
Uptake and Distribution of Nitrogen from Acidic Fog within a Ponderosa Pine (*Pinus ponderosa* Laws.)/Litter/Soil System

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ABSTRACT. The magnitude and importance of wet deposition of N in forests of the South Coast (Los Angeles) Air Basin have not been well characterized. We exposed 3-yr-old ponderosa pine (*Pinus ponderosa* Laws.) seedlings growing in native forest soil to acidic fog treatments (pH 3.1) simulating fog chemistry from a pine forest near Los Angeles, California. Fog solutions contained either $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$, or unlabeled N. The fog treatments were applied in open-top chambers in six 5-hr exposures. Soil treatments within each of the fog exposures were bare soil, soil overlain with L- and F-litter, and soil covered with plastic during the fog events to prevent fogwater from contacting soil. Seedlings were harvested and samples were collected 15 wk after the fog treatments. Uptake of ^{15}N by roots was by far the dominant pathway for plant assimilation of fog-deposited ^{15}N . Deposition of N in fog supplied 9.4% and 8.7% of the total N in current-year crown biomass in the litter-overlay and bare-soil treatments, respectively. Total N concentrations in every plant fraction except current-year stems were significantly higher in the bare-soil treatment than in the plastic-covered soil treatment. Less than 5% of the ^{15}N deposited directly to the seedling crowns was retained by the plants in the covered-soil treatment, whereas 57% of the ^{15}N deposited to the seedling/litter/soil systems was incorporated into plant biomass. The litter layers retained $^{15}\text{NH}_4^+$ more effectively than $^{15}\text{NO}_3^-$. Data from this study suggest that N deposited from fog may be an important source of N for plant growth in forests of the SCAB where fog occurrence and pollution exposure coincide. FOR. SCI. 41(4):645-663.

ADDITIONAL KEY WORDS. Nitrogen deposition, nitrogen saturation, nutrient cycling, wet deposition, ammonium, nitrate.

ATMOSPHERIC DEPOSITION, IN BOTH WET AND DRY FORMS, constitutes a significant N input to forest ecosystems exposed to high levels of air pollution (Aber et al. 1989, Lindberg et al. 1990, Lovett and Lindberg 1993). Dry deposition of N in the San Gabriel and San Bernardino Mountains near Los Angeles, CA, is among the highest in North America (Bytnerowicz et al. 1987a, 1987b, Fenn and Bytnerowicz 1993, Solomon et al. 1992). Dry deposition of N at a highly exposed site in the San Bernardino Mountains was estimated to be $29 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn and Bytnerowicz 1993). Dry deposition of N is generally thought to be of greater importance as a source of atmospheric N than wet deposition in forests of the SCAB (Bytnerowicz et al. 1987a, 1987b, Fenn and Bytnerowicz 1993, Riggan et al. 1985, Solomon et al. 1992, Young et al. 1988). However, a reappraisal of past assumptions of the comparative importance of dry deposition

and wet deposition of N in forests of the SCAB may be in order if preliminary data suggesting high N deposition from rain, fog, rime ice, and snow in the San Bernardino Mountains are indicative (Berg et al. 1991, and unpublished data from our laboratory). No studies of stand level inputs of N from wet deposition or fog have been reported for the mixed conifer forests in southern California. However, fog in the SCAB, and to a lesser degree rain, are enriched with N and are highly acidic (see Table 1 and references therein).

Ionic constituents are more concentrated in cloudwater, fogwater, and rime ice than in rain or snow (Berg et al. 1991, Collett et al. 1990, Lovett 1992, Miller et al. 1993, Waldman et al. 1985). However, the annual volume of water in fog or cloudwater deposition in low- to mid-elevation forests is usually less than that for incident precipitation. Concentrations of NH_4^+ and NO_3^- in fogwater were 63 to 87 times higher than in rainwater at Henninger Flats in the SCAB, while the total deposition of NH_4^+ and NO_3^- in fogwater was of comparable magnitude to input in incident rainfall (Waldman et al. 1985). Concentrations of NH_4^+ and NO_3^- in cloudwater in the Sierra Nevada Mountains were more than ten times those observed in precipitation. Collett et al. (1990) concluded that cloudwater in the Sierra Nevada Mountains in California contributes significantly to the regional acid deposition load, and that cloud interception may be the dominant deposition mechanism for isolated conifers and ridgetop canopies. Scavenging and transfer of atmospheric N and S to the forest canopy by cloud droplets was 12 to 30 times more efficient than by dry deposition processes in a high-elevation forest in New York (Miller et al. 1993). Fogwater or cloudwater deposition of N in western forests influenced by anthropogenic emissions warrants further study considering the potential for high N inputs and ecological effects; primarily, N saturation, NO_3^- contamination of groundwater and surface waters (Riggan et al. 1994, Stoddard 1994), altered forest composition and health, soil acidification and nutrient leaching, plant nutritional imbalance (Ericsson et al. 1993, Schulze 1989), and increased greenhouse gas emissions (Aber et al. 1989).

Much of the N deposited (both wet and dry) to the forest canopy and floor is transported by throughfall to the forest floor and soil where it may be utilized by vegetation or microorganisms, adsorbed to mineral soil and organic matter, or lost from the system as leachate or as trace N gases produced during nitrification or denitrification (Gundersen 1991, Raison and Stottlemeyer 1991, Van Miegroet et al. 1992a, 1992b). Direct uptake of atmospheric N by forest canopies (Lovett and Lindberg 1993, Potter et al. 1991) or root uptake of N from throughfall or precipitation percolating into the forest floor and soil would have the most immediate effects on plant physiology, nutrition, and growth. Nitrogen not incorporated into plant biomass shortly after deposition, yet retained within the ecosystem, may eventually contribute to plant-available N.

