concentrations in foliage, litter, and soil and increasing forest growth. This effect leads to stand densification and increased fuel accumulation, which increases the risk of stand destruction by fire in these areas of long-term fire suppression. Greater foliar N content in young foliage, as a result of N deposition or from resorption from senescing foliage, appears to help pine trees compensate for ozone-induced needle loss (Beyers et al., 1992; Temple and Riechers, 1995) and to offset ozone-caused reductions in aboveground tree growth in southern California forests (Grulke and Balduman, 1999; Fenn and Poth, 2001). In fact, radial bole growth in ponderosa pine and California black oak trees in the most polluted site in the SBM responded positively to four years of N fertilization treatments (Fenn and Poth, 2001), reinforcing the conclusion that N offsets aboveground growth decreases caused by ozone injury.

Recent studies indicate that atmospheric concentrations of nitric acid vapor (HNO_3), a component of photochemical smog, may be high enough to cause direct toxicity effects on foliage of wildland shrub and tree species in the Los Angeles Air Basin (Bytnerowicz et al., 1998, 1999b). Further studies are needed to evaluate the occurrence, severity and extent of injury caused by HNO_3 under field conditions.

5.2. Foliar senescence effects of ozone exposure in combination with nitrogen deposition

Major plant growth perturbations occur in ponderosa pine trees exposed to air pollutants in highly-polluted sites in the SBM. The combined effects of ozone and N are believed to result in greater physiological disruption and nutrient cycling impacts, both within individual trees and at the stand level, than either pollutant acting alone (Grulke and Balduman, 1999; Takemoto et al., 2001). Fine root biomass and carbohydrate allocation belowground were significantly reduced in ponderosa pine trees exposed to high ozone and elevated N deposition (Grulke et al., 1998, 2001). Ozone causes premature abscission of pine foliage, while increased N fertility causes more rapid foliar growth and premature abscission. This results in greater foliar biomass production and turnover resulting in increased litter buildup on the forest floor and C storage in aboveground woody biomass. In many trees in the western SBM, only the current-year foliage over-winters, resulting in ponderosa pine trees with biomass allocation similar to that of a deciduous tree with one overwintering age class. As a result of their dramatically altered foliar senescence Grulke and Balduman (1999) referred to these pine trees as “deciduous conifers.” In summary, the physiological functioning of ozone-sensitive ponderosa pine is dramatically altered by the combined effects of ozone and N deposition.

5.3. Altered carbon cycling and sequestration

The phenological effects discussed above drive major changes in C cycling and storage in mixed conifer forests. The net result of N enrichment, in combination with ozone exposure is greater C storage in aboveground woody tissue (Grulke et al., 1998, 2001) and significant litter accumulation on the forest floor (Fenn and Poth, 1999b). The latter effect was also found in simulations with the CENTURY model that indicate that long-term needle fall is accelerated by the combination of ozone and N deposition more than by either pollutant alone (Arbaugh et al., 1999). High N concentrations in the litter in sites with high N deposition likely contributes to reduced long-term decomposition rates as has been frequently reported (Berg, 2000), although the initial stages of litter decomposition in the SBM are enhanced by N deposition (Fenn and Dunn, 1989; Fenn, 1991).

In ponderosa pine, and possibly in oak trees, in the highly-polluted western SBM, the bole functions as an important C storage organ (Grulke and Balduman, 1999; Fenn and Poth, 2001). Carbon allocation to coarse and fine roots is dramatically reduced as a result of air pollution exposure (Grulke et al., 1998; Grulke et al., 2001). This implies that C sequestration from root-derived organic matter is probably lower. However, C normally allocated to roots is shifted to storage in woody aboveground biomass, a relatively long-term storage pool. These findings suggest that overall C sequestration in these forests is increased, at least as long as fire suppression is maintained, by the combined effects of ozone and N deposition because of increased C storage in a large pool of recalcitrant organic matter on the forest floor and in soil, and increased C storage in aboveground woody biomass. The end result of these air pollution effects is an increased accumulation of fuel, which is expected to exacerbate the risk of wildfire and to make it more difficult to safely implement prescribed fire. An additional downside is that after fire in N saturated watersheds in southern California, nitrate concentrations in streamwater reach extremely high levels (more than 1.5 times the drinking water standard of 714 $\mu\mathrm{eq}\,\mathrm{L}^{-1}$) as the accumulated N is mobilized by fire and nitrification of the N liberalized from organic matter (Riggan et al., 1994).

