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Evidence for nitrogen saturation in the San Bernardino Mountains in southern California

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Abstract

Elevated N deposition has occurred in the Los Angeles Basin in southern California for at least the last 40 years. Elevated streamwater NO_3^- fluxes and high nitric oxide (NO) fluxes from soil, indicators of N saturation, have recently been reported for chaparral watersheds exposed to chronic N deposition in the San Gabriel Mountains north/northeast of Los Angeles. A number of nutritional and edaphic parameters across a deposition gradient in the San Bernardino Mountains (SBM) support the hypothesis that the mixed conifer forest in the western end of the range is also N saturated. Concentrations of NO_3^- in the soil solution or in soil extracts during the summer months were 14 to 44 times higher at Camp Paivika (CP), a western high N deposition site, than at Camp Osceola (CAO) or Barton Flats (BF), eastern low-pollution sites. Accumulation of NO_3^- in foliage of bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) and overstory species was also much greater at CP than at CAO and a site near BF. Nitric oxide fluxes in mid-August from relatively dry soil at CP were ca. 20 times higher than for typical forests in North America. Nitrous oxide (N_2O) emissions, on the other hand, were low in the SBM sites. However, emissions of NO and N_2O were several-fold higher at CP than at BF, a relatively low-pollution site. High NO emissions from otherwise undisturbed and well-drained forest soils of the western US may prove useful as a diagnostic indicator of N saturation. Nitrogen mineralization was greater at CP and Dogwood (high-pollution sites) than at CAO and Heartbar (low-pollution sites). Additional indicators of N enrichment at CP compared with the low N deposition sites include: low C:N ratios in soil and foliage, high foliar N:P ratios, higher nitrification rates and high soil acidity. Lower pH and base saturation were observed in soil from two high-pollution sites compared with two low-pollution sites. In summary, high NO emissions and elevated NO_3^- concentrations in the soil solution and in foliage, and high foliar N:P ratios at CP, indicate N in excess of biotic demand, with potential above-normal loss of N from the ecosystem – and thus, a N-saturated condition. Model outputs from the nutrient cycling model (NuCM) agreed well with field data from the SBM on elevated soil solution NO_3^- concentrations, reduced soil base saturation, and lack of a growth response to increasing N deposition.

Keywords: Nitrogen trace gases; Nitrate accumulation; Nutrient ratio

1. Introduction

Northern temperate forests have long been considered to be N-limited (Aber et al., 1989; Vitousek and

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Howarth, 1991). However, a growing number of forest ecosystems exhibit symptoms of the contrasting condition of N saturation (Foster, 1985; Van Breemen et al., 1987; Johnson et al., 1991, 1993; Driscoll and Van Dreason, 1993; Stoddard, 1994; Boxman et al., 1994a; Dise and Wright, 1995; Bredemeier et al., 1995). Nitrogen saturation has been variously defined as a condition in which (1) available N is frequently in excess of total biotic demand, (2) vegetation within an ecosystem no longer exhibits a positive growth response to N addition (Nilsson, 1986), even though other growth factors are not growth limiting, and (3) sustained N losses approximate or exceed N inputs – the N retention capacity of the system has been exceeded. These definitions are functionally related, and for purposes of this study, we will consider Definition 1 as the core concept of N saturation; which, however, will frequently result in the conditions given in Definition 2 and possibly Definition 3. Aber (1992) lists three environmental components impacted by N saturation: soil chemistry and water quality, forest composition and productivity, and fluxes of trace gases that are chemically or radiatively active. Excess soil NO_3^- may also impact forest ecosystems by altering the susceptibility of trees to disease and insect pests (Skeffington and Wilson, 1988), and by affecting mycorrhizal symbioses (Termorshuizen, 1993). Soil/plant nutrient relations (Katzensteiner et al., 1992; Boxman et al., 1994a, b) can also be affected by high nitrification rates and excess soil NO_3^-, causing increased soil acidification (Falkengren-Grerup, 1989) and cation leaching with possible nutrient deficiencies in sites with marginal nutrient reserves (Schulze, 1989; Johnson and Ball, 1990).

Sources of N leading to a N saturated condition usually include atmospheric N and available N from N mineralization and nitrification. Nitrogen saturation can also result from non-anthropogenic N sources such as biological N fixation (e.g. forests with a significant alder component; Van Miegroet and Cole, 1984). The primary diagnostic characteristics of N saturated ecosystems are thought to include: excess NO_3^- leached beyond the rooting zone and/or

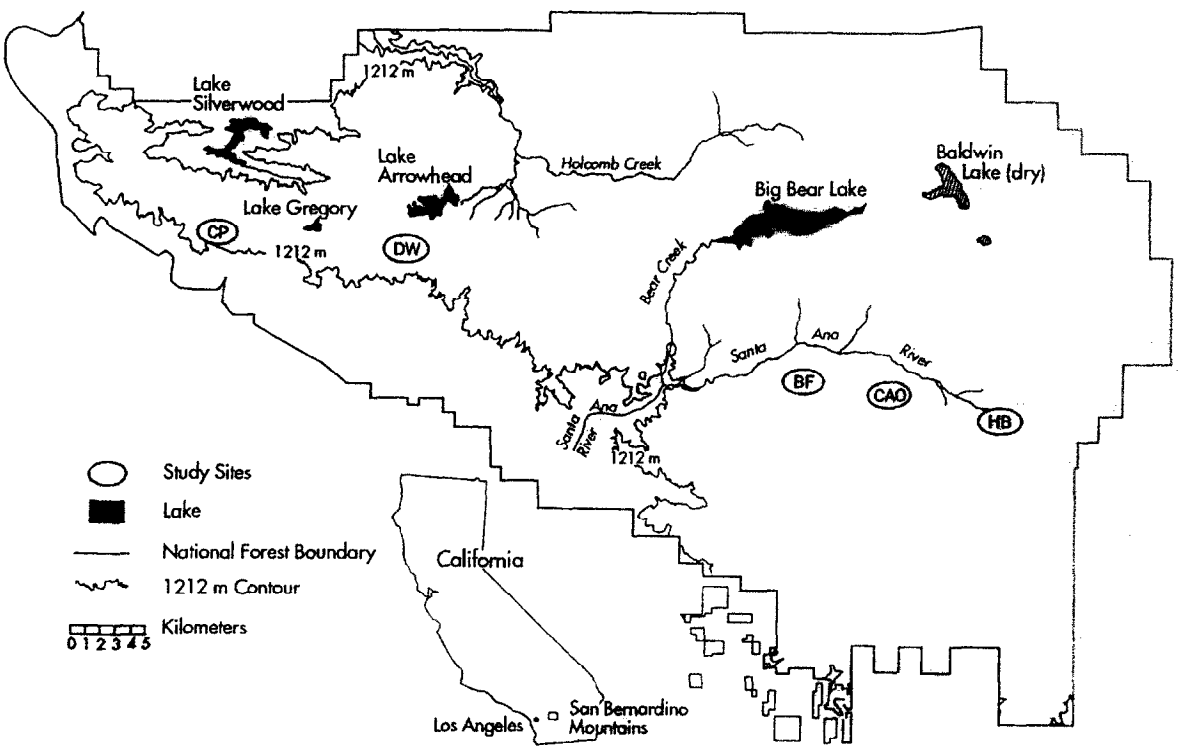

Fig. 1. Locations of the six study sites in the San Bernardino Mountains used in this study. Modified from Miller et al. (1986).

above-normal NO_3^- fluxes in streamwater, elevated losses of trace N gases from soil, lowered C:N ratios in soil, high N:nutrient ratios in foliage, elevated storage levels of NO_3^- (Stams and Schipholt, 1990) and free amino acids (Ericsson et al., 1993) in vegetation, and lack of a plant growth response following N amendment (Ågren and Bosatta, 1988; Aber et al., 1989; Aber, 1992; Stoddard, 1994).

Dry deposition of N in the Los Angeles Air Basin is among the highest in North America (Bytnerowicz et al., 1987; Solomon et al., 1992). N inputs from fog (Waldman et al., 1985), rime ice, snow (Berg et al., 1991), and rain also contribute in varying degrees to the total atmospheric N input in forests near Los Angeles. High streamwater fluxes of NO_3^- in chaparral watersheds in the San Gabriel Mountains north/northeast of Los Angeles (Riggan et al., 1985, 1994) demonstrate the potential for N saturation in natural ecosystems within the Los Angeles Air Basin. In the San Bernardino Mountains (SBM) east of Los Angeles, L-litter decomposition rates, species diversity of decomposer fungi, and concentrations of N in soil, foliage and litter were greatest in the western high-pollution sites of the atmospheric deposition gradient (Fenn and Dunn, 1989; Fenn, 1991). Nitrogen deposition at Camp Paivika (CP) in the western SBM is estimated to be 35–45 kg ha^{-1} $year^{-1}$ (Fenn and Bytnerowicz, 1993; Fenn et al., 1995). Nitrogen deposition during the summer 'smog' season occurs mainly in dry forms, with oxidized N pollutants (i.e. HNO_3, NO_3^-) more prevalent than reduced forms of N. In this paper we present results for a number of nutritional and edaphic indicators and from nutrient cycling model (NuCM; Liu et al., 1992; Johnson et al., 1993) simulations which support the hypothesis that the forest at CP is N saturated.