Only a few studies report direct measurements of N uptake and partitioning from wet-deposited N. Uptake of NH_4^+ by foliage and stems in several studies was greater than uptake of NO_3^- (Bowden et al. 1989, Brumme et al. 1992, Eilers et al. 1992, Garten and Hanson 1990, Lumme 1994, Pearson and Stewart 1993, Wilson 1992). The literature reports conflicting results regarding preferences of forest species for root uptake of NH_4^+ or NO_3^- . In general, NH_4^+ appears to be the preferred ion for root uptake in acidic soils (Haynes 1986, Haynes and Goh 1978, Krajina et al. 1973, McFee and Stone 1968, Pang 1985, Schulze 1989, Van Den Driessche 1971). Tree and grass species from calcareous soils, such as in the

San Bernardino Mountains, generally prefer NO_3^- as a N source (Haynes 1986, Krajina et al. 1973, Pang 1985, Raven 1988). Haynes (1986) suggests that for the majority of plant species a predominance of NO_3^- plus lower amounts of NH_4^+ in soil, such as occurs in the San Bernardino Mountains (Fenn and Poth 1994), produces the greatest growth. In forests of the SCAB, deposition of NO_3^- is several-fold greater than deposition of NH_4^+ (Bytnerowicz et al. 1987a, 1987b, Fenn and Bytnerowicz 1993). Nitrate concentrations in soil solution and in soil extracts at a high-pollution site in the San Bernardino National Forest were 14 to 44 times higher than those at moderate- and low-pollution sites (Fenn et al. 1995). The high NO_3^- availability in soil of the high-pollution sites may favor plant species which prefer NO_3^- as a N source.

The main objectives of this study were (1) to determine the fate of N deposited in fog to a simulated pine seedling/forest-floor/mineral-soil system, (2) to determine if foliar and root uptake of N deposited from fog contribute significantly to the N requirements of ponderosa pine seedlings, and (3) to compare crown and root uptake of wet-deposited NO_3^- and NH_4^+ in ponderosa pine.

MATERIALS AND METHODS

SEEDLING PREPARATION AND SOIL TREATMENTS

Two-year-old ponderosa pine seedlings from the Chico Tree Improvement Center in Chico, CA, were transplanted in November 1990 into black polyethylene pots 18 cm in diameter and 40 cm deep. Each pot contained approximately 11 kg of mineral soil collected near Green Valley Lake in the San Bernardino Mountains. The seedlings were maintained in an air-conditioned greenhouse receiving charcoal-filtered air.

Seedlings were randomly assigned to one of six exposure chambers. Ten seedlings with soil overlain with litter were placed in each of two control chambers receiving unlabeled acid fog. Each of the four remaining exposure chambers used for ^{15}N -labeled fog was assigned: (1) 11 seedlings with plastic covering the soil to exclude fogwater, (2) 11 seedlings with the soil overlain with L-litter (relatively fresh needle litter) and F-litter (partly decomposed plant residues, generally recognizable as to origin, Green et al. 1993), (3) 14 seedlings with bare soil, and (4) 10 seedlings killed by heating the potted plants in an oven (70°C for 2.5 hr) prior to the fog treatments (Table 2). Dead seedlings were included to determine the extent of physical adsorption of $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ to the plant components, although microorganisms colonizing dead tissues could also contribute to ^{15}N retention in dead plants (Lovett and Lindberg 1993).

The litter-overlay treatment consisted of 65 g of air-dried F-litter placed on the surface of the mineral soil, and 40 g of L-litter placed on top of the F-litter layer. The litter used in this study was collected at Camp Paivika, a site near Crestline, CA, on the western end of the mixed conifer forest zone in the San Bernardino Mountains. All seedlings were placed in open-top chambers one day prior to the acid fog treatments.

ACID FOG EXPOSURE

Seedlings were exposed to acid fog in six modified open-top chambers 3.0 m in diameter and 2.4 m tall (Hogsett et al. 1985) under ambient environmental con-

ditions at the Forest Fire Laboratory in Riverside, CA. Atomized fog was emitted into the chambers at an angle perpendicular to chamber walls by four nozzles mounted equidistantly around the inside perimeter of each chamber 1.5 m above the chamber bottom.

The acid fog mixture used in this study simulated fog chemistry measured in a pine forest at Henninger Flats 25 km northeast of Los Angeles (Table 1; Hogsett et al. 1989, Waldman et al. 1985). The pH of the acid fog solutions was adjusted to 3.1 with 0.5 N NaOH. The simulated fog mixtures contained 1.46 mEq

TABLE 1.

Nitrate and ammonium concentrations ($\mu\text{Eq L}^{-1}$) in fog and rain from various sites in the Los Angeles Basin.

Location	Landscape ^a	NO_3^-	NH_4^+	Reference
Fog				
Riverside (simulated fog)	Exposure ^b chamber	1460	580	This paper
Henninger Flats	Pine forest 780 m	1472 (161–16300) ^c	579 (62–7420)	Waldman et al. (1985)
Los Angeles area—3 sites	Urban	(130–12000)	(370–7870)	Waldman et al. (1982)
Los Angeles area—3 sites	Urban	(252–7900)	(759–2860)	Jacob et al. (1985)
Los Angeles basin—16 sites	Urban	1110 (581–2928)	1580 (420–4260)	Brewer et al. (1983)
Riverside	Urban	(7050–17400)	(9588–22926)	Munger et al. (1990)
Rain				
Tanbark Flats	Chaparral- montane 800 m	(13–20)	(9–14)	Young et al. (1988); Blanchard and Tonnessen (1993)
Mt. Wilson-San Gabriel Mts.	Pine forest 1740 m	10	8	Blanchard and Tonnessen (1993)
San Gabriel and San Bernardino Mts.—3 sites	Pine forest 1740–2067 m	(11–23)	(1–36)	Liljestrand and Morgan (1981)
Los Angeles basin—6 sites	Urban	(19–44)	(14–36)	Liljestrand and Morgan (1981)
Los Angeles basin—6 sites	Urban	(9–44)	(8–44)	Zeldin and Ellis (1984)
Los Angeles basin—6 sites	Urban	(14–25)	(19–45)	Blanchard and Tonnessen (1993)

^a Numbers in the landscape column are meters above sea level.

^b Fog solution addition rate was 2.2 mm hr⁻¹. ¹⁵N (99 atom% excess) addition rate was 99 $\mu\text{moles hr}^{-1} \text{ plant}^{-1}$.

^c Nitrate and ammonium concentrations in parentheses represent the range of values reported for that site or sites. Values not in parentheses are volume-weighted averages or median values for individual fog collection dates.