5.4. Ozone effects on understory species

The effects of N deposition on understory species has not been studied, except for comparisons of the N status of bracken fern at sites with varying N deposition. In high pollution sites in the SBM, fern fronds accumulate high levels of NO_3^- during the early part of the growing season, and total N content is also much higher in this nitrophilous species (Fenn et al., 1996). More is known of ozone injury in understory species, partially because of research looking for native ozone injury bioindicator species. Even still, information on ozone injury to understory plants in California is limited for a variety of reasons (Temple, 1999), including the research focus on ozone effects on overstory species. Ozone, in concert with long-term fire suppression, has also altered understory communities by increasing mortality of ponderosa and Jeffrey pine and favoring shade-tolerant understory tree species such as incense cedar (*Calocedrus decurrens* [Torr.] Florin) and white fir (Minnich et al., 1995). Ozone injury was not observed in indicator understory plants at the Forest Health Monitoring biosites in the Sierra Nevada in the first year of the survey (Campbell et al., 2000c), although injury was observed in ponderosa and Jeffrey pine. Injury was usually only seen in pine needles 3 years old or older, apparently due to cumulative exposure effects. Another reason injury was not seen in understory plants in the first year of the survey is probably because most sites were in the northern Sierra or at high elevation where ozone levels are lower. In subsequent years, additional sites were added at lower elevation, and foliar ozone injury was observed on susceptible forest understory species, particularly blue elderberry (*Sambucus mexicana* C. Presl.) and mugwort (*Artemisia douglasiana* Besser) growing on the western slopes of the southern Sierra (P.J. Temple, unpublished data).

Most understory herbaceous plants are active for short periods in spring (e.g., April to June) when ozone levels are lower, while understory shrubs active in the summer are predominantly drought- and ozone-tolerant. Nonetheless, several understory species have shown ozone injury under field conditions. Blue elderberry and mugwort are examples of understory woody and perennial plants showing distinctive ozone injury symptoms in the SBM (Temple, 1999). Annual understory plants, such as *Gayophytum diffusum*, *Lepidium virginicum* var. *pubescens*, and *Cordylanthus rigidus*, also show moderate-to-severe ozone injury symptoms in the western SBM.

Elymus glaucus L. (blue wildrye) is a native California perennial bunchgrass found throughout the state below 2500 m, often growing in association with oaks and conifers. Temple (1999) reported that although blue wildrye is considered to be ozone sensitive, symptoms in the field do not appear to be characteristic of ozone injury. Yoshida et al. (2001) studied the effects of ozone on plant growth, mycorrhizal colonization, and microbial communities in soil of *E. glaucus*. Two populations were studied, one from the Stanislaus National Forest in northern California and one from Sky Forest, a high-ozone site in the San Bernardino National Forest. Total plant biomass was reduced by ozone exposure; however, the aboveground biomass response was more significant with the southern population, while the reduction in mycorrhizal root colonization was greater in the northern population (Yoshida et al., 2001). Furthermore, it was found that in the northern plant populations, active soil bacterial biomass was reduced and fungal populations were increased, suggesting that ozone indirectly affects soil processes.

6. Other stressors impacting forest health in California

6.1. Stressors causing loss of vigor and increased tree mortality

Reduced vigor of forest trees and tree mortality are often caused by multiple stress factors, both naturally-occurring and anthropogenic. In California forests, the dominant natural stressor is the extended periods of drought that occur periodically when annual precipitation amounts are below normal in successive years. One of the most important human-caused stress factors in California forests is stand densification as a result of successful long-term fire suppression efforts. Dense stands are stressed by competition for resources, such as water, nutrients, and solar radiation. Both severe drought stress and stand densification exacerbate forest insect damage. Bark beetle attack is frequently the ultimate cause of death in stressed trees in California forests (Page, 1981; Savage, 1994, 1997; Smith et al., 1994; Ferrell, 1996).