2. Methods

2.1. Study area

The study sites are located along a 55-km west to east air-pollution gradient within the mixed conifer forest zone in the SBM east of Los Angeles, California (Fig. 1). Ponderosa (*Pinus ponderosa* Laws.) or Jeffrey pine (*P. jeffreyi* Grev. and Balf.) are the dominant overstory species in the study areas. Major overstory species associated with ponderosa or Jeffrey pine in the plots are white fir (*Abies concolor* Gord. and Glend.), California black oak (*Quercus kelloggii* Newb.), incense cedar (*Calocedrus decurrens* (Torr.), and sugar pine (*Pinus lambertiana* Dougl.). Bracken fern (*Pteridium aquilinum* var. *pubescens* Underw.) understory are frequently dense in the western plots. The sites chosen for this study have not burned within the past 40 years to our knowledge. Since 1905 when fire control programs were initiated in the SBM, the average fire frequency in the ponderosa and Jeffrey pine types has been 22 and 29 years, respectively (McBride and Laven, 1976).

Sample collection sites in this study are located adjacent to permanent research plots established in 1972 and 1973 (McBride and Miller, 1977). The air pollution gradient was originally established as such based on atmospheric ozone (O_3) concentrations (Miller et al., 1986). More recently, it was confirmed that a gradient in N and S deposition also exists from west to east in the SBM (Fenn and Bytnerowicz, 1993). Air pollution exposures are greatest on the western end of the gradient due to the proximity of major urban centers in the valley to the west. Camp Paivika (CP) is located on the crest overlooking the urban region to the west and is the site with the highest air pollution exposure. Dogwood (DW) is located ca. 9 km east of CP, and is a highly polluted site, although not to the same degree as CP. Barton Flats (BF), Camp Osceola (CAO), and Heart Bar (HB) are the most easterly sites with the lowest air-pollution exposures. Samples at BF were collected from permanent research plots (Plots 1–3) and near the BF monitoring station established in 1991.

The parent material of the soils in the plots is partially weathered or decomposed granitic rock, except for HB, which is primarily mixed alluvium derived from granitic and metamorphic rock (Arkley et al., 1977). Soils in the SBM are sandy with considerable very fine gravel (2–5 mm; Arkley, 1981). All soils in the plots sampled in this study, have weakly developed B horizons and become increasingly coarse textured with depth (Arkley, 1981). At CP and DW soils are mainly coarse-loamy, mixed, mesic, Ultic Haploxerolls (Arkley, 1981), of the Shaver series. The Shaver series is dark in color to a

depth of greater than 50 cm with no significant clay accumulation in the subsoil (Lund and Page, 1973; Arkley et al., 1977). Soils at BF, CAO, and HB are mostly coarse-loamy, mixed, frigid, Xerumbrepts and Xerochrepts (Arkley, 1981).

2.2. Soil chemical analyses

Six or seven soil samples were collected in April, July, and October 1993 at CP and CAO from a depth of 5–25 cm from locations traversing a 200 m × 70 m plot. The surface litter layers were removed prior to collecting the soil samples. Soils were collected in polyethylene bags and stored at 4°C until analysis. Nitrate, ammonium and sulfate concentrations in saturated soil extracts (Rhoades, 1982) were determined using liquid ion chromatography (Dionex[1] series 4000i, Sunnyvale, CA). Total C and N and pH were also measured for the soils collected in October. Soil pH was determined on a 1:2 mixture of soil and 0.01 M $CaCl_2$. Total soil C and N concentrations were determined by combustion analysis with a combustion analyzer (Carlo Erba Instruments, Milan, Italy; Model NA 1500, Series 2). Soil pH and total C and N were also determined in March 1994 from soils collected at CP and CAO. Five soil samples were collected from each of these sites from an area ca. 0.7 ha in size.

Soil samples were collected for soil solution analysis at CP, Barton Flats Monitoring Station (BF1) and HB on March 22, 1994. Samples were collected at Barton Flats Plot 2 (BF2) on March 29, 1994. The soils appeared to be near field capacity at the time of collection. Each replicate soil sample was a composite of four subsamples. Subsample sites were located 2 to 3 m apart along a grid line. Samples were collected by removing forest floor material, digging small pits, and taking soil samples from the sides of the pits at depths of 0 to 8 cm and 15 to 23 cm. Three composite samples per soil depth were obtained in each plot. Soil solution was collected by the centrifugal filtration method of Davies and Davies (1963) as described by Soon and Warren (1993), with slight modifications. Glass fiber filter disks were used instead of glass wool plugs to cover the drainage holes of the false-bottom soil tubes, the tubes were centrifuged at 5000 rpm instead of 3000 rpm, and 20 g of soil was used instead of 25 g (Soon and Warren, 1993). From 0.75 to 2.03 ml of soil solution were collected from the 20 g soil samples subjected to centrifugation. Soil solutions were analyzed for NO_3^-, NH_4^+, SO_4^{2-}, Cl^-, and major cations.

2.3. Trace gas fluxes from soil

A modified static box method (Anderson and Poth, 1989) was used to determine the fluxes of nitrous oxide (N_2O) and nitric oxide (NO) from soil. Stainless steel collars circumscribing 0.58 m^2 ground area were inserted into the soil to a depth of 2 cm and the top of the flux boxes were set over the collars to form a sealed headspace. The procedure employs real time measurement of NO using a Luminox nitrogen dioxide (NO_2) detector (Model LMA-3, Scintrex-Unisearch, Toronto, Canada). For analysis of N_2O, samples were taken through a silicone rubber septum on the top of the flux box with 50-ml syringes, and samples were injected into a gas chromatograph (Model 5790, Hewlett Packard Corporation, Palo Alto, CA) with an electron capture detector and stainless steel column packed with Porapak Q 80/100 mesh. Details of the flux boxes and procedures for NO and N_2O analysis are given in Anderson and Poth (1989).

Six replicate flux boxes were employed at CP and six at BF. Flux boxes at CP were located in partial shade. However, three of the boxes at BF were located in an area receiving full sun in the morning and early afternoon. Therefore, at BF, only data from the three flux boxes in partial shade were considered, in order to reduce environmental variability between sites. At each plot, flux boxes were arranged in clusters of three. The boxes within a cluster were closely spaced, separated by ca. 0.5 m. At CP the two clusters were ca. 7 m apart. Flux measurements were taken at BF on August 9, 1993 and at CP on August 16, 1993. This is late in the summer–fall drought period typical of the Mediterranean climate. Trace gas fluxes were first measured on dry soils. Subsequently, we added enough water to the soil to remove any water limitation on the microbes in-

[1] Mention of trade names or products is for information only and does not imply endorsement by the US Department of Agriculture.

volved in trace gas production. Because of the thickness of the litter layers at CP, 8 l of distilled water were added, and 3 l were added at BF which has a relatively thin forest floor. Water contents never exceeded field capacity in these well drained soils. We waited 1 h after wetting before fluxes were remeasured.

2.4. Nitrogen mineralization rates and base saturation

Ammonium and nitrate production in soil from CP, DW, CAO, and HB were determined from the top 0–2 cm of soil, and in the F-litter (the partially decomposed layer above the mineral soil and underneath the undecomposed L-litter). At HB the litter layers are very thin, and the litter collected at HB was not as decomposed as at the other sites. The F-litter layer at CP on the other hand, is a relatively thick decomposed horizon. Each litter and soil sample was a composite of litter or soil collected under one or two ponderosa or Jeffrey pine trees, and one or two co-dominant species; California black oak and white fir at DW, CAO, and HB, or California black oak at CP. Three replicate composite samples were collected per plot. The nine sampled trees per plot encompassed an area of ca. 1000 m^2. Litter and soil were collected from the same forest-floor locations below mid-canopy. Soils were prepared by sieving through a 2-mm sieve. Time zero soil samples were taken for KCl extraction prior to placing soil and litter in plastic cups and adding water to ca. 75% saturation content. Cups with soil or litter were covered with aluminum foil and incubated at room temperature for 10 weeks. At weekly or biweekly intervals 3 g of moist soil or litter from each of three replicate beakers per soil horizon–forest site combination were extracted with 30 ml of 2 N KCl. The concentrations of N as NH_4^+, and $NO_2^- + NO_3^-$ in the soil extracts were determined with a Technicon TRAACS autoanalyzer. Concentrations of NH_4^+ and $NO_2^- + NO_3^-$ were calculated on a soil or litter dry weight basis. The maximum N-mineralization rate of soil and litter at each plot was determined from the slope of a linear regression of the data covering the 3- to 4-week period with the highest mineralization rate (sum of NH_4^+, NO_2^-, and NO_3^- production).

Percent base cation saturation was also determined for the same composite soil samples used for the N-mineralization assays. The cation exchange capacity of the soils was determined by K^+ saturation with 2 N KCl, followed by ethanol rinse and NH_4^+ replacement. Analyzed K^+ was used to calculate number of exchange sites. Exchangeable cations in 1 M SrCl extracts were determined with atomic absorption spectroscopy (Perkin–Elmer 5000, Norwalk, CN). Cations measured were Ca^{+2}, Mg^{+2}, K^+, and Na^+.