$\text{NO}_3^- \text{ L}^{-1}$ and $0.58 \text{ mEq NH}_4^+ \text{ L}^{-1}$, a 2.5:1 ratio of NO_3^- to NH_4^+ . This ratio is consistent with the concentrations and deposition of $\text{NO}_3^- + \text{HNO}_3$, and $\text{NH}_4^+ + \text{NH}_3$ in forests within the SCAB (Bytnerowicz et al. 1987a, 1987b, Fenn and Bytnerowicz 1993, Waldman et al. 1985). Two replicate chambers received acid fog with 99% excess $(^{15}\text{NH}_4)_2\text{SO}_4$ as the sole source of NH_4^+ , and two chambers received acid fog labeled with 99% excess $^{15}\text{NO}_3^-$ in the form of $^{15}\text{HNO}_3$ plus three $^{15}\text{NO}_3^-$ salts (Hogsett et al. 1989, Waldman et al. 1985). Two chambers received fog containing unlabeled NH_4^+ and NO_3^- in order to determine background levels of atom% excess ^{15}N .

Fog treatments were applied from 0600 until 1100 hr and again from 1500 to 2000 hr on each of three consecutive days from June 6 to June 8, 1991, for a total of 30 hr. Thirty hours of fog exposure represents 20% of the approximately 150 hr/yr of fog that occurs at the Henninger Flats area (Waldman et al. 1985). Chamber blowers were turned off during the fog exposures to prevent disturbance of fog deposition. At the end of each fog event, chamber blowers remained off for an additional hour. The average fog deposition rate for the six chambers was $15.7 \text{ L ch}^{-1} \text{ hr}^{-1}$ (equal to 2.2 mm hr^{-1}). We calculated the fogwater deposition velocity (rate of fog deposition per area of exposed surfaces) for our seedling/soil system to be 0.25 mm h^{-1} , which is similar to the conservative estimate used by Waldman et al. (1985) for fogwater deposition to pine canopies (0.20 mm hr^{-1}). The ^{15}N (99 atom% excess) addition rate was $99 \mu\text{mole hr}^{-1} \text{ plant}^{-1}$.

On June 10, 1991, all of the seedlings were returned to the greenhouse. The plants were watered weekly with no more than 900 ml of tap water to avoid saturating the soil and leaching N from the system. The foliage was not watered or washed after the fog treatments.

SAMPLE PREPARATION AND ANALYSIS

Plant harvest and soil collection from the pots began on September 18, 1991, and continued until September 26 (15 to 16 wk after the first fog event). Plant and soil samples were divided into the following fractions: current-year needles (91N) and stems (91S), previous-year needles (90N) and stems (90S), roots, soil, L-litter, and F-litter. Sample sizes are given in Table 2. Soil was collected by removing all of the soil from the pots, mixing the soil and subsampling the mixed soil. All plant and soil samples were oven-dried at 70°C for 24 hr. After drying, needles were

TABLE 2.

Number of plants (sample sizes) for each fog/soil treatment combination. For each combination, plants were divided among two replicate chambers.

Soil treatment	Fog treatment		
	$^{15}\text{NO}_3^- + ^{14}\text{NH}_4^+$	$^{14}\text{NO}_3^- + ^{15}\text{NH}_4^+$	$^{14}\text{NO}_3^- + ^{14}\text{NH}_4^+$
Bare	28	28	—
Litter-overlay	22	22	20
Plastic-covered	22	22	—
Heat-killed plants	20	20	—

separated from stems, and plant and litter samples were ground in a Wiley mill and weighed. Further subsamples of the dried soil were pulverized to fine powder in a Shatterbox pulverizer (Model 8511, Spex Industries Inc., Edison, New Jersey). Plant samples that were not ground sufficiently by the Wiley mill were also processed in the Shatterbox. The processed samples were analyzed for ^{15}N and total N by continuous-flow-isotope ratio mass spectrometry (Barrie et al. 1989) on a Europa Scientific Automated Nitrogen, Carbon Analysis-Mass Spectrometry system (Europa Scientific, Cincinnati, Ohio).

CALCULATIONS OF ^{15}N CONCENTRATIONS AND DEPOSITION

The concentration of N in the plant, litter, and soil samples that came from the NH_4^+ or NO_3^- in the fog was calculated as follows (Powlson and Barraclough 1993):

$$F = T(A_S - A_B)/A_F$$

where F is the concentration of N in the sample derived from labeled fog, T is the total concentration of N in the sample, A_S is atom% excess ^{15}N in the labeled sample, A_B is atom% excess ^{15}N in control samples exposed to unlabeled fog, and A_F is atom% excess ^{15}N in the labeled fog solutions (Powlson and Barraclough 1993). Atom% excess is defined as the atom% ^{15}N in a material minus 0.3663.

The amount of ^{15}N within the plant fractions as a result of fog deposition to the crowns was determined from ^{15}N analysis of the seedlings with plastic-covered soil. Root uptake of ^{15}N from fog was determined as ^{15}N uptake in plants with the crown and soil exposed (the bare-soil treatment), minus the ^{15}N content of plants with plastic-covered soil. We estimated the extent of botanical uptake (B) of N from fog as follows:

$$B = T - D$$

where T is the total ^{15}N content of the plant fraction, and D is the ^{15}N content of the corresponding fraction of the dead (heat-killed) plants.

We calculated the amount of ^{15}N deposited to the seedling crowns in order to determine the retention efficiency (percent of ^{15}N deposited from fog and retained in the plant at harvest) of the crowns for ^{15}N deposited in fog. We estimated fogwater deposition to the live crowns from the fogwater deposition velocity described above (0.25 mm hr^{-1}) and the average crown surface area of the seedlings. The surface area of the seedling crowns was estimated from measurements of the length and diameter of each needle fascicle and from stem segments from a subsample of 11 seedlings.

STATISTICAL ANALYSES

Plant and soil data in this study were analyzed by analysis of variance (ANOVA). Two designs were used, depending on the variable being analyzed. For analyses that distinguished the two ions (NO_3^- or NH_4^+) that were the alternative sources of labeled N (i.e., analyses of concentration, content, or proportion of ^{15}N within a given component of the system), the labeled ionic species was considered to be a full-chamber effect, with two replicate chambers at each level. Soil treatment (bare soil, soil covered with plastic, or soil overlain with litter) was a within-

chamber effect, applied independently to each pot. A split-plot approach was used for these situations.

For variables involving total N, or biomass, the ion that was the source of the labeled N was not relevant, so that all of the chambers were regarded as replicates of a common level of full-chamber treatment. In these cases the chambers were viewed as blocks, and only the within-chamber effects were tested.

