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Increased Site Fertility and Litter Decomposition Rate in High-Pollution Sites in the San Bernardino Mountains

MARK FENN

ABSTRACT. Some possible factors causing enhanced litter decomposition in high-pollution sites in the San Bernardino Mountains of southern California were investigated. Nitrogen concentration of soil, as well as foliage and litter of ponderosa pine (*Pinus ponderosa* Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) were greater in high-pollution plots than in moderate- or low-pollution plots. Nitrogen concentration of soil, foliage, and litter of ponderosa pine (ozone-sensitive), and of the ozone-tolerant species, sugar pine (*Pinus lambertiana* Dougl.) and incense cedar (*Calocedrus decurrens* [Torr.] Florin.), were all higher at a higher pollution site than at a moderate-pollution site. The rate of litter decomposition for all three species was also greater at the high-pollution site. Results suggest that the primary factor causing enhanced decomposition of L-layer litter in high-pollution plots is greater site fertility, leading to the production of foliage and litter that is higher in N than litter from moderate- or low-pollution plots.

Although foliage of ponderosa pine trees exhibiting symptoms of severe ozone damage in high-pollution plots abscissed 2–4 years earlier than foliage of trees in low-pollution plots, retranslocation of N and P prior to needle abscission was not inhibited in high-pollution plots. Higher N levels in litter in the high-pollution plots does not appear to be due to reduced retranslocation of N from senescing foliage. Litter from ponderosa pine trees with severe symptoms of ozone damage (chlorotic mottle) decomposed at the same rate as litter from adjacent trees with no visible chlorotic mottle.

Treating ponderosa and Jeffrey pine litter from four plots with 2, 20, or 200 mM NH_4NO_3 significantly increased the rate of litter decomposition at one or more N concentrations in three of the four plots. Total CO_2 generated by the decomposing litter during a 15 or 17 day period tended to increase with N amendment, but was significantly increased only with litter from the dogwood plot treated with 200 mM NH_4NO_3. In some areas in the San Bernardino Mountains, chronic N deposition may stimulate litter decomposition by: (1) increasing site fertility, leading to higher concentrations of N in foliage and litter, and (2) accumulation of N onto litter and plant canopies, which stimulates litter decomposition upon wetting. FOR. SCI. 37(4):1163–1181.

ADDITIONAL KEY WORDS. Nutrient cycling, air-pollution gradient, ozone, nitrogen deposition, retranslocation of nitrogen.

THE MIXED CONIFER FOREST of the San Bernardino Mountains has been exposed to high levels of oxidant air pollution since the early 1950s. Ponderosa pine (*Pinus ponderosa* Laws.) is a principal component of the mixed conifer forest and has been seriously affected by oxidant air pollutants (Miller 1983). An ozone (O_3) gradient has been defined in the San Bernardino Mountains, with O_3 concentration decreasing from west to east (Miller 1983, Miller et al.

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1986). Pollutants other than O_3, such as N and to a lesser degree S compounds, also occur in the pollutant mixture to which mountains downwind of the Los Angeles Basin are exposed (Bytnerowicz et al. 1987a,b, Miller and Ryan 1977, Riggan et al. 1985).

The decomposition rate of L-layer needle litter of ponderosa pine and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) decreases along with pollution levels from west to east in the San Bernardino Mountains (Bruhn 1980, Bruhn et al. 1980, Fenn and Dunn 1989). A high correlation was found (r = 0.91) between N concentration of ponderosa and Jeffrey pine litter and the rate of CO_2 evolution from decomposing litter (Fenn and Dunn 1989). Fungal diversity was also significantly higher in the western, high-pollution plots. The principal factor(s) leading to higher N concentration, decomposition rates, and fungal diversity in litter of the western high-pollution plots were not determined (Fenn and Dunn 1989).