This type of drought occurred in the mid-1970s (Page, 1981) and again from 1987 to 1992 throughout California, resulting in widespread tree death (Savage, 1994, 1997; Smith et al., 1994; Ferrell, 1996). As a result of the latter drought, by 1991 in the Sierra Nevada, mortality in pine-dominated forests was estimated to be as much as fifteen times normal levels (Savage, 1994). Stand structure analysis was used to characterize patterns of mortality in a mixed conifer forest in the San Jacinto Mountains in the Transverse Ranges (San Bernardino NF) in southern California (Savage, 1994). Climate and forest type at this study site are similar to those in the Sierra and results of this study may be indicative of the similar trends reported in the Sierra Nevada. Because of greater distance from the major urban areas surrounding Los Angeles, air pollution levels in the San Jacinto Mountains are lower than those that occur in the SBM. Although the role of the various stresses is not easy to evaluate, it was concluded that drought was the main contributing factor in the increased tree mortality, with chronic fire suppression and possibly air pollution as additional predisposing factors. Insect attack appears to have been the ultimate cause of tree mortality (Savage, 1994). Stand densification and litter accumulation favored regeneration and recruitment of shade-tolerant and fire-sensitive species such as white fir and sugar pine (*Pinus lambertiana* Dougl.). Ponderosa, Jeffrey and Coulter (*P. coulteri* D. Don) pines appeared to be more susceptible to insect attack than the other species. Savage (1994) concluded that a possible fate of this stand is devastation by crown fire because of the high forest density, the large numbers of dead trees, and high litter content. To reduce this risk in the Sierra Nevada, most forests are routinely salvage logged to reduce the fuels (Page, 1981). However, salvage logging is not normally done in the national parks (Ferrell, 1996), except in areas where visitor safety is a concern.

In a subsequent study, Savage (1997) compared stand structure and tree mortality in two sites in the SBM (Holcomb Valley and BF) with long-term fire suppression and a similar forest in San Pedro Martir, Baja California (La Corona Arriba), that is unmanaged and subject to a natural fire regime. Trees were sampled in 1994, following a major drought from 1987 to 1992. In the SBM sites the percentage of standing dead trees was 14%, compared to only 4% in the San Pedro Martir site. The drought appears to have been equally severe in both study regions. This data supports the hypothesis that the more open structure of the Baja California forests, maintained by frequent surface fires, results in less severe stress to the trees during drought years (Savage, 1997). These studies suggest that fire suppression, like air pollution, is an anthropogenic stress factor that increases forest susceptibility to naturally-occurring stress factors, such as bark beetle attack and drought stress. Each additional stressor may further reduce forest sustainability in the long term.

6.2. Stand structural changes with fire suppression

Minnich et al. (1995) compared stand structure in the SBM shortly after the beginning of the fire suppression era with stand structures 60 years later. It was concluded that in the pre-suppression era ground fires in the SBM were widespread with a fire return interval of 15–30 years. The rate of stand thickening over the 60-year period of fire suppression was positively correlated with precipitation. In general, stands are changing from old-growth age structure to young growth, and a compositional shift is occurring from ponderosa and Jeffrey pine to white fir and incense cedar. Parallel trends were found in forests in the Sierra Nevada, but magnified by the increased precipitation of the Sierra Nevada. The forest changes as a result of fire suppression have important conservation consequences for bird species diversity and for impacts on individual bird species (Minnich et al., 1995). Furthermore, California forests of 60 years ago were remarkably similar to modern forests in the Sierra San Pedro Martir in Baja California where fire suppression is not practiced. These studies confirm that fire suppression is the cause of abnormally high stand densification in many California forests.

6.3. Multiple stress impacts in the Sierra Nevada

The stress factors leading to tree mortality in the Sierra Nevada are the same as those in the Transverse Ranges in southern California. Drought stress is the most important of these factors, and recurrent droughts are characteristic of the Sierra Nevada climate. Prominent examples of widespread and sometimes catastrophic tree mortality in the Sierra Nevada is that which occurred after the severe 1975–1977 drought and again after the 1987–1992 extended drought. The ultimate cause of tree mortality in both cases was commonly bark beetle infestations, but successful bark beetle kills are usually preceded by such stress factors as drought, fire scorching, disease or overly dense stands (Page, 1981; Ferrell, 1996). Air pollution does not appear to have been a major factor in the widespread tree mortality observed in the Sierra in the 1990s, since the most severe losses occurred on the east side of the Sierra, where air pollution levels are generally very low. Mortality of pine and fir stands on the east side was sometimes higher than 80% of the standing volume (Smith et al., 1994). Mortality after severe drought affects low- and mid-elevation forests first, usually causing increased mortality at higher elevations only if the drought is protracted (Ferrell, 1996).

Surveys have shown that 75 to 90% of the tree mortality in California forests is a result of multiple organisms or an interaction of site and stand conditions and insects. Three common interactions include dwarf mistletoe–bark beetle complexes, root disease–bark beetle complexes, and overstocking–bark beetle complexes. In all of these situations, the pathogen or stand condition (including drought stress) reduces tree vigor and natural defenses, predisposing trees to successful bark beetle attack (Smith et al., 1994). The drought between 1975 and 1977 was one of the most severe on record. Tree mortality rose dramatically within one year of the onset of drought and then decreased precipitously when precipitation returned to more normal levels (Smith et al., 1994). More than two-thirds of the dead trees during this period were either ponderosa pine or white fir. In the initial years of the drought (1975–1976), 69% of the trees had some combination of insects and pathogens. In the middle year (1977–1978), this proportion dropped to 53%. Immediately after precipitation returned to normal (1979–1980), the proportion of mortality associated with multiple biotic agents dropped to 22%. As the importance of multiple agents declined, bark beetles became the dominant organism involved in the mortality.