Data were log transformed to stabilize variance. Pairwise contrasts were used to test differences among soil treatment levels for each ion, and for total N and biomass. For comparisons of the levels of ^{15}N content or concentration among different components of plant or soil, the observed differences were computed for each pot and then analyzed; for each set of such differences (representing a given ion and soil treatment), a Bonferroni adjustment for multiplicity was applied to the significance tests. All data analyses were performed with the PC-SAS software program (SAS Institute, Cary, North Carolina).

RESULTS

^{15}N CONCENTRATIONS

Concentrations of ^{15}N in plant tissue were an order of magnitude greater in plants with exposed soil (bare-soil and litter treatments) than in plants in which only the crown was exposed (Figure 1; $P < 0.01$ for the null hypothesis). Concentrations of ^{15}N were greater in current-year needles and stems than in older needles and stems and were greater in foliage than in stems of the same age (Figure 1). In seedlings with exposed soil, ^{15}N concentrations in the plant fractions were four to five times greater in the $^{15}\text{NO}_3^-$ treatment than in the $^{15}\text{NH}_4^+$ treatment (Figure 1; $P < 0.01$ for the null hypothesis). In seedlings with plastic-covered soil (application of ^{15}N to the crowns only), ^{15}N concentrations in the plant fractions were three to four times greater in the $^{15}\text{NO}_3^-$ treatment than in the $^{15}\text{NH}_4^+$ treatment (Figure 1; $P = 0.01$ to 0.09 for the null hypothesis). Likewise, in the heat-killed plants ^{15}N concentrations were two to seven times greater in the $^{15}\text{NO}_3^-$ treatment than in the $^{15}\text{NH}_4^+$ treatment.

DISTRIBUTION OF FOG-APPLIED N

The ^{15}N content (biomass \times ^{15}N concentration) within the various fractions of the plant/soil/litter system is presented in Figure 2. The lowest ^{15}N content was nearly always in the 91S fraction because of the low biomass of the 91S. Absolute values for ^{15}N content were high in the soil, and to a lesser degree in the root fractions, relative to the other fractions. Differences in ^{15}N content between roots and soil and most of the other fractions were not statistically significant, presumably because of variability among the seedlings in the size of the plant fractions. In the litter-overlay soil treatment, 54% of the ^{15}N ($^{15}\text{NH}_4^+ + ^{15}\text{NO}_3^-$) applied to the plant/soil systems in fog was in the plant fractions (crown and roots), 9% in litter, and 37% in soil. In the bare-soil treatment 57% of the ^{15}N was in the plant tissues and 43% in soil.

PERCENT NITROGEN FROM ACID FOG

In current-year crown biomass (91N + 91S), 9.4%, and 8.7% of the total N originated from fog (mass-weighted average) in plants of the litter-overlay and

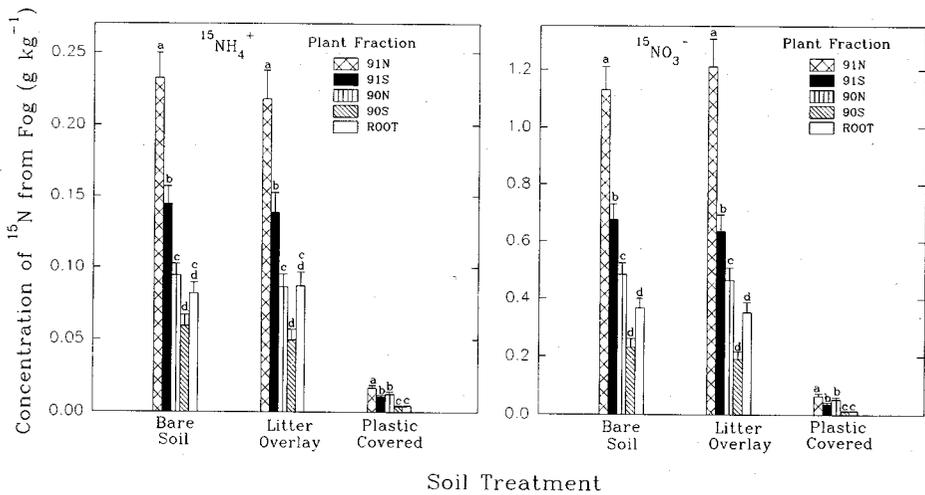


FIGURE 1. Concentrations of ^{15}N from fog in ponderosa pine seedling fractions, exposed to fog containing $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$. Error bars represent one standard error. Letters above the bars indicate significant differences ($\alpha = 0.05$; Bonferroni adjusted within each combination of ion and soil treatment) between plant components within a given soil treatment. 91N = 1991 needles, 91S = 1991 stems, 90N = 1990 and older needles, 90S = 1990 and older stems, and ROOT = all roots.

bare-soil treatments (Figure 3). Total N in older crown biomass (90N + 90S) originating from acid fog was 6.3% and 6.7% in the litter-overlay and bare-soil treatments. In the covered-soil treatment, the percentage of total N from fog in the soil and plant fractions was significantly lower than in the bare-soil or litter-overlay treatments ($P \leq 0.001$ for $^{15}\text{NO}_3^-$ and $P \leq 0.04$ for $^{15}\text{NH}_4^+$). Fog contributed 0.5% to 0.6% of the total N in the aboveground plant parts in the covered-soil treatment (Figure 3).

Less than 0.7% of the total N in the L-litter, F-litter, and soil fractions came

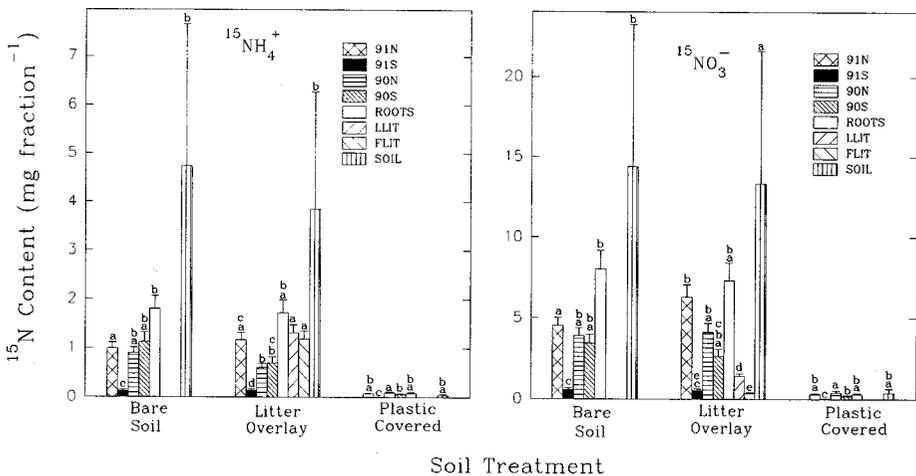


FIGURE 2. Content of ^{15}N from fog within the components of the plant/litter/soil systems for the plastic-covered, bare-overlay, and litter-overlay soil treatments. Error bars and abbreviations are as described in Figure 1. LLIT = L-litter and FLIT = F-litter.