In this study, the following factors are evaluated for their possible role in causing higher N concentration in litter and increased litter decomposition rates in plots exposed to high-pollution levels in the San Bernardino Mountains: (1) higher soil N levels leading to foliage and litter with higher N concentrations, (2) ozone-induced premature foliar abscission or tissue damage, (3) reduced retranslocation of N due to ozone stress, or (4) increased input of N from atmospheric deposition. In some experiments the ozone-tolerant species, sugar pine (*Pinus lambertiana* Dougl.) and incense cedar (*Calocedrus decurrens* [Torr.] Florin.) were included along with ponderosa pine (ozone-sensitive) to compare nutrient concentrations of foliage and litter, and litter decomposition rates of species which differ in ozone sensitivity, but occur together in the mixed conifer forest across the air-pollution gradient.

MATERIALS AND METHODS

STUDY AREA

Plant and soil samples were collected from 11 plots located along an air-pollution gradient in the San Bernardino Mountains east of Los Angeles, CA (Figure 1). Not all 11 plots were sampled in every experiment, however. Nine of the 11 plots were initially selected in 1972 and 1973 as part of a large interdisciplinary study of the effects of air pollution on the mixed conifer forest in the San Bernardino Mountains (McBride and Miller 1977). The area containing the plots spans a west-east distance of 55 km, with O_3 concentration decreasing from west to east and from south to north (Miller et al. 1986). Plots were selected for this study based on 24-hr averages of O_3 concentration measured for 15 to 68 days during July and August of 1974 to 1978 (Miller 1983, Miller et al. 1986). A 24-hr average consists of hourly O_3 concentrations averaged over a 24-hr time period. Ozone concentrations have decreased slightly in the last 10–15 yr (Miller et al. 1986). For plots in which O_3 data were not available, O_3 concentration was estimated by interpolation or extrapolation, based on location of the plots in relation to nearby plots where O_3 was measured (Miller 1983, Miller et al. 1986). Plots were classified as receiving either a low-, moderate-, or high-pollution exposure based on three O_3 concentration ranges. Concentration gaps were purposely included between the three categories in order to ensure separation in O_3 concentrations between the three classes. Plots with 24-hr average concentrations of 196 μg

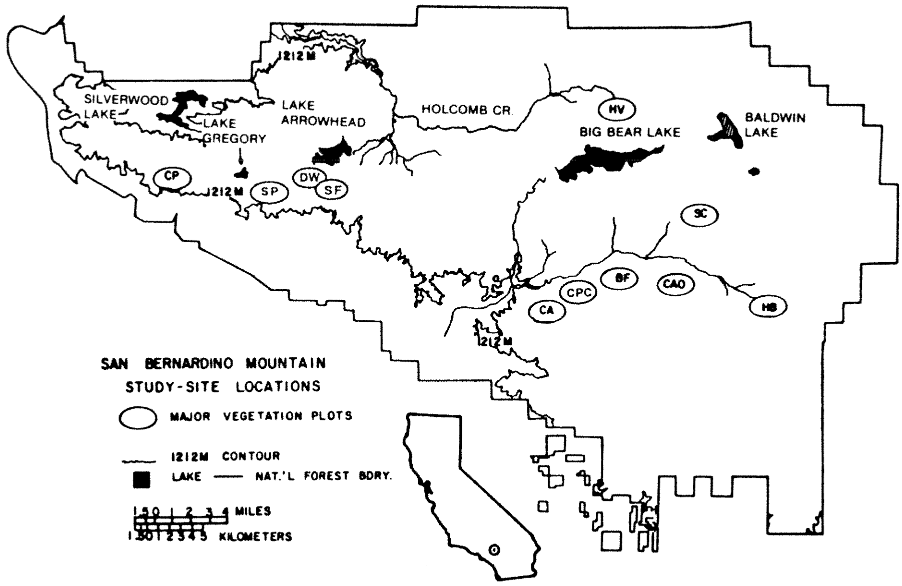

FIGURE 1. Locations of the 11 plots in the San Bernardino Mountains used in this study. Modified from Miller et al. 1986.

O_3 m^{-3} or greater were considered high. Plots with average O_3 concentrations of 118 to 157 μg O_3 m^{-3} were classified as moderate, and plots with exposures equal to or less than 98 μg O_3 m^{-3} were classified as receiving a low dose (Table 1). Along the west-east gradient total annual precipitation declines from 1100 mm near Lake Arrowhead to approximately 500 mm at Big Bear Lake (Miller 1983). Temperature decreases, and the dominant pine species shifts from ponderosa pine to the closely related Jeffrey pine along the same gradient.