2.5. Enumeration of nitrifier organisms

Populations of nitrifiers (ammonium oxidizers) were estimated in soils from CP, DW, BF, CAO and HB using the most probable number dilution technique (Alexander, 1982). Soils used for nitrifier enumeration were subsamples of the soils collected for saturation soil extracts and for N mineralization assays, and on the dates of trace gas flux measurements as described above. Serial dilutions of soils were from 10^{-1} to 10^{-6}, with five replicate tubes for each dilution. A precipitate-free NH_4^+ oxidizer medium (Schmidt and Belser, 1982) was added to each culture tube at the beginning of the incubation. Positive tubes were identified with a diphenylamine nitrate spot test reagent after 21–23 days of incubation in the dark at 27.5°C (Schmidt and Belser, 1982).

2.6. Foliar C, N, P, S, NO_3^-, and NH_4^+

Foliage of ponderosa pine, Jeffrey pine, California black oak, and bracken fern were collected (when available) in late April, July, and October, 1993 from CP and CAO. However, since bracken fern is not found at CAO, fern samples for the low-pollution site were actually collected ca. 4 km west of CAO near the BF area, and only on the July and October sampling dates. Foliage was collected from the same study areas as the soils collected for chemical analysis as described above. Ponderosa pine was sampled at CP, but at CAO Jeffrey and ponderosa pine co-occur. No attempt was made to identify the sampled pine trees to species, so that trees of either species may have been sampled at CAO, although Jeffrey pine is more common than ponderosa pine at CAO. Seven or eight pine and oak trees, distributed

throughout the 200 m × 70 m plots, were sampled per plot on each date. In April, oak foliage was not collected at CAO because the spring flush of oak foliage was only beginning to emerge. Oak foliage collected at CP in late April was newly emerged and mostly red/purple in color, although some leaves had turned green. Pine foliage collected in April at CP and CAO was from the previous year, while current-year pine needles were collected in July and October. Four annual whorls of pine needles were collected from each replicate tree (one whorl from each geographic quadrant) on each sampling date. Leaves were collected from all sides of each replicate oak tree at a height of 1.5 to 2.5 m. Fern fronds were collected in open areas near the oak and pine trees sampled at CP. At the low-pollution site seven or eight replicate frond samples were collected along three parallel 60- to 80-m transects (ca. 6 m apart) in an area with a dense fern cover.

Nitrate and ammonium concentrations were determined for foliage collected in April, July, and October 1993. For the determination of foliar NO_3^- and NH_4^+ concentrations, 0.5 g of dried and ground leaf material was shaken with 25 ml demineralized water for 4 h as described by Stams and Schipholt (1990) and Breimer (1982). The solution was centrifuged for 20 min, and NO_3^- and NH_4^+ concentrations were determined colorimetrically with a Technicon TRAACS 800 autoanalyzer. Total C, N, and S in foliage collected in October 1993 were determined by combustion analysis, and total P was determined from nitric-perchloric digestion and analysis with a Technicon TRAACS 800 autoanalyzer (Glaubig and Poth, 1993).

2.7. Nutrient cycling model

The nutrient cycling model (NuCM) is a stand-level nutrient cycling model, designed primarily for humid forest ecosystems, in which the forest ecosystem is represented as a series of vegetation and soil components. The major objectives for using NuCM were to test its performance under the semi-arid conditions in the SBM, and as a tool for evaluating the potential for and mechanisms of N saturation as evidenced by field results. Using mass balance and transport formulations, the model tracks 16 solution-phase components including the major cations and anions, ANC (acid-neutralizing capacity), an organic acid analog, and total aluminum (Liu et al., 1992). The model routes precipitation through the canopy and soil layers, and simulates evapotranspiration, deep seepage, and lateral flow. The soil includes multiple layers and each layer can have different physical and chemical characteristics. Nutrient pools associated with soil solution, the ion exchange complex, minerals, and soil organic matter are all tracked explicitly. The processes which govern interactions among these pools include user-specified rates for decay, nitrification, anion adsorption, cation exchange, and mineral weathering. Cation exchange is represented by the Gapon equation (Bohn et al., 1979).

NuCM was calibrated for the BF site using data collected from the site for vegetation and soil nutrient concentrations, soil and litter mass, and soil solution concentrations. At the time of this exercise, no data for biomass from the BF site was available, so the data on a ponderosa pine stand from Klemmedson (1975) was used. Procedures outlined in the user's manual (Munson et al., 1992) were used in the calibration. Details are described elsewhere (Liu et al., 1992; Johnson et al., 1993). Five N deposition scenarios were run: inputs of 1.9, 9.5, 19.2, 38.2, and 95.6 kg ha^{-1} $year^{-1}$ (0.1 ×, 0.5 ×, 1 ×, 2 ×, and 5 × scenarios). The 9.5 kg ha^{-1} $year^{-1}$ scenario is approximately equal to annual atmospheric N input at BF (Bytnerowicz et al., 1995), and the 38.2 kg ha^{-1} $year^{-1}$ scenario is the approximate annual N loading at CP (Fenn and Bytnerowicz, 1993; Fenn et al., 1995). Each simulation was run from the same initial conditions, with no input variable changes except N deposition. Model runs simulated 40 years of forest growth.

2.8. Statistical analyses

Data analysis for comparing results between sites were performed using SigmaStat™ statistical software from Jandel Scientific Software (San Rafael, CA). Differences between the high and low pollution sites for foliar nutrient ratios and for fluxes of NO and N_2O from soil were tested with ANOVA and a paired *t*-test. When the data failed the normality test, the Mann–Whitney rank sum test was used (Fox et al., 1994). Differences in concentrations of ions in

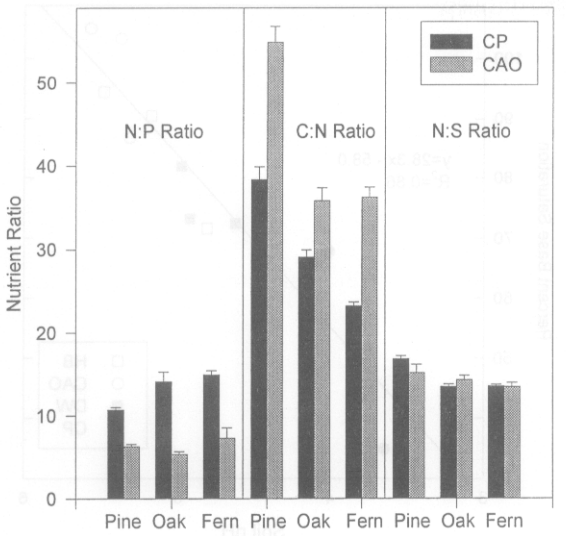

Fig. 2. Nutrient ratios in current-year foliage of ponderosa or Jeffrey pine, California black oak, and bracken fern from a high- (CP) and low-pollution (CAO) site in the SBM. Foliage was collected for nutrient analysis on Oct. 19–20, 1993. The N:P and C:N ratios were all significantly different between CP and CAO, while N:S ratios were not significantly different between the two plots. Error bars represent standard errors of the mean for each plot/species combination. Fern foliage for CAO was collected 4 km to the west of the CAO pine and oak site.

soil solution among sites were tested by one-way ANOVA and Bonferroni's all pairwise multiple comparison procedures. Repeated measures ANOVA procedures were used for comparing data between sites when data was collected sequentially from the same plots (N mineralization, foliar extracts, saturation soil extracts). Bonferroni pairwise multiple comparison procedures were used to test differences among plots. In some cases data were log transformed to stabilize the variance or to achieve normality of distribution. When normality was not achieved, the Friedman one-way repeated measures ANOVA on ranks procedure was used followed by the Student–Newman–Keuls multiple comparison procedures (Fox et al., 1994).

3. Results

3.1. Foliar N:nutrient ratios

Foliar N:P and C:N ratios were compared for ponderosa pine, California black oak, and bracken fern at CP and at CAO (Fig. 2). For all three plant species N:P ratios were higher ($P < 0.001$) and C:N ratios were lower ($P < 0.005$) at CP than at CAO (foliage collected on October 19, 1993; fern foliage for CAO was from a site 4 km to the west of CAO). The N:S ratios for current-year pine, oak and fern foliage were not significantly different at CP and CAO (Fig. 2). For all three plant species N and

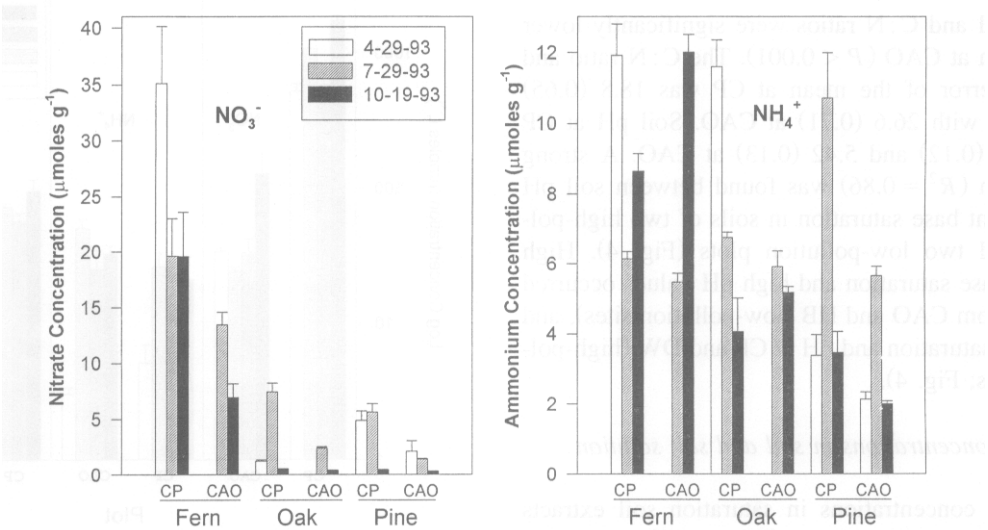

Fig. 3. Concentrations of NO_3^- and NH_4^+ in water extracts of dried foliage of ponderosa or Jeffrey pine, California black oak, and bracken fern from CP and CAO. Error bars, sites, and foliage collection are as described for Fig. 2. Fern foliage for CAO was collected 4 km to the west of the CAO pine and oak site.