This shift in the makeup of the organisms contributing to tree mortality has been explained by Smith et al. (1994). The trees that died early in the drought were already weakened by pathogens. A short-term drought thus functions to cleanse the forest of trees with existing debilitations. After many of these less vigorous trees were killed, drought and increased insect populations continued to cause the mortality of trees that had been relatively healthy. Site and stand characteristics are also important in determining forest health and stand responses to drought and other stressors.

As discussed above, abnormal stand densification is a major stress factor in the Sierra Nevada. This is primarily due to long-term fire suppression and past logging practices that favored the growth of shade tolerant species such as firs and cedars. This stand structure leads to drought stress of overstory species such as ponderosa pine that are normally drought resistant, thus making them more susceptible to bark beetles during droughts. In forests such as these, with a mix of dead and dying trees and with a dense tree understory, a fuel ladder structure is created, resulting in stands susceptible to stand-destroying wildfires. Overly dense stands are also more susceptible to insects and pathogens (Ferrell, 1996). Another negative consequence of fire suppression is that regeneration of giant sequoia and ponderosa pine is inhibited in stands that have not burned for many years, because a mineral seedbed is required for regeneration of these and some other conifer species (Hartesveldt and Harvey, 1967; Tappeiner and McDonald, 1996).

In summary, drought is a recurring phenomenon in California forests, such as those in the Sierra Nevada. However, abnormally high stand density in the Sierra Nevada results in greatly increased susceptibility to insects and pathogens and favors the occurrence of stand-replacing crown fires. In the southwestern Sierra Nevada, where the most severe air pollution exposures occur, N deposition may have subtle effects on forest health by increasing forest growth, thus exacerbating stand densification, susceptibility to insects and pathogens, drought stress, and the danger of catastrophic fire. However, these effects of N deposition, in addition to ozone effects on tree health, litter production (due to premature foliar senescence), and tree susceptibility to bark beetles, are likely to be more evident if air pollution levels increase as the human population and livestock operations expand in the coming years.

6.4. Air pollution interactions with other stressors

Results from a number of studies in the SBM suggest that ozone stress predisposes ponderosa pine trees to bark beetle attack. Oxidant injury results in reduced oleoresin yield, rate of flow, and exudation pressure, sapwood and phloem moisture content and phloem thickness—all of which are important in defense of the tree against beetle attack (Stark and Cobb, 1969; Pronos et al., 1999). In ozone damaged pine trees fewer attacking parent adults of the western pine beetle (*Dendroctonus brevicomis*) were required to produce a similar number of emerging adults (Dahlsten et al., 1997). These and other results indicate that in stands with a greater number of ozone damaged trees, a given population of western pine beetle could kill more trees and increase at a greater rate compared to a stand with a lower proportion of damaged trees (Pronos et al., 1999). Experimental studies in the field (James et al., 1980) and in ozone fumigation chambers (Fenn et al., 1990) indicate that ozone-stressed ponderosa and Jeffrey pine trees are more susceptible to root diseases. However, field observations and surveys in California forests do not support a relationship between air pollution exposure and disease incidence or severity (Pronos et al., 1999). This is likely due to the spotty nature of disease incidence and disease center development.

Even without insect infestations, nitrogen deposition and ozone, the two major pollutant types in California forests, both exacerbate the problem of excessive fuel accumulation in mixed conifer forests that have not burned for many decades. Nitrogen deposition increases biomass and litter production, thus contributing to the stand densification and fuel accumulation problem. Ozone causes foliar injury in sensitive trees, which results in premature foliar abscission. In combination with N, it causes litter and fuel accumulation. This problem is particularly severe in more mesic microsites (e.g., based on topographic position) where ponderosa or Jeffrey pine is a major component of the overstory. In these sites, foliar uptake of ozone and ozone injury (Grulke et al., 2003), fuel production, and N cycling rates are higher, magnifying the effects of these pollutants. These forest responses to air pollution have been documented for the more polluted western sites in the SBM. The extent that similar impacts may occur at sites such as Mountain Home State Park in the southern Sierra is not known.

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