N and P Concentration in Soil, Foliage, and Litter in Sites Across an Air-Pollution Gradient

Concentration in Soil

Total N and P concentration of soil from seven plots across the air-pollution gradient were determined. Soil was collected from two plots in each pollution category, plus from an additional moderate-pollution plot (CPC) where foliage and litter of three tree species were collected. At each of the plots, six soil samples were collected from randomly selected open spaces in the stand. Surface litter was removed, and mineral soil was collected from a depth of approximately 21–26 cm below the soil surface. Soil samples were placed into polyethylene bags and stored at 4°C until processing. Soil was sieved through a 2 mm mesh screen, and total N and P concentration of soil was determined by Kjeldahl digestion and subsequent analysis with a Technicon (Traacs 800) autoanalyzer.

Concentration in Foliage and Litter of Ponderosa and Jeffrey Pine

L-layer litter and foliage of ponderosa or Jeffrey pine were collected in October 1988 from 10 plots spanning the air-pollution gradient (Figure 1). Current-year

TABLE 1.

Pollution severity categories and estimated O_3 exposures of 11 plots traversing an air-pollution gradient in the San Bernardino Mountains.

Plot	Estimated O_3 concentration 24-hr average ($\mu g\ O_3\ m^{-3}$)[a]	Pollution severity category[b]
Camp Paivika (CP)	235	High
Strawberry Peak (SP)	216	High
Dogwood (DW)	196	High
Sky Forest (SF)	196	High
Camp Angelus (CA)	157	Moderate
Cedar Pines Camp (CPC)	137	Moderate
Barton Flats (BF)	118	Moderate
Camp Osceola (CAO)	98	Low
Heart Bar (HB)	59	Low
Sand Canyon (SC)	59	Low
Holcomb Valley (HV)	59	Low

[a] The 24-hr averages of O_3 concentration were measured for 15 to 68 days during July and August of 1974 to 1978. A 24-hr average consists of hourly O_3 concentrations averaged over a 24-hr time period. For plots in which O_3 data were not available, O_3 concentration was estimated based on their location along the O_3 gradient (Miller et al. 1986). Ozone concentrations have decreased slightly in the last 10–15 yr (Miller et al. 1986).

[b] Plots with 24-hr average concentrations of 196 $\mu g\ O_3\ m^{-3}$ or greater were considered high. Plots with average O_3 concentrations of 118 to 157 $\mu g\ O_3\ m^{-3}$ were classified as moderate, and plots with exposures equal to or less than 98 $\mu g\ O_3\ m^{-3}$ were classified as receiving a low dose.

(1988) foliage was collected from 20 trees (total tree height of 6–10 m) at each of the ten plots by pruning off a branch 2 to 3 m above ground level between the 1988 and 1987 needle whorls. One branch was sampled within each of the four geographic canopy quadrants per tree. L-layer litter was collected from under ten mature ponderosa or Jeffrey pine trees at the ten plots. Needles were collected from an area under the canopy within approximately 3 m from the base of each tree. Litter from each tree was mixed thoroughly, and a subsample was oven-dried at 70°C for 24 hr, and then ground in a Wiley mill. Green foliage was stripped from the branches, dried at 70°C for 24 hr, and ground in a Wiley mill. The concentration of N and P in litter and foliage was determined as described above for soil analysis.