S concentrations in foliage were significantly greater ($P \leq 0.01$) at CP while P concentrations were greater ($P < 0.02$) at CAO.

Average total N concentrations in pine, oak, and fern at CP were 12.9, 17.1, and 20.0 g kg^{-1} compared with 9.0, 13.5, and 12.9 g kg^{-1} at CAO. Average total P concentrations in pine, oak, and fern at CP were 1.21, 1.27, and 1.35 g kg^{-1} compared with 1.44, 2.55, and 2.17 g kg^{-1} at CAO. Average total S concentrations in pine, oak, and fern at CP were 0.77, 1.28, and 1.48 g kg^{-1} compared with 0.61, 0.95, and 0.97 g kg^{-1} at CAO.

3.2. Foliar NO_3^- and NH_4^+

Nitrate concentrations in pine, oak and fern foliage were greater ($P \leq 0.03$) at CP than at CAO. However, by late October NO_3^- concentrations in pine and oak had dropped precipitously at both sites to low levels (Fig. 3). Ammonium concentrations in pine ($P < 0.01$) foliage were greater at CP than at CAO. Ammonium concentrations in fern were slightly greater at CP in July, but were much greater at CAO than at CP in October (Fig. 3). Ammonium concentrations in oak foliage were not significantly different between the sites.

3.3. Soil C:N ratios, base saturation and soil pH

Soil pH and C:N ratios were significantly lower at CP than at CAO ($P < 0.001$). The C:N ratio and standard error of the mean at CP was 18.8 (0.65) compared with 26.6 (0.71) at CAO. Soil pH at CP was 4.01 (0.12) and 5.42 (0.13) at CAO. A strong correlation ($R^2 = 0.86$) was found between soil pH and percent base saturation in soils of two high-pollution and two low-pollution plots (Fig. 4). High percent base saturation and high pH values occurred in soils from CAO and HB (low-pollution sites), and low base saturation and pH at CP and DW (high-pollution sites; Fig. 4).

3.4. Ion concentrations in soil and soil solution

Nitrate concentrations in saturation soil extracts were 14 to 44 times greater ($P < 0.002$) at CP than at CAO (low pollution) throughout the growing season (Fig. 5). By comparison, NH_4^+ and SO_4^{2-} concentrations in the saturation extracts were much lower than for NO_3^-, but concentrations were similar among the two plots (Fig. 5).

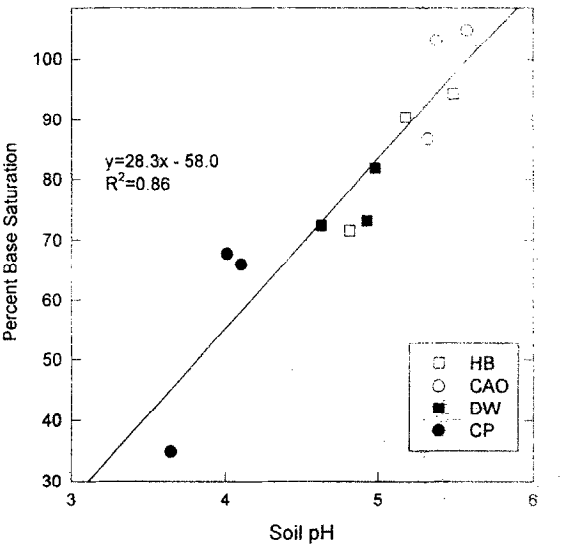

Fig. 4. Base saturation versus pH of soil from the A horizon at two low-pollution sites (HB and CAO) and two high-pollution sites (DW and CP).

Nitrate concentrations in soil solution were higher

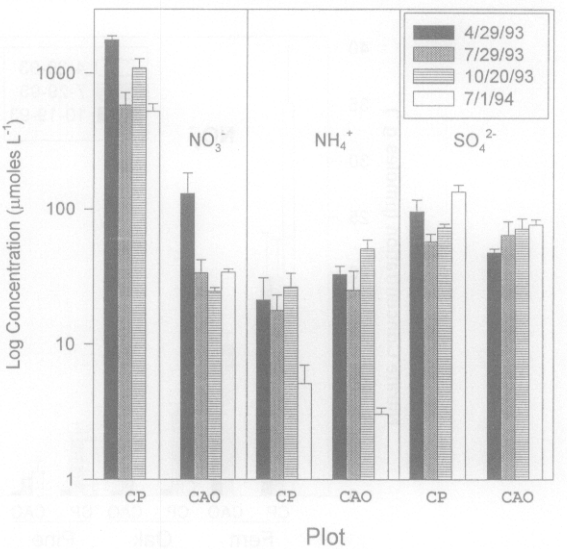

Fig. 5. Log concentrations of NO_3^- and NH_4^+ in saturation extracts of soil from a high- (CP) and low-pollution (CAO) sites. Error bars represent standard errors of the plot mean.

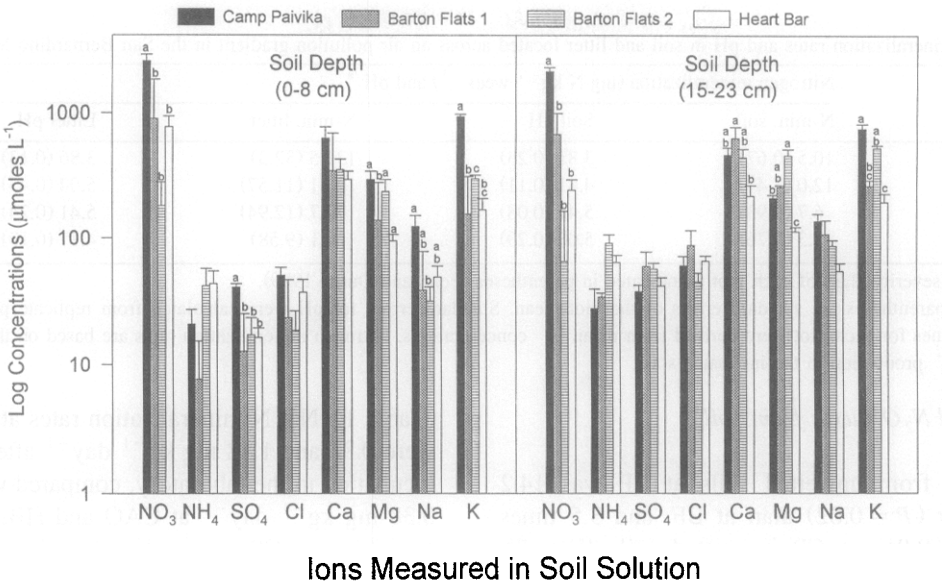

Fig. 6. Log ionic concentrations in soil solution collected by the soil centrifugation method. Soils were collected in late March 1994. Plots from which soils were collected are indicated in the figure legend. Error bars represent standard errors of the plot mean.

than any other ion at CP for both soil depths. Ion concentrations were similar from soil of the top 8 cm and from a depth of 15–23 cm (Fig. 6). Ammonium and sulfate concentrations in soil solution were orders of magnitude lower than NO_3^- concentrations at all the sites (Fig. 6).

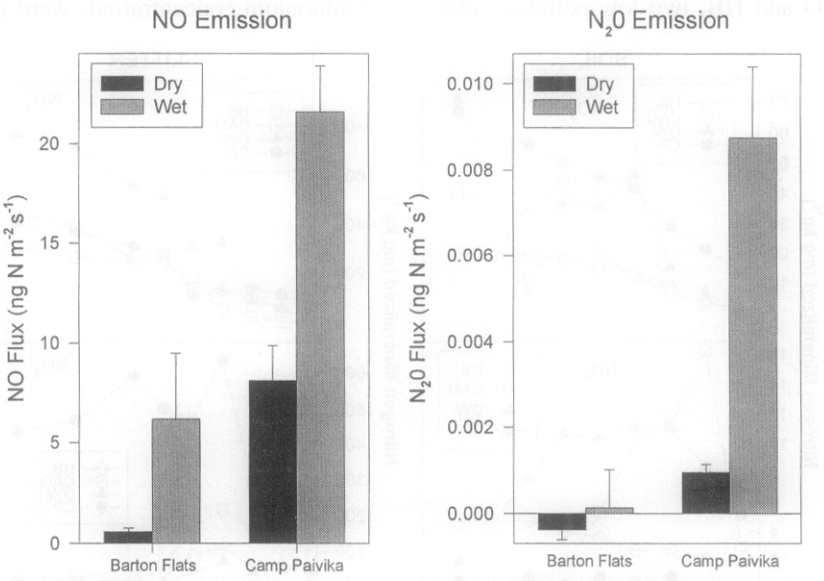

Fig. 7. Nitric oxide (NO) and nitrous oxide (N_2O) emissions from field soils at a low-pollution site (Barton Flats) and a high-pollution site (Camp Paivika) on August 9 and August 16, 1993 respectively. The dry treatment refers to untreated soils, and the wet treatment refers to soils treated with water 1 h prior to beginning flux measurements. Error bars represent standard errors of the plot mean ($n = 6$ replicate flux boxes at CP and $n = 3$ boxes at BF).