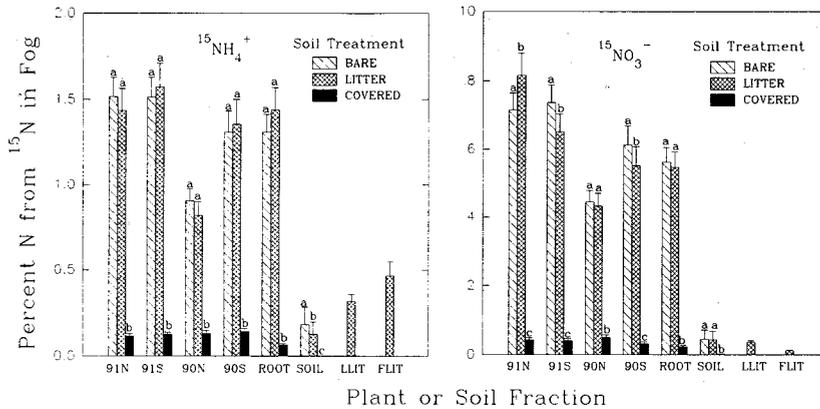


FIGURE 3. Percent of total N in plant tissue, soil, or litter originating from $^{15}\text{NH}_4^+$ - or $^{15}\text{NO}_3^-$ -labeled acid fog treatments. Soil treatments, error bars and abbreviations are as described in Figures 1 and 2. Letters indicate significant differences ($\alpha = 0.05$) between soil treatments within a given sample fraction.

from the acid fog treatments regardless of soil treatment ($^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ data combined; Figure 3). In soil, the percentage of total N from fog was higher in the $^{15}\text{NO}_3^-$ treatment than in the $^{15}\text{NH}_4^+$ fog treatment ($P < 0.01$) for each of the soil treatments (Figure 3). In the F-litter fraction, the percentage of total N from fog was higher in the $^{15}\text{NH}_4^+$ treatment than in the $^{15}\text{NO}_3^-$ treatment ($P < 0.04$), but no significant difference was found between the two N forms in the L-litter (Figure 3). The percentage of total soil N from $^{15}\text{NH}_4^+$ was lower ($P < 0.07$) in soil overlain with litter than in the bare-soil treatment (Figure 3).

CANOPY UPTAKE AND ADSORPTION OF ^{15}N

In the bare-soil treatment we estimated that physical adsorption + microbial uptake accounted for 3–9% of the ^{15}N content in the plant fractions (based on the ^{15}N content of the heat-killed plants). By comparison, in the plastic-covered soil treatment 50–100% of the ^{15}N content in the plant fractions was attributed to physical adsorption + microbial uptake. In the covered-soil treatment <0.3% of the total N content in the canopy fractions was attributed to botanical uptake by the crown, and <0.6% to physical adsorption + microbial uptake (Table 3). In the bare-soil treatment, 4.9–8.4% of total N content was attributed to botanical uptake and 0.3–0.5% to physical adsorption + microbial uptake (Table 3).

TOTAL NITROGEN CONCENTRATIONS

Total N concentrations in many of the plant fractions were often slightly greater when the soil was exposed to fog (Figure 4). Total N concentrations in the 91N ($P = 0.06$) and 90S ($P = 0.08$) fractions were slightly higher in the bare-soil treatment than in the litter-covered soil treatments. Total N concentrations were higher ($P = 0.001$ to 0.04) in the bare-soil treatment than in the plastic-covered soil treatment for all the plant fractions except the 91S fraction (Figure 4). Total N concentrations of soil did not differ among the bare-soil, plastic-covered, or litter-overlay treatments (Figure 4).

TABLE 3.

Percent of total N in plant fractions from botanical uptake, or physical adsorption + microbial uptake of $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ in fog.

Fraction	Botanical uptake ^a		Physical adsorption ^a + microbial uptake	
	$^{15}\text{NH}_4^+$	$^{15}\text{NO}_3^-$	$^{15}\text{NH}_4^+$	$^{15}\text{NO}_3^-$
Bare soil				
91N	1.48	6.84	0.03	0.26
91S	1.45	6.96	0.06	0.40
90N	0.83	4.05	0.08	0.39
90S	1.19	5.81	0.12	0.31
Root	1.24	5.18	0.07	0.44
Plastic-covered soil				
91N	0.08	0.19	0.03	0.24
91S	0.05	0.02	0.06	0.38
90N	0.02	0.10	0.09	0.40
90S	0.00	0.00	0.21	0.35

^a Botanical uptake refers to ^{15}N content per fraction minus ^{15}N content in the corresponding dead plant fraction. Physical adsorption + microbial uptake refers to the ^{15}N content of the plant fractions of the heat-killed seedlings.

PLANT BIOMASS

Current-year foliage was the only plant fraction for which soil treatment affected plant biomass. The average dry weight of current-year needles was higher in the litter ($P = 0.001$) and plastic-covered soil treatments ($P = 0.08$) than in the bare-soil treatment (Figure 5).

DISCUSSION

UPTAKE OF ^{15}N

Root uptake was the dominant pathway of ^{15}N input into the ponderosa pine seedlings. The amount of ^{15}N in the plant fractions was dramatically reduced when the soil was covered with plastic, thus preventing root uptake of ^{15}N . Sheppard et al. (1993) also reported reduced foliar N concentrations in red spruce (*Picea rubens* Sarg.) seedlings exposed to acid mist if the soil was covered with plastic. Of the ^{15}N measured in the aboveground tissue in the bare-soil treatment in our study, 92% was attributed to root uptake, 2% to crown uptake, and 6% was adsorbed to plant surfaces or assimilated by phyllosphere microorganisms. In the covered-soil treatment only 4.5% of the estimated ^{15}N deposited to the crowns was either adsorbed to or incorporated into plant tissue 16 wk after the fog exposures. Inefficient retention of wet-deposited $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ by pine foliage is presumably due to the epicuticular waxy layer and cuticle which cover pine foliage (Leyton and Juniper 1963, Scherbatskoy 1989).