Concentration in Soil, and Foliage and Litter of Three Tree Species

Foliage from ten ponderosa pine, ten sugar pine, and ten incense cedar trees, and six soil samples were collected in October 1989 at Camp Paivika (CP) and at Cedar Pines Camp (CPC). Camp Paivika is located on the western extreme of the air-pollution gradient and has a 24-hr average O_3 concentration of 235 $\mu g\ O_3\ m^{-3}$ during July and August (Miller et al. 1986). CPC is located approximately 36 km to the east and 8 km to the south of CP (Figure 1). It was chosen for this study because it is one of the more easterly and thus less polluted sites where ponderosa pine, sugar pine, and incense cedar trees are found together. Based on the location of CPC along the air-pollution gradient, it is estimated that the average 24-hr O_3 concentration during July and August is approximately 137 $\mu g\ O_3\ m^{-3}$. Current-year foliage was collected from ponderosa pine trees as described above. Foliage was collected from the sugar pine and incense cedar trees by pruning off

12–15 branch terminals from around the canopy of each tree at a height of 2 to 3 m above ground level. Soil samples were collected, and N and P concentrations of the soil and foliage were determined as described above. At both sites the combined foliage from each tree, and each of the six soil collections, were treated as replicate samples.

Litter was collected in April 1989 from under five replicate ponderosa pine and five replicate sugar pine trees at CP and CPC. Litter from incense cedar was collected by breaking off dead and dry foliage which was still attached to branches. When necessary, incense cedar litter was collected from several trees to obtain sufficient material for one replicate sample. Five replicate litter samples of incense cedar were collected at CP and at CPC. The concentration of N and P of the litter samples was determined as described.

Concentration in Foliar-Age Classes of Ponderosa and Jeffrey Pine

Nitrogen and P concentrations in ponderosa pine needles of different age classes were determined at two high-pollution sites (Camp Paivika and Strawberry Peak), and for Jeffrey pine needles at two low-pollution sites (Camp Osceola and Heart Bar). The purpose of this experiment was to compare retranslocation of N and P in trees growing on sites along the air-pollution gradient. Samples were obtained in November 1989 by pruning off two branches from each of seven replicate trees per plot. The branches were cut into sections, with one annual whorl per section, and stored in paper bags at room temperature for 2–4 wk. At CP and at Strawberry Peak (SP), seven replicate trees, which retained 2 years of live needles, were sampled. The current year's needles from 1989, and the previous year's needles from 1988, were green, while most of the 1987 needles which were still attached to the branch were dead. Many of the 1987 needles had already abscissed and fallen to the ground or onto lower branches. At Camp Osceola (CAO) and at Heart Bar (HB, low-pollution sites) two branches were collected from each of seven replicate trees that retained 4 years of green needles (1989, 1988, 1987, and 1986) plus dead but still attached needles from 1985. In many cases, the 1985 whorls also contained a few green needles. In all cases, live and dead needles from the same year were sorted and analyzed separately. At CP and SP, two branches per tree were also collected from seven to ten replicate trees that retained only 1989 (current-year) needles. In all experiments where total N and P concentrations of the foliar age classes were determined, each of the two branches sampled per tree were processed and analyzed separately. Values for the two branches per tree were averaged to obtain the result for each replicate tree. All needles were dried, ground, digested, and the total N and P concentration determined by Kjeldahl digestion and subsequent analysis.

Concentration in Mottled and Unmottled Foliage

In the experiments described above, some of the ponderosa pine trees exhibited varying degrees of visible ozone injury (chlorotic mottle). Moderate and severe chlorotic mottle was mainly observed on trees retaining only 1 to 2 years of foliage. In another experiment, foliage was collected from ponderosa pine trees which were selected based on the presence or absence of chlorotic mottle, in order to determine whether foliage with visible ozone injury differed in concentration of N and P from foliage with no visible injury. On November 21, 1989, seven pairs of adjacent ponderosa pine trees (companion trees) were selected at two high-pollution sites (CP and SP) in which one of the trees had foliage that was severely mottled and the other tree had little or no visible mottle on its needles. At CP, 1989 needles with severe chlorotic mottle were collected from trees that retained only the current year's (1989) needles. For comparison, needles from 1989 with little or no mottling were collected from companion trees which retained at least 2 years of live needles (1989 and 1988). At SP, 1989 needles rarely had symptoms of chlorotic mottle. For that reason, at SP severely mottled 1988 needles were collected from trees which retained 2 years of live foliage. Unmottled needles produced in 1988 were also collected at SP from trees which retained 3 years of live needles and which were adjacent to the mottled trees. From each replicate tree sampled in this study, five annual whorls were collected and combined to make a composite sample. Each of the seven composite samples per plot was dried and ground. Two subsamples of the ground tissue from each tree were digested and analyzed for N and P. Results from analysis of the two subsamples per tree were averaged to obtain the values for each replicate tree.