Table 1
Maximum N-mineralization rates and pH in soil and litter located across an air pollution gradient in the San Bernardino Mountains

Plot [a]	Nitrogen mineralization (mg N kg^{-1} $week^{-1}$) and pH [b]			
	N-min. soil	Soil pH	N-min. litter	Litter pH
CP (high)	10.5 (0.67)	3.81 (0.23)	131.5 (32.3)	3.86 (0.13)
DW (high)	12.0 (3.47)	4.81 (0.11)	101.1 (11.57)	5.04 (0.43)
CAO (low)	6.7 (0.93)	5.41 (0.08)	70.7 (12.94)	5.41 (0.24)
HB (low)	5.3 (0.76)	5.08 (0.20)	60.1 (9.58)	4.31 (0.19)

[a] Air pollution severity class of each plot is indicated in parentheses (Fenn and Dunn, 1989).
[b] Numbers in parentheses are standard errors of the plot mean. Standard errors for pH were calculated from replicate pH values, while average pH values for each plot were derived from mean H^+ concentrations. Nitrogen mineralization rates are based on the sum of NH_4^+, NO_2^-, and NO_3^- production in the incubated soils.

3.5. NO and N_2O fluxes from soil

NO flux from unwetted soils at CP was 14.2 times higher ($P = 0.02$) than at BF, and 3.5 times higher ($P < 0.01$) at CP in wetted soils (Fig. 7). $NO:N_2O$ ratios in unwetted soils were 8.5×10^3 at CP and 1.5×10^3 at BF. $NO:N_2O$ ratios in wetted soils were 2.5×10^3 at CP and 4.7×10^4 at BF.

3.6. Nitrogen mineralization

Maximum N mineralization rates ($NH_4^+ + NO_2^-, + NO_3^-$) in soil and litter were approximately twice as high at CP and DW, two high-pollution sites, than at CAO and HB, two low-pollution sites (Table 1). Net N mineralization rates at CP and DW were 0.88 and 1.18 mg kg^{-1} day^{-1} after 8 weeks of incubation in the laboratory, compared with 0.67 and 0.38 mg kg^{-1} day^{-1} at CAO and HB. Nitrate concentrations at CP were at least ten times greater than in soil from the other plots at the beginning of the incubation. Nitrate in the mineral soil generally increased with time of incubation in soil from all the plots, but the rate of increase was greatest ($P < 0.001$) and most consistent for the CP soil (Fig. 8). Ammonium concentrations in all the soils except HB decreased as nitrate increased. Ammonium concentrations in soil from CP, on the other hand, dropped to and remained near zero after 1 week, (Fig. 8). Ammonium concentrations were greatest at DW and

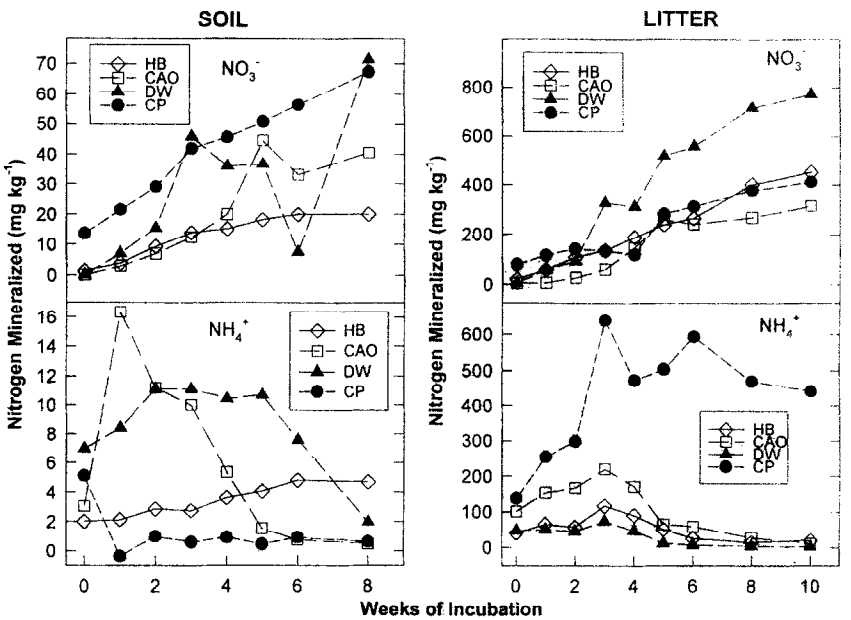

Fig. 8. Nitrogen mineralization in soil and litter from four sites traversing the air pollution gradient in the San Bernardino Mountains.

CAO in the first few weeks of incubation, intermediate at HB, and lowest at CP (Fig. 8), although in the latter part of the experiment, NH_4^+ production dropped rapidly as NO_3^- production increased at DW and CAO.

Nitrate production from litter generally increased with time of incubation for all four plots, but NO_3^- production was greatest at DW. Nitrate concentrations were similar for litter from CP, CAO, and HB (310 to 430 mg N kg^{-1} by Week 10), but NO_3^- concentration in litter from DW by Week 10 was 780 mg N kg^{-1} (Fig. 8). Ammonium production increased to 630 mg N kg^{-1} after 3 weeks with the litter from CP, while NH_4^+ production of litter from the other three plots peaked at 80–200 mg N kg^{-1} after 3 weeks. Ammonium concentrations at DW, CAO, and HB then declined to 5–40 mg N kg^{-1} by the 8th week, whereas NH_4^+ concentrations at CP were still as high as 460 mg N kg^{-1} by Week 10 (Fig. 8). The major temporal pattern for N-mineralization in litter after Week 3 was diminishing NH_4^+ and increasing NO_3^- concentrations (Fig. 8). The pH of the soil and litter from the N-mineralization experiment are presented in Table 1. For both soil and litter, pH was lowest at CP and highest in the low-pollution plots.

3.7. Nitrifier populations

Assays for nitrifier populations from soils across the air-pollution gradient yielded mixed results. Most probable number (MPN) counts of nitrifiers in soil collected in July 1994 were 30 times greater ($P < 0.05$) at CP than at CAO (882 vs. 29 nitrifiers g^{-1} MPN count). No differences were found between nitrifier MPN counts in soils collected at CP, DW, CAO, and HB in September 1994 (263–610 nitrifiers g^{-1} MPN count). Likewise, MPN counts were not significantly different in soils collected from CP and BF in August 1994 (420 at CP and 3198 at BF). In some instances the standard deviations were large relative to the mean, so that only order of magnitude differences between sites were discernible.

3.8. NuCM simulations

Simulation results for NO_3^- leaching, soil solution NO_3^-, soil pH, and soil base saturation at BF indicate

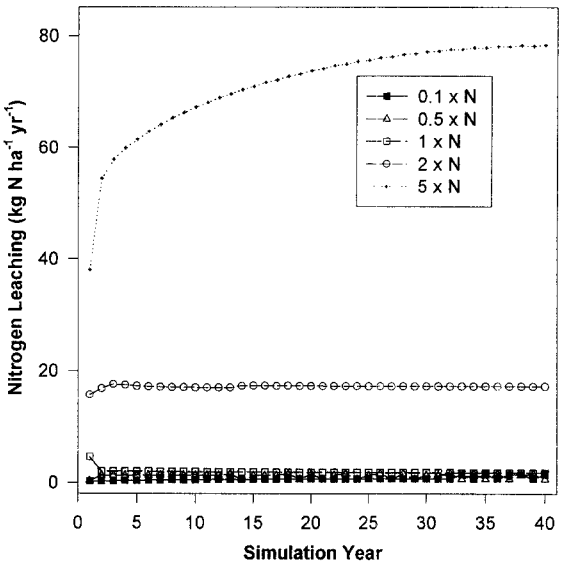

Fig. 9. Simulated N leaching below the B horizon (10–37 cm depth) at BF for 40 years under various N deposition scenarios: 0.1× = 1.9, 0.5× = 9.5, 1× = 19.2, 2× = 38.2, and 5× = 95.6 kg ha^{-1} $year^{-1}$.