In a number of studies of N uptake from fog or cloudwater (mainly seedling

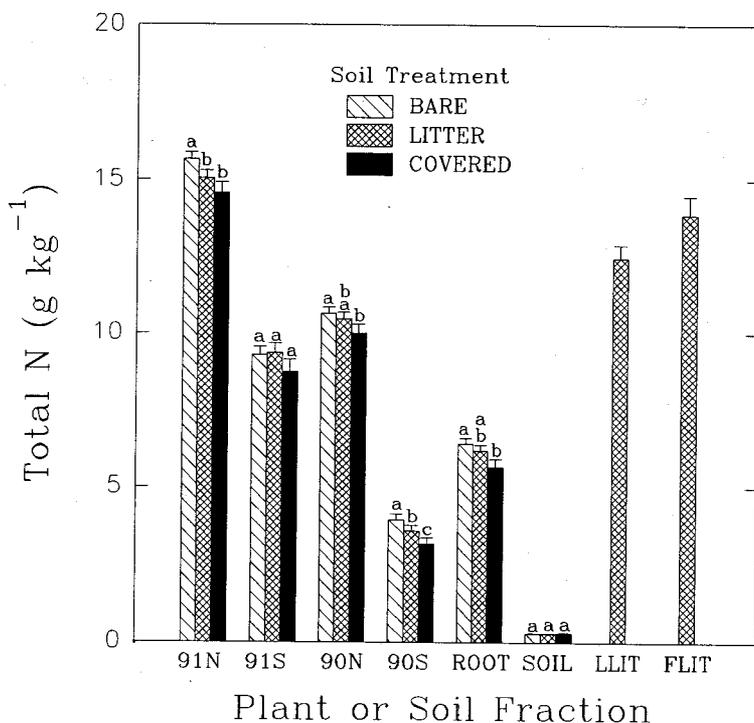


FIGURE 4. Total N concentrations by soil treatment in the components of the seedling/litter/soil systems exposed to acidic fog (data from the $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ treatments combined). Soil treatments, error bars and abbreviations are as described in Figure 1. Letters indicate significant differences ($\alpha = 0.10$) between soil treatments within a given sample fraction.

studies) canopy assimilation of atmospheric N often constituted a small but discernible fraction of the total foliar N content (Bowden et al. 1989, Lumme 1994, Thornton et al. 1990, 1992). Concentrations of N in red spruce seedlings at a high-elevation site in the southern Appalachians were higher in seedlings exposed to cloudwater than in seedlings with cloudwater excluded. The authors suggested that greater N concentrations in the exposed seedlings were likely due to foliar deposition and uptake of N from cloudwater (Thornton et al. 1990, 1992). Bowden et al. (1989) exposed the crowns of red spruce seedlings to acid mist labeled with $0.14 \text{ mM } ^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$. Extrapolating their results to yearly inputs at a high-elevation red spruce stand, they estimated that 1.3% of the N required for new foliar growth would be taken up by the crown as NH_4^+ and 0.3% as NO_3^- in cloudwater. Bowden et al. (1989) concluded that a small but significant portion of foliar N uptake in red spruce was attributable to direct movement into foliage and young twigs.

In our study only 0.24% of the N in new foliage and stems (after subtracting ^{15}N adsorbed to dead 91N and 91S) was supplied by deposition of N in fog to the crown. With more extended fog exposures, or possibly with plants in the field, greater crown uptake of N might have occurred. Bowden et al. (1989) exposed red spruce seedlings to simulated cloud water for 50 hr in 5 days, compared to 30 hr in 3 days in our study. In another study, exposure of red spruce seedlings to acid mist containing $0.15 \text{ mM } \text{NO}_3^-$ for 17 hr day^{-1} for 4 consecutive days did not induce nitrate reductase activity, although exposure to gaseous HNO_3 or NO_2 did

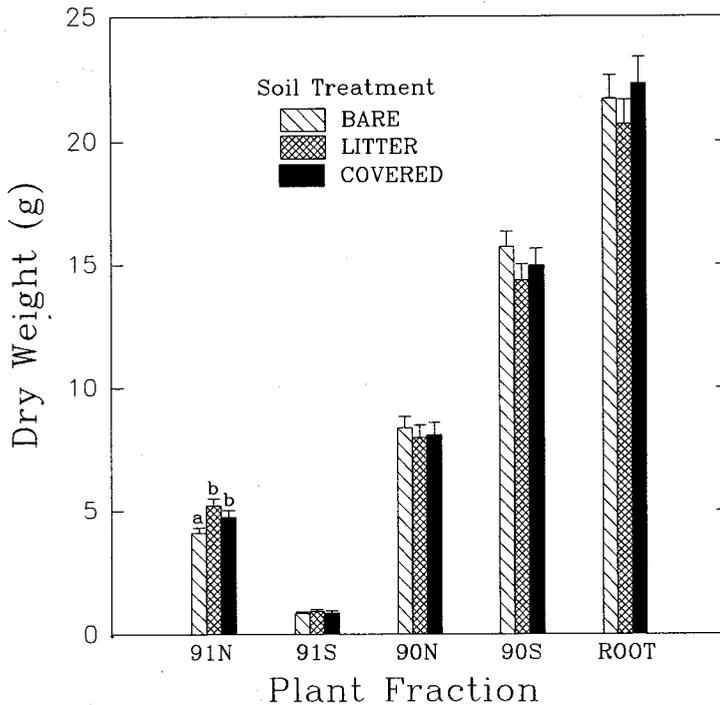


FIGURE 5. Dry weight of plant components by soil treatment (data from $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ treatments combined). Significant differences in dry weight between the soil treatments were found only in the 91N fraction ($P = 0.001$ for bare soil vs. litter; $P = 0.08$ for bare soil vs. covered). Abbreviations are as in Figure 1.

(Norby et al. 1989). It was suggested that very little foliar uptake of NO_3^- from mist occurred.

With longer exposures to high N concentrations in fog, greater canopy uptake of N can occur. Crown uptake of N from wet deposition to red spruce and Norway spruce (*Picea abies* Karst.) has been reported with deposition treatments applied for 12 to 20 wk (Eilers et al. 1992, Jacobson et al. 1989). A maximum of 5–7% of the total N in foliage was supplied by wet deposition of N to the crowns of young Norway spruce and beech (*Fagus sylvatica* L.) trees at nearly the same concentration as in our study. However, the treatments were applied 3 times a week for 4 to 5 months (Brumme et al. 1992, Eilers et al. 1992).