Rate of Decomposition of Litter from Sites across an Air-Pollution Gradient

Rate for Litter of Three Tree Species at a High- and a Moderate-Pollution Site

Decomposition rates were compared for litter of ponderosa pine, sugar pine, and incense cedar trees at CP (high pollution) and CPC (moderate pollution). Rates were determined 1, 8, and 15 days after wetting the litter, by measuring the rate of CO_2 evolution from litter. Litter was placed in PVC tubes (11.5 cm × 4 cm i.d.) and moistened with distilled water. The tubes were plugged on each end with polyester filter floss. Air was pumped through the tubes until the concentration of CO_2 in the airstream had reached equilibrium. The concentration of CO_2 in the air exiting the PVC tubes was then determined with an infrared gas analyzer, and the rate of CO_2 evolution per gram of litter was calculated (Fenn and Dunn 1989).

Rate for Unmottled and Mottled Foliage

To determine whether needles with severe chlorotic mottle decompose at a different rate than needles without mottle, 1-yr-old (1988) needles were collected from four pairs of adjacent ponderosa pine trees at Strawberry Peak, a high-pollution site, on August 17, 1989. Each pair of trees consisted of one tree with severe chlorotic mottle and one tree with slight or no visible chlorotic mottle on the 1988 needles. Mottled and unmottled foliage was collected instead of L-layer litter, because it isn't possible to differentiate litter originating from mottled foliage from litter originating from unmottled foliage. Three to four whorls were collected from each tree and placed into paper bags. The needles were allowed to dry in the greenhouse in paper bags for 4 weeks, at which time approximately 7 g of needles were placed into litter bags made of hardware cloth (1 mm mesh) bags. On October 13, 1989, the litter bags were taken to Camp Osceola, which is a low air-pollution site in the San Bernardino Mountains, and placed under a Jeffrey pine tree. A low-pollution site was selected for placement of the litter bags to avoid confounding effects of high levels of atmospheric deposition during field incubation. On February 2, 1990, the litter bags were brought back to the laboratory for determination of CO_2 evolution from the decomposing litter. Litter from each source tree was removed from the mesh bags and combined with other litter samples from the same tree. Five grams fresh weight of litter from each source tree were placed into each of five PVC cylinders. Other litter subsamples were also weighed, dried overnight at 70°C, and reweighed to determine litter moisture content. To determine decomposition rate, the litter was moistened with distilled water, and CO_2 evolution over time was measured as described. Values for CO_2 evolution rates of the five litter subsamples for each tree were averaged to obtain values for each of the four replicate trees per treatment. Measurements of CO_2 evolution were taken 1, 3, 5, and 10 days after wetting the needles. Two litter subsamples from each tree were dried, ground, and digested for determination of litter N and P concentration.

Rate for Litter Amended with NH_4NO_3

In November 1988, subsamples of the litter collected in October 1988 from under ten Jeffrey pine trees at the Holcomb Valley plot (low pollution) were combined. Subsamples of the litter collected from ten ponderosa pine trees at the Dogwood plot (high pollution) were also combined. From the composite samples, 3.5 g fresh weight of litter was placed into PVC tubes for incubation and measurement of CO_2 evolution over a period of 15 days as described above. In this experiment, however, four replicate litter subsamples per plot were sprayed to runoff with either distilled water, or 2, 20, or 200 m*M* NH_4NO_3 solutions. The litter needles were sprayed with the treatment solutions at the beginning of the experiment and again 8 days later. Treating litter with solutions of NH_4NO_3 is assumed to simulate the wetting (by precipitation) of ammonium and nitrate accumulated on litter surfaces from dry deposition, or the wetting of litter by throughfall containing nutrients washed from the overstory.