N saturated conditions at the 2× (38.2 kg N ha^{-1} $year^{-1}$) and 5× (95.6 kg N ha^{-1} $year^{-1}$) deposition scenarios (Figs. 9–12). Nitrogen leaching below the B soil horizon, which was virtually all as NO_3^-, was near baseline levels in the three lowest deposition scenarios. Nitrate leaching in the 38.2 and 95.6 kg ha^{-1} $year^{-1}$ scenarios were 17 and 78 kg ha^{-1} $year^{-1}$ after 40 simulation years (Fig. 9). However, NO_3^- leaching was high in these high deposition scenarios during the entire 40 years. Soil solution NO_3^- concentrations in the B soil horizon (depth = 10–37 cm) were similar in Year 2 and Year 40 in all the scenarios except for the highest N deposition rate (5×; 95.6 kg ha^{-1} $year^{-1}$), in which concentrations in the soil solution peaked at 4833 μmol l^{-1} in Year 2 and 7717 μmol l^{-1} in Year 40 (Fig. 10). By comparison, in the 1.9 to 19.2 kg ha^{-1} $year^{-1}$ N deposition scenarios, the highest soil solution concentration was 360 μmol l^{-1} (Fig. 10).

Soil pH (Fig. 11) and base saturation (Fig. 12) decreased considerably in all the scenarios after 40 years. Decreases were much greater however, in the 2× and 5× deposition scenarios. Simulated stand biomass increased only gradually in the 0.1× deposition scenarios during the 40-year simulation. Stand

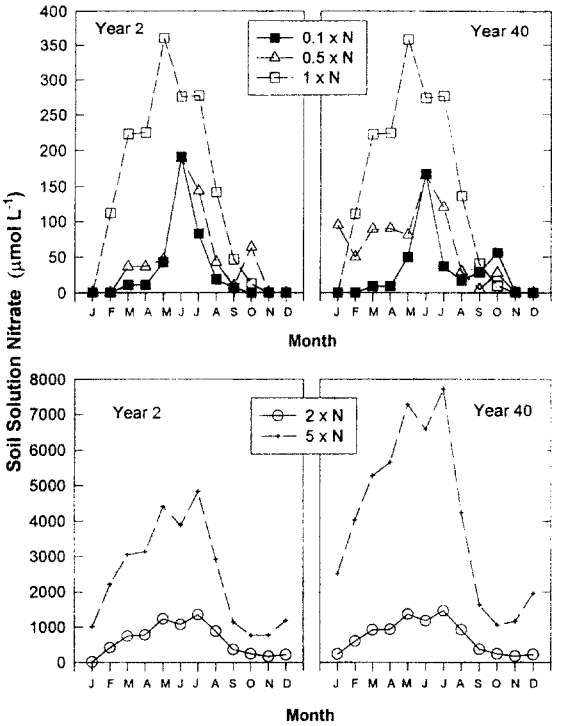

Fig. 10. Simulated soil solution nitrate concentrations in the B horizon (10–37 cm depth) in Years 2 and 40 at BF under various N deposition scenarios: 0.1× = 1.9, 0.5× = 9.5, 1× = 19.2, 2× = 38.2, and 5× = 95.6 kg ha^{-1} year^{-1}.

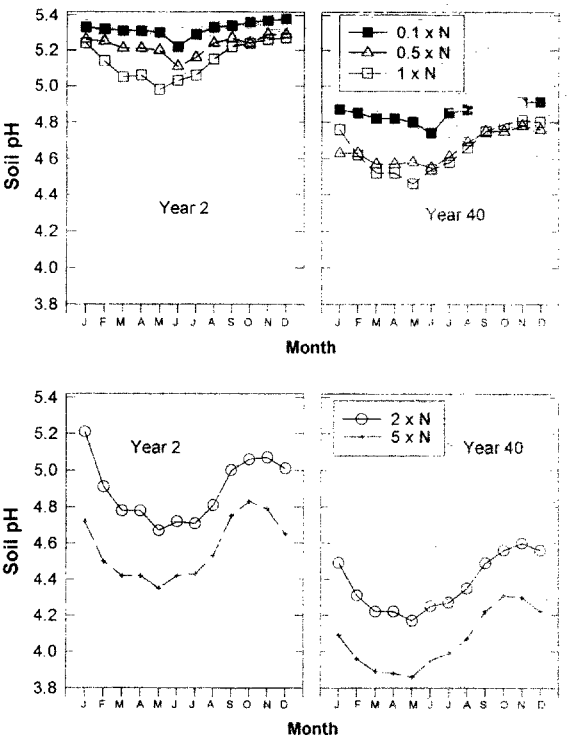

Fig. 11. Simulated soil solution pH in the A horizon in Years 2 and 40 at BF under various N deposition scenarios: 0.1× = 1.9, 0.5× = 9.5, 1× = 19.2, 2× = 38.2, and 5× = 95.6 kg ha^{-1} year^{-1}.

biomass increased more rapidly in the 0.5× –2× deposition scenarios, but showed no further increase in the 5× scenario (Fig. 13). Approximately 10% of the total stand overstory biomass in all the deposition scenarios was from the deciduous component and the remainder was coniferous overstory.

4. Discussion

4.1. Evidence for N saturation

None of the parameters presented in this paper taken alone conclusively demonstrates that the mixed conifer forest at CP is N saturated. However, the accumulated evidence indicates a N saturated condition at CP. The amount of available N in the ecosystem at CP appears to be greater than the biotic demand, based on the high NO_3^- concentrations sustained in soil throughout the growing season, and

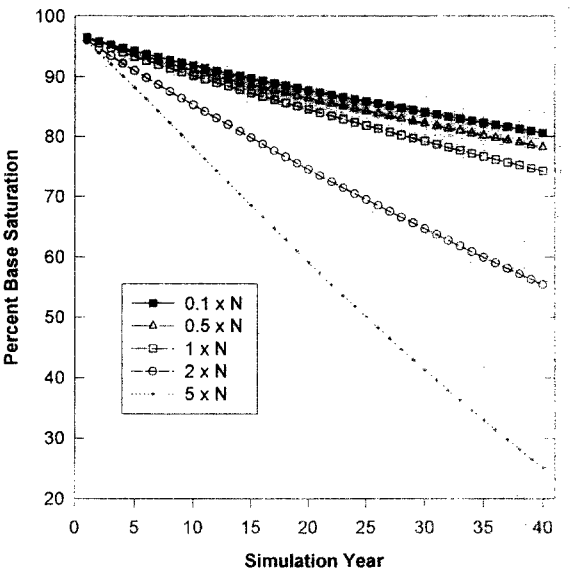

Fig. 12. Simulated soil base saturation in the A horizon at BF for 40 years under various N deposition scenarios: 0.1× = 1.9, 0.5× = 9.5, 1× = 19.2, 2× = 38.2, and 5× = 95.6 kg ha^{-1} year^{-1}.

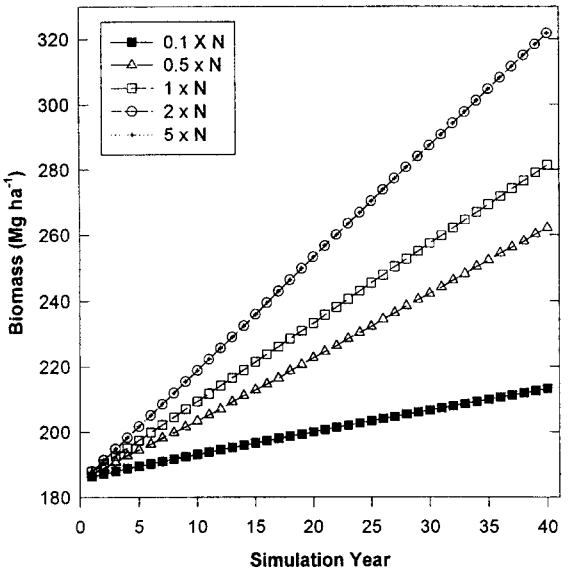

Fig. 13. Simulated total overstory biomass at BF under various N deposition scenarios: 0.1× = 1.9, 0.5× = 9.5, 1× = 19.2, 2× = 38.2, and 5× = 95.6 kg ha^{-1} $year^{-1}$. Note that simulations for the 2× and 5× scenarios track conjointly.

further evidenced by elevated soil NO fluxes. High N:P ratios, low C:N ratios, and high NO_3^- concentrations in foliage at CP are additional indicators of N enrichment, possibly due to chronic N deposition.

Nitrogen deposition at CP was reported to be > 30 kg N ha^{-1} $year^{-1}$, but winter deposition was greatly underestimated (Fenn and Bytnerowicz, 1993). More recently, bulk winter deposition of N in rain, and snow at CP was 11.9 kg ha^{-1}, and fog deposition was also highly elevated compared with more easterly sites in the SBM (Fenn et al., 1995). Annual atmospheric N deposition at CP is probably as high as 35–45 kg ha^{-1}. Net annual N incorporation in the growing biomass of a forest stand is roughly 5–10 kg ha^{-1} $year^{-1}$ (Glatzel, 1990; Zöttl, 1990). The net annual vegetation increment of N (N necessary to build woody tissue) in dry environments such as in the SBM is probably less than 5 kg ha^{-1} $year^{-1}$ (Johnson, 1992). Vegetation N increment accounted for nearly all ecosystem N retention in 19 of 24 forests reviewed by Johnson (1992). There is an obvious potential for N saturation in the SBM if annual vegetation N increment is ca. 5 or even 10 kg ha^{-1} $year^{-1}$ and annual N deposition inputs are 35–45 kg ha^{-1} $year^{-1}$.