ION PREFERENCE

Our results indicate that NO_3^- was the preferred ion for root uptake in the ponderosa pine seedlings. Labeled N concentrations were four to five times higher in plants with soil exposed to $^{15}\text{NO}_3^-$ compared to plants with soil exposed to $^{15}\text{NH}_4^+$. However, the greater ^{15}N concentration in the $^{15}\text{NO}_3^-$ treatment is at least partially due to the 2.5:1 molar ratio of $^{15}\text{NO}_3^-$ to $^{15}\text{NH}_4^+$ in the acid fog mixtures.

Crown uptake rates were negligible in our study, and the preferred ion for canopy uptake of ^{15}N was unclear. Further studies are needed using equivalent concentrations of $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ in order to compare crown and root uptake

and assimilation of NH_4^+ and NO_3^- in ponderosa pine. It appears from the literature that forest canopies more effectively retain wet-deposited NH_4^+ than NO_3^- (Bowden et al. 1989, Brumme et al. 1992, Eilers et al. 1992, Garten and Hanson 1990, Jacobson et al. 1989, Lumme 1994, Pearson and Stewart 1993, Wilson 1992). Shoots of Norway spruce absorbed NH_4^+ from solution, but Scots pine (*Pinus sylvestris* L.) released NH_4^+ to the solution. Neither species demonstrated uptake of NO_3^- from solution (Wilson 1992). In throughfall studies NH_4^+ is commonly reported to be removed from precipitation by forest canopies. Nitrate is also removed from incident precipitation by forest canopies (Parker 1983, Potter et al. 1991). Lovett and Lindberg (1993) reported canopy consumption of atmospheric N in throughfall studies at 11 forested sites in North America and one in Europe. Consumption of NO_3^- was generally greater than for NH_4^+ on an absolute basis, but when expressed as a percentage of atmospheric inputs, canopy consumption varied from 10–90% with a mean of about 50% for each ion.

^{15}N DISTRIBUTION IN SEEDLINGS

Current-year biomass was the strongest sink for ^{15}N from fog, as evidenced by higher ^{15}N concentrations in 1991 needles and stems compared to older plant components. In Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) the concentration of ^{15}N from fertilization also increased from old to current growth (Pang 1985). In our study, ponderosa pine foliage accumulated higher concentrations of ^{15}N than stems of the same age. Similarly, foliage of beech (Brumme et al. 1992) and Norway spruce (Eilers et al. 1992) accumulated greater concentrations of ^{15}N than stems following prolonged crown treatment with solutions containing labeled N. However, Bowden et al. (1989) found greater ^{15}N concentrations in stems of red spruce seedlings than in foliage.

LITTER AND SOIL RETENTION OF ^{15}N

In the $^{15}\text{NH}_4^+$ treatment, the F-litter retained more ^{15}N ($P < 0.03$), and the L-litter retained similar levels of ^{15}N , than in the $^{15}\text{NO}_3^-$ treatment, even though $^{15}\text{NO}_3^-$ concentrations were 2.5 times that of $^{15}\text{NH}_4^+$ in the fog treatments. Litter in the $^{15}\text{NH}_4^+$ treatment apparently retained enough $^{15}\text{NH}_4^+$ from fog to result in lower ^{15}N levels in soil of the litter treatment compared to the bare-soil treatment. However, the reduction of ^{15}N in soil of the litter-overlay treatment in the $^{15}\text{NH}_4^+$ chambers was not great enough to affect concentrations of ^{15}N in the plant fractions. The greater affinity for $^{15}\text{NH}_4^+$ than for $^{15}\text{NO}_3^-$ of the partially humified F-litter, and possibly of the L-litter, is probably due to the high cation exchange capacity typical of humus and soil organic matter (Brady 1974). L- and H-pine litter have been shown to retain significant quantities of $^{15}\text{NH}_4^+$ after fertilization with ^{15}N -labeled urea (Foster et al. 1985, Nömmik and Popović 1971). Sitka spruce litter immersed in NH_4^+ solutions reduced the NH_4^+ concentration in solution due to litter retention of NH_4^+ (Duckworth and Cresser 1991). Chemical fixation of $^{15}\text{NH}_4^+$ in L- and H-litter of Jack pine (*Pinus banksiana* Lamb.) was greater than microbial immobilization of $^{15}\text{NH}_4^+$ (Foster et al. 1985).

In contrast to our results, Duckworth and Cresser (1991) found marked NO_3^- retention in the more humified F and H horizons of reconstituted organic soil profiles (L, F, and H layers) from a Sitka spruce (*Picea sitchensis*) forest in

northeast Scotland. The authors suggested that greater NO_3^- retention in the humified layers, compared to the L layer, may be due to differences in microflora populations and activities in adjacent soil layers, or due to modified drainage characteristics and longer contact time. Differences in NO_3^- retention characteristics between organic soil horizons in our California forests and in the Sitka spruce forest in Scotland are undoubtedly due to major differences in climate, vegetation, soil type, and forest floor characteristics.

Total N concentrations in soil were not significantly affected by the acid fog treatments in any of the treatment combinations. The total amount of N deposited from fog to the seedlings and soil amounted to 1.5% of the total soil N pool. This underscores the likelihood that the fog treatments contributed to total plant N content by increasing available N in the soil solution without significantly affecting the total N content of the mineral soil.

INPUTS AND UTILIZATION OF N FROM DRY, WET, AND FOG DEPOSITION

We hypothesize that the primary mechanism for plant utilization of wet-deposited N in coniferous forests entails: (1) scavenging of precipitation or fog by the canopy, (2) transport of N to the forest floor and into the soil as precipitation, throughfall, or stemflow, and (3) root uptake of a portion of the solubilized available N. Direct canopy uptake of N from precipitation or fog may be of lesser importance, except under conditions of prolonged canopy exposure to rain, fog or cloud water enriched with N.