Measurements of CO_2 evolution were taken 2 hr, and 1, 3, 7, 8, 9, 11, and 15 days after the initial wetting of the needles. The total amount of CO_2 evolved during the experiment was estimated by multiplying the rate of CO_2 evolution at the end of each time interval times the duration of the interval. The amount of CO_2 evolved during the intervals was summed to determine the total amount of CO_2 evolved per gram of litter. This experiment was repeated in December 1988 with litter collected in October 1988 from ponderosa pine trees at CP (high pollution) and from Jeffrey pine trees at HB (low pollution). An additional measurement was taken 17 days after wetting in the experiment with litter from CP and HB.

Statistical Analysis of Data

Differences in the N and P concentration of foliage and litter from the various plots and within the various treatments were determined by performing analysis of variance and subsequent comparison by Tukey's test for means comparison. Effects of NH_4NO_3 on rates of litter decomposition were tested for significant effects by repeated-measures analysis of variance (Milliken and Johnson 1984). Pairwise comparisons of litter decomposition rates between the water-control treatment and the N treatments were tested for significant differences by use of single degree of freedom contrasts, as described previously (Fenn and Dunn 1989). Differences in the total amount of CO_2 evolved from litter treated with water or NH_4NO_3 were tested for significance by analysis of variance and by Tukey's test for means comparison.

The relationship between litter N concentration and CO_2 evolution, from decomposing needles of ponderosa pine, sugar pine, and incense cedar was tested with the Pearson correlation coefficient. Data for N concentration and CO_2 evolution of litter for all three species was combined for this analysis.

RESULTS

A listing of the experiments in this study, and the figures and tables where results are presented, is given in Table 2.

N and P Concentration in Soil, Foliage, and Litter in Sites Across an Air-Pollution Gradient

Concentration in Soil, and Foliage and Litter of Ponderosa and Jeffrey Pine

The N concentration of the soil samples, and of the foliage and litter from ponderosa and Jeffrey pine trees was significantly higher in the high-pollution plots as contrasted with the moderate- and low-pollution plots (Figure 2). However, pine foliage in the moderate- and low-pollution plots did not follow the trend of N deposition. The concentration of foliar N was significantly higher in the low-pollution plots than in the moderate-pollution plots (Figure 2).

No clear trend was apparent for P concentrations of soil, foliage, and litter of the three pollution categories. Soil in the low-pollution plots was significantly lower in P content compared with the high- and moderate-pollution plots (Figure 2). Foliar P concentration did not differ significantly between the high- and low-pollution plots, although foliage from the low-pollution sites were significantly higher in P than foliage from the moderate sites. Litter P concentration was not significantly different among the three pollution categories (Figure 2).

Concentration in Soil, and Foliage and Litter of Three Tree Species

Nitrogen concentration in the soil, as well as in foliage and litter of ponderosa pine, sugar pine, and incense cedar trees was significantly higher on a high-pollution site

TABLE 2.

Listing of the experiments in this study, and the table or figure where results of each experiment are presented.

A. Nitrogen and phosphorus concentration in soil, foliage, and litter in sites across an air-pollution gradient.
   1. Concentration in soil, and foliage and litter of ponderosa and Jeffrey pine in sites traversing the air-pollution gradient (Figure 2).
   2. Concentration in soil, and foliage and litter of ponderosa pine, sugar pine, and incense cedar at a high- (CP) and a moderate-pollution (CPC) site (Figures 3 and 4).
   3. Concentration in foliar-age classes of ponderosa and Jeffrey pine at two high-pollution sites (CP and SP), and at two low-pollution sites (CAO and HB, Tables 3 and 4, Figure 5).
   4. Concentration in mottled and unmottled foliage from ponderosa pine trees at Camp Paivika and Strawberry Peak (high-pollution sites; see text).

B. Rate of decomposition of litter from sites across an air-pollution gradient.
   1. Rate for litter of ponderosa pine, sugar pine, and incense cedar at a high- (CP) and a moderate- (CPC) pollution site (Figure 6).
   2. Rate for unmottled and mottled foliage of ponderosa pine from Strawberry Peak (see text).
   3. Rate of CO_2 evolution (Figure 7) and total CO_2 evolution (Table 5) during a 15- or 17-day period for litter from two low- (HB and HV) and two high-pollution (CP and DW) sites amended with NH_4NO_3.