A mixed conifer forest (2060 m elevation) in the San Gabriel Mountains near Los Angeles with annual throughfall N deposition of 12.4 kg ha^{-1} was not N saturated based on the dramatic foliar biomass increase in fertilized Jeffrey pine trees compared with unfertilized trees (Kiefer, 1995). However, chaparral watersheds (ca. 850 m) in the San Gabriel Mountains (Riggan et al., 1985) with annual throughfall N deposition of 23.3 kg ha^{-1} were N saturated, as evidenced by high streamwater NO_3^- losses. These findings from the San Gabriel Mountains and the present study from the SBM are in accordance with a survey of N inputs and outputs from 65 forested plots and catchments throughout Europe (Dise and Wright, 1995). Below a deposition threshold of about 10 kg N ha^{-1} $year^{-1}$ no significant NO_3^- leaching occurred, while at intermediate levels of 10–25 kg N ha^{-1} $year^{-1}$ leaching occurred at some sites. Above a deposition level of 25 kg N ha^{-1} $year^{-1}$ significant N leaching (N saturation) occurred at all sites (Dise and Wright, 1995). NuCM model simulations for BF in the SBM also suggested that N saturation becomes apparent at some deposition level between 19 and 38 kg N ha^{-1} $year^{-1}$.

4.2. Nitrogen mineralization

Nutrient cycling processes such as litter decomposition and N mineralization are typically higher in N saturated sites than in more N-limited sites (Aber et al., 1989; Van Miegroet et al., 1992). Maximum N mineralization rates in soil were higher at CP and at DW than at CAO and HB, two low-deposition sites in the SBM. At CP, concentrations of NO_3^- in the mineral soil increased steadily throughout the 8-week incubation period, while NH_4^+ concentrations dropped precipitously after 1 week and remained near baseline values for the entire incubation. On the other hand, NH_4^+ levels in soil were commonly several-fold greater in the other three plots than at CP during much of the experiment. The rapid oxidation of NH_4^+ at CP suggests a substantial and active nitrifier population, and is probably the major source of persistently high NO_3^- concentrations in the soil solution. However, in two out of three assays for soil nitrifier populations, MPN counts were not significantly different at CP compared with the low-pollution sites. This may be due to the inadequacy of the

MPN dilution technique to accurately quantify soil nitrifier populations. Nitrification in litter was greater at DW, while NH_4^+ accumulation was greatest at CP. Nitrification seems to have been inhibited in litter at CP due to unknown factors.

Nitrate and ammonium production in soils collected under chaparral canopies (burned 54 to 80 years prior) in San Diego County in southern California (Fenn et al., 1991) were highly similar to NO_3^- and NH_4^+ production determined with the same methodology for soils from CP and DW, suggesting that N mineralization rates in the SBM are not unusually high compared with other ecosystems in southern California.

4.3. Trace N gas emissions, N deposition, and stand disturbance

NO fluxes from unwetted soils at CP and at BF were 24 and four times higher than for typical temperate forest soils in the United States (Williams et al., 1992). High NO fluxes from chaparral soils in the South Coast (Los Angeles) Air Basin (SCAB) have been reported previously (Anderson et al., 1988). NO fluxes from unburned dry and wetted soils in the San Dimas Experimental Forest (SDEF) near Los Angeles were 9.7 and 21.4 ng N m^{-2} s^{-1}, respectively (Anderson et al., 1988), and were nearly identical to the NO flux rates measured at CP in this study (8.1 and 21.6 ng N m^{-2} s^{-1} in dry and wetted soils). Riggan et al. (1985, 1994) also found high streamwater NO_3^- fluxes from chaparral watersheds in the SDEF with high air-pollution loadings. Thus, both streamwater losses of NO_3^-, elevated soil solution NO_3^-, and high NO emissions from soil suggest that chaparral and mixed conifer ecosystems in the SCAB with high air-pollution exposure are N saturated.

Disturbances other than air pollution can also stimulate trace N gas emissions from forest soils and NO_3^- export from watersheds. Nitrate losses from forests as a result of stand disturbance are well documented (Vitousek and Melillo, 1979). NO emission rates as high as 14 ng N m^{-2} s^{-1} were measured after light rain in a mixed conifer forest in northern California which had been whole-tree harvested and all the litter removed from the forest floor (Iris Anderson, personal communication, 1994). The flux rate in the undisturbed control site was < 1 ng N m^{-2} s^{-1}. Whole tree harvesting and litter removal can cause reduced N immobilization and greater pool sizes and losses of NO_3^- (Vitousek, 1981; Vitousek and Matson, 1985). Greater pool sizes of NO_3^- are likely to result in increased emissions of N trace gases (Matson et al., 1992). Based on elevated NO emission rates and NO_3^- losses from high-pollution chaparral and mixed conifer forest sites in the San Gabriel and San Bernardino Mountains, we hypothesize that long-term chronic atmospheric deposition may represent a disturbance of similar magnitude to whole tree and litter harvesting or forest-type conversion; at least in terms of effects on ecosystem N cycling.

Nitrous oxide fluxes at CP and BF were low compared with other US forests. Nonetheless, N_2O fluxes from moistened soils at CP were ten times greater than at BF. Nitrous oxide fluxes from the coarse-textured soils of the SCAB are expected to be low compared with more humid forests with finer-textured soils. In a central California grassland, NO and N_2O production began within minutes of adding water to dry soil. Below field capacity, NO production was greater than N_2O production, while above field capacity N_2O production was greater. Nitrification was the main source of NO, while denitrification was the dominant source of N_2O when soil was above field capacity (Davidson, 1992). Davidson (1991, 1993) reported that NO emissions are much higher than emissions of N_2O in soils with $< 60\%$ water-filled pore space, with chemoautotrophic nitrification as the dominant source of both N_2O and NO. Given that the form of gaseous N emissions (NO, N_2O, or N_2) is controlled by water-filled pore space in the Davidson model, we should be able to compare NO and N_2O emission rates in common units of ng of N. Comparing our NO flux measurements with a review of N_2O fluxes from fertilized agricultural soils, we found that our high-pollution forest site (CP) had equivalent or higher fluxes than 60 of the 88 studies reviewed (Eichner, 1990). Since many forests of the western US have well-drained soils and are generally more water-limited that eastern forests, we expect that NO emissions will predominate from western forest soils.

4.4. Foliar nutrients and nutrient ratios

Greater N:P ratios and lower C:N ratios in foliage of ponderosa pine, California black oak, and bracken fern demonstrate N enrichment at CP compared with CAO. Foliar N:P ratios are reportedly better indicators of excess N than foliar N concentrations alone (Zinke, 1980, Mohren et al., 1986; Ericsson et al., 1993). Ericsson et al. (1993) reported that above a threshold N:P ratio of 12.5–14.0 elevated arginine concentrations, an indicator of excess available NO_3^-, were detected in foliage of Norway spruce (*Picea abies* (L.) Karst.). N:P ratios in pine, oak, and fern at CP were 10.7, 13.5, and 14.8, but were only 5.3–6.3 at CAO (all foliage collected in mid-October). Measurements of free amino acid concentrations in foliage across the atmospheric deposition gradient in the SBM could provide additional information on the N status of vegetation and the degree of N saturation.

Zinke (1980) also reported greater N:P ratios in bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) in high-pollution montane sites than in less-polluted sites in the SCAB. More recently, Poth et al. (1991) studied the effects of air pollution on growth and nutrient status of bigcone Douglas-fir in the SBM. Foliar N concentrations in bigcone Douglas-fir were negatively correlated with P concentrations ($r = -0.57$; Poth et al., 1991), as proposed for the N saturation hypothesis (Aber et al., 1989). The average foliar N:P ratio for the eight plots in the high-pollution region was 8.5 compared with a N:P ratio of 6.4 for nine plots in the eastern less-polluted region of the SBM. The relatively low N:P ratios of bigcone Douglas-fir in the SBNF are expected in these stands with poorly developed nutrient-poor soils. Bigcone Douglas-fir in the SBNF inhabits rough and steep terrain on the slopes of dissected canyons, where soils are typically shallow and poorly developed (McDonald, 1990).

When plant or soil nutrient supplies are marginal, chronic N deposition can induce nutrient deficiencies or imbalances (Schulze, 1989; Johnson and Ball, 1990). Mechanisms of N-induced deficiencies include growth stimulation from high levels of available N or due to cation leachate losses as counterbalancing ions for leached NO_3^-. To date there is no evidence of N-induced nutritional disorders in forests of southern California, presumably because the soils are not highly leached nor low in cations. Concentrations of macronutrient and micronutrient cations did not vary greatly between two high-pollution sites and two low-pollution sites in the SBM, although in some cases concentrations were greater in the high-pollution plots (M.A. Poth, unpublished data, 1993). Likewise, in this study, foliar S concentrations were greater at CP compared with CAO, which explains why N:S ratios were similar at both sites.