The results of this study may have relevance to the processing of dry-deposited N in Western forests. Dry forms of N, and of other compounds, accumulate on vegetation, the forest floor, and on soil between precipitation events. Approximately 60–70% of dry-deposited N is typically washed from coniferous canopies by rain (Cadle et al. 1991, Hanson and Garten 1992, Lovett and Lindberg 1993, Marshall and Cadle 1989), and transported into the soil as throughfall (McColl and Bush 1978, Parker 1983, 1990). Thus, washoff of dry-deposited N follows a similar pathway as wet-deposited N for transport to the forest floor and rooting zone. Lovett and Schaefer (1992) and Potter et al. (1991) list factors affecting net throughfall fluxes including: the duration of rain and of the antecedent dry period, dry deposition rate, canopy cover, rainfall amount and intensity, chemical gradients between plant-surface water and plant tissue, and rainfall acidity. The application of $^{15}\text{NH}_4^+$ and of $^{15}\text{NO}_3^-$ in acidic fog solutions to ponderosa pine seedlings may grossly simulate the washing of dry-deposited NH_4^+ and NO_3^- from foliage and litter. Assuming that fogwater throughfall percolating into the soil is analogous to throughfall transport of accumulated dry-deposited compounds into the soil, we estimated the potential nutritional contribution of dry atmospheric N to current-year biomass. We calculated the amount of N which would accumulate from dry deposition onto the seedlings and to the soil surface if the seedlings were placed at a high-pollution (Camp Paivika, CP) and a low-pollution (Camp Osceola, CAO) site in the San Bernardino Mountains. These calculations were performed using the dry deposition flux rates for NO_3^- and NH_4^+ to ponderosa and Jeffrey pine trees at CP and CAO (Fenn and Bytnerowicz 1993). At CP, the calculated seasonal dry deposition of N to the pine seedlings and soil was 3.8 mmoles N plant⁻¹, which is similar to the 3.0 to 3.1 mmoles ^{15}N deposited from fog per plant/soil system in this study (bare-soil and litter-overlay treatments). The calculated dry

deposition to plants located at CAO for the 6 dry months of the "smog season" was 1.2 mmoles N plant⁻¹.

Our ¹⁵N wet-deposition data and calculations for dry deposition of N to ponderosa pine seedlings at CP suggest that fog deposition and dry deposition could each supply as much as 10% of the annual N content of current-year foliage. Wet deposition from rain and snow also contribute N to the forest ecosystem (Berg et al. 1991). However, in order for fog, wet and dry deposition combined to supply 20% of the annual N content of seedlings, N not absorbed by the canopy must be transported to the rooting zone when root activity and plant demand for N are favorable for N uptake and assimilation. Furthermore, competition for N with other plants and microbes, and ecosystem losses of N, must not be excessive.

Annual N inputs from fog, wet deposition, and dry deposition appear to be of similar magnitude at Camp Paivika, based on literature data (Fenn and Bytnerowicz 1993, and sources cited in Table 1 herein) and recent unpublished data from our laboratory on N concentrations in fog and wet deposition at Camp Paivika. However, fog incidence is not a common occurrence in all forested areas of the SCAB. Fog frequency varies according to location, elevation, and site-specific meteorological conditions. Likewise, the magnitude of N deposition from fog will vary considerably from site to site. On the other hand, chronic dry deposition of N is prevalent during the long dry "smog season" in all exposed sites located downwind of urban centers. More in-depth studies will be needed to quantify total N deposition, and the relative contributions of fog, wet, and dry deposition inputs in forests of the SCAB.

Background levels of total N deposition in remote montane sites in the western United States are generally 1–3 kg ha⁻¹ yr⁻¹ (Young et al. 1988). Total N deposition at 11 sites in North America ranged from 5–27 kg ha⁻¹ yr⁻¹, although only two of the sites had N deposition greater than 10 kg ha⁻¹ yr⁻¹ (Lovett and Lindberg 1993). Dry deposition of N at CP was estimated to be approximately 29 kg ha⁻¹ yr⁻¹, but wet deposition has not been well quantified at CP (Fenn and Bytnerowicz 1993). Fog deposition alone could represent an annual N deposition input of 26 kg ha⁻¹ at Henninger Flats near Los Angeles, based on the deposition rates to foliage and fog frequencies reported by Waldman et al. (1985), and assuming a stand total-sided leaf area index of 3.

ECOLOGICAL EFFECTS OF CHRONIC N DEPOSITION

Initially, elevated N deposition results in a positive growth response in N-limited ecosystems (Aber et al. 1989). However, chronic excess available N, from any combination of natural and anthropogenic sources, can lead to N saturation of forest ecosystems (Aber et al. 1989). An array of nutritional indicators support the hypothesis that N deposition over the last 40–50 yr at CP has contributed to N saturation (Fenn et al. 1995). Among the principal factors indicating a N saturated condition at CP are: sustained high concentrations of NO₃⁻ in the soil solution and in soil extracts, elevated emissions of nitric oxide from soil, high NO₃⁻ concentrations in foliage of understory and overstory species, high N:P ratios in foliage, and lack of a growth response to N amendments (Fenn et al. 1995).

The high potential for N saturation of natural ecosystems in the SCAB is further

demonstrated by persistently high NO_3^- fluxes in streamwater from chaparral watersheds experiencing chronic N deposition (Riggan et al. 1985, 1994). Long-term consequences of chronic N deposition at CP and other polluted sites in the SCAB are not known with certainty, but areas of concern include effects on forest health and composition, plant nutrition, soil chemistry, water quality, and greenhouse gas emissions (Aber et al. 1989, Ericsson et al. 1993, Fenn et al. 1995, Riggan et al. 1985, 1994, Schulze 1989).

CONCLUSIONS

The ^{15}N fog treatments provided 9.4% of the N in current-year crown biomass of seedlings in the litter-covered soil treatment. The main pathway for plant assimilation of fogwater ^{15}N was via root uptake of throughfall N. The total deposition of N to the seedling/litter/soil systems from simulated fog in the bare-soil and litter treatments (3.0 and 3.1 mmoles ^{15}N), plus the calculated dry deposition of N to ponderosa pine seedlings at a high-pollution site in the San Bernardino Mountains (3.8 mmoles ^{15}N) equalled approximately 20% of the N in current-year crown biomass. Further studies are needed in forests of southern California to determine the magnitude and effects of atmospheric N from fog, precipitation, and dry deposition on plant nutrition and health, soil chemistry and nutrient cycling, water quality, and trace N gas emissions. Manipulative studies and field investigations along air-pollution gradients in mountains of the SCAB may prove insightful in understanding the N retention capacity, and the primary processes of N retention in Mediterranean ecosystems.

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