Nitrogen enrichment at CP is further evidenced by the greater accumulation of NO_3^- in bracken fern and in overstory species at CP compared with CAO. Bracken fern has been shown to accumulate high concentrations of total N (Gerloff et al., 1966) and NO_3^- (Stams and Schipholt, 1990) in foliage compared with other plant species in the same habitat. Total foliar N concentrations in fern were greater than in pine and oak at CP and greater than pine at CAO. Nitrate concentrations in bracken fern were also much greater than in pine or oak foliage at CP and CAO. However, NO_3^- concentrations in bracken fern in the SBM sites (6.9 to 35.1 μmol g^{-1}) did not accumulate to the extreme levels (80 to 320 μmol g^{-1}) reported for bracken fern (Stams and Schipholt, 1990) in a highly N-saturated oak-birch stand in the Netherlands (Van Breemen et al., 1987). By comparison, NO_3^- concentrations in spinach foliage in unfertilized agricultural soils were 10–20 μmol g^{-1}, and 280–1100 μmol g^{-1} in soils fertilized with 200 or 225 kg NO_3-N ha^{-1} (Breimer, 1982).

Foliar NH_4^+ concentrations in understory and overstory species in the oak–birch stand in the Netherlands were generally at least twice as high as in the California sites (Stams and Schipholt, 1990). The greater foliar NO_3^- and NH_4^+ concentrations in the Netherlands site, were probably due to excessive available N in the soil solution (Van Breemen et al., 1987) as a result of high atmospheric N inputs and high N mineralization rates typical of deciduous forests (Vitousek and Melillo, 1979). Direct foliar uptake of atmospheric N may have also been a contributing factor.

Nitrogen will accumulate in plant tissue beyond the level needed to achieve maximum growth (Zhen and Leigh, 1990). Nitrate, one of the primary storage forms of N in plants, is stored in the vacuole (Granstedt and Huffaker, 1982), but does not accu-

mulate until growth requirements for N are satisfied (Zhen and Leigh, 1990), or until the capacity for NO_3^- assimilation is exceeded (Lee et al., 1986). The higher accumulation of NO_3^- in foliage of pine, oak, and fern at CP than at CAO may indicate that the growth requirements for N at CP are satisfied. Nitrogen fertilization of mature ponderosa pine trees at CP in two separate experiments did not cause a significant growth response in current-year foliar biomass, while fertilization did stimulate foliar growth at CAO (Fenn, 1996). Similarly, NuCM also simulated no stand biomass response upon increasing N inputs over the level of N deposition loading that occurs at CP.

4.5. Soil acidification

In the high-deposition plots (CP and DW), pH and percent base saturation in the A horizon was lower than in the low-deposition plots (CAO and HB). Lower percent base saturation at CP and DW may be a result of higher cation leaching losses as counter-balancing ions for leached NO_3^- and possibly SO_4^{2-}. Likely proton sources in the high-deposition sites include acidic deposition, enhanced nitrification rates, and root uptake of NH_4^+. Our results and other studies on western granitic soils (Clayton et al., 1991) suggest that proton exchange for base cations is the major soil pH buffering mechanism. Proton consumption via sulfate adsorption (Clayton et al., 1991) may also be operative in the SBM soils, but no data is available to support this possibility. Comparison of our data with soil pH and C : N ratios from a U.S. Environmental Protection Agency-sponsored study in the mid 1970s (Arkley et al., 1977) suggest that in the past 20 years soil has acidified and become N enriched at a faster rate in the western, high-pollution sites compared with the low-pollution sites. However, comparisons between the previous data and our results are speculative, since details of chemical analysis methods, sampling protocols, and statistical analyses are not given for the earlier data. However, Wood et al. (1992) also reported large-scale surface soil acidification of chaparral soils in the San Gabriel Mountains since the 1970s. Soil pH measurements from over 700 different locations obtained in the 1970s were compared to over 300 recently-measured pH values. Lower elevation sites had the highest soil NO_3^- and SO_4^{2-} levels, and soil pH did not decrease with increasing elevation, as would normally be expected (Wood et al., 1992). Thus, data from the San Gabriel and San Bernardino Mountains suggest that soil acidification has increased in the last 20 years in areas exposed to chronic atmospheric deposition.

4.6. NuCM simulations

The NuCM model was designed primarily for more humid forest ecosystems, yet it performed well in this semi-arid forest. NuCM predicted relatively high soil solution NO_3^- concentrations in these systems, even with low N deposition rates – a result of the prolonged summer droughts. This prediction seems to have been confirmed by soil solution data from HB (low-pollution site), which were collected after the simulations were run. Similarly, the extremely high soil solution NO_3^- concentrations measured at CP were predicted by NuCM for the high deposition scenarios in advance of the collection of that data. NuCM predicted a reduction in base saturation with increasing N deposition which was also subsequently observed in the field. Model simulations and field data both indicated decreasing soil pH with time, and greater soil acidification with higher N deposition. The accuracy of other NuCM predictions (such as lower growth rates at N deposition rates less than 38 kg ha^{-1} $year^{-1}$) have not been fully evaluated. Nitrogen saturation, defined as no further growth response to N addition, occurred at some level between the $2 \times$ (38.2 kg N ha^{-1} $year^{-1}$) and $5 \times$ (95.6 kg N ha^{-1} $year^{-1}$) scenarios in the simulations. Similarly, lack of foliar growth response following N fertilization at CP (Fenn, 1996) also supports the NuCM simulation of no stand growth response to further N addition.

The temporal development of N saturation at CP is not known, but the computer simulations suggest that high N inputs rapidly lead to elevated NO_3^- leaching and high NO_3^- concentrations in the soil solution of the B horizon. An increasing number of manipulative field studies utilizing N deposition addition or reduction treatments also demonstrate that N saturation (defined as excess NO_3^- losses) of

forest ecosystems can be induced or reversed within only a few years (Adams et al., 1993; Kahl et al., 1993; Boxman et al., 1994a, 1995; Norton et al., 1994; Dise and Wright, 1995; Bredemeier et al., 1995; Wright et al., 1995). Biotic responses to altered N inputs, such as changes in foliar nutrient status or growth, tend to respond more slowly, although in some cases responses are observable within the first several years (Boxman et al., 1994a, 1995).

4.7. Consequences and ecological significance of N saturation

Positive evidence of N saturation does not imply that forest health will be adversely impacted (Skeffington, 1990). No symptoms have been observed of declining forest health, vegetation injury, or nutrient imbalances/deficiencies due to excess N deposition in montane ecosystems of the Los Angeles Air Basin. However, oxidant injury to ponderosa pine in the SBM is well known (Miller et al., 1986), yet very little is known of the possible interactive effects of high ozone and N deposition in the SBM. Indicators of cumulative effects of chronic N deposition in these ecosystems are observed in soil and plant nutrient pools (Fenn, 1991), in soil acidification (Wood et al., 1992), and as elevated N losses in soil leachate, in streamwater (Riggan et al., 1985, 1994), or as N trace gases emitted from soil (Anderson and Poth, 1989). It is not clear what adverse long-term ecological effects may occur in these southern California ecosystems as a result of N saturation. Certainly streamwater quality in terms of excess NO_3^- from polluted watershed is of concern, and has been well documented from chaparral watershed in the San Gabriel Mountains (Riggan et al., 1985, 1994). Analogous streamwater NO_3^- data is not available from the SBM, because of the lack of gauged watersheds and the confounding factor of residential sources of groundwater and streamwater NO_3^-. However, based on the persistently high NO_3^- concentrations in soil solution and saturation soil extracts in the SBM, and on preliminary streamwater analyses from the San Gorgonio Wilderness in the SBM, it would not be surprising if watersheds in the SBM exposed to high N deposition also exhibit high streamwater NO_3^- fluxes.

5. Conclusions

Evidence from this study suggests that the mixed conifer forest at CP is N saturated or is approaching N saturation. The following factors support this conclusion: (1) high total N concentrations in soil, foliage and litter compared with the low-pollution sites, (2) high foliar N:P ratios, (3) high concentrations of NO_3^- in foliage of bracken fern and overstory species, (4) low C:N ratios in soil and foliage, (5) greater soil acidification and decreased percent base saturation compared with low-pollution sites, (6) sustained high NO_3^- concentrations in soil solution, (7) elevated NO emissions from soil, and (8) high soil nitrification rates. Lack of a foliar growth response in ponderosa pine to N fertilization at CP also indicates that N is non-limiting (Fenn, 1996). NuCM simulations of high NO_3^- concentrations in the soil solution, reduced base saturation of soils, and lack of a growth response to increasing N deposition agreed well with field data in the SBM.

High soil NO fluxes from otherwise undisturbed sites in the western US may be diagnostic of N saturation. Little is known of the potential long-term effects of N saturation on forest composition, health and sustainability in forests of the Los Angeles Air Basin. High NO_3^- concentrations in water from local N-saturated watersheds is of particular concern, and could exacerbate the problem of high NO_3^- levels in some local aquifers.

Further studies are needed to more fully evaluate the degree and geographic extent of N saturation and ecological effects of N deposition in southern California. Periodic data collection throughout the year on nitrate fluxes in soil solution and in streamwater, and on N trace gas emissions from soil will identify seasonal trends of N processing and biogeochemical responses to high and low atmospheric N inputs. Mechanistic studies are also needed on the factors controlling N retention and of the N retention capacity of forest ecosystems under the climatic conditions prevalent in California, and in other dry Western forests. Management practices in forests with high potential for release of excess N may require management strategies with greater focus on increasing N retention (e.g. maintaining relatively young, nutrient consuming stands) and reducing N outputs from forested watersheds (Glatzel, 1990; Aber et al., 1991).

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