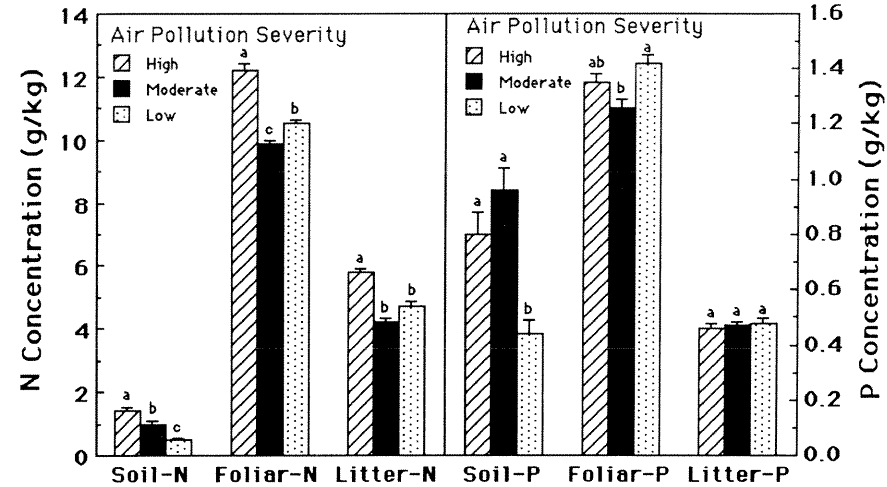

FIGURE 2. Concentration of N and P in soil, and in ponderosa and Jeffrey pine foliage and litter from plots exposed to high, moderate, and low pollution concentrations. Letters above the standard error bars indicate significant differences ($P = 0.05$) between air pollution categories (for a given variable) according to Tukey's test for means comparison.

(CP) compared to that found at a moderate-pollution site (CPC, Figure 3). Results of P analysis of soil, foliage, and litter of the three tree species at CP and CPC did not follow a similar trend (Figure 4). Soil collected from the high-pollution site was higher in P than soil collected from the moderate-pollution site. However, the

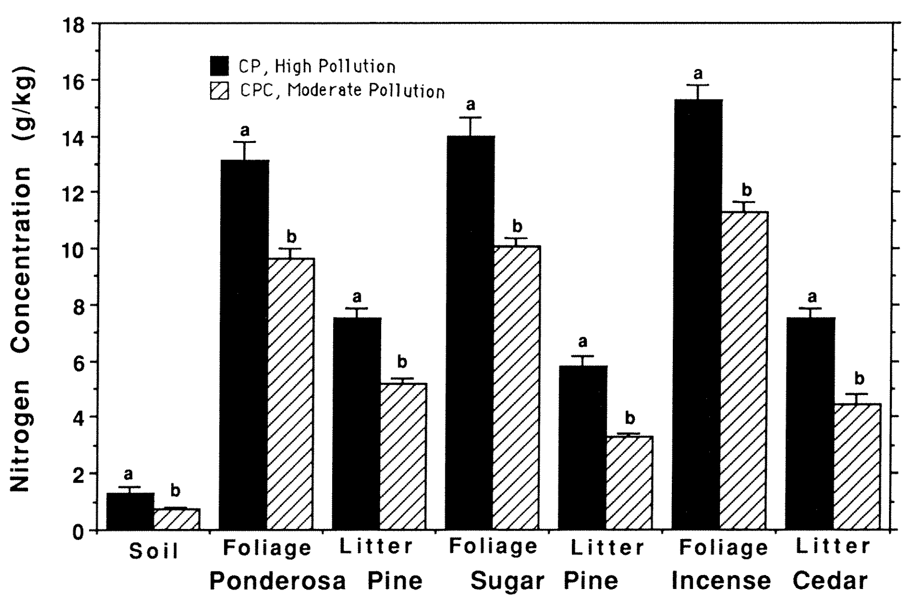

FIGURE 3. Nitrogen concentration in soil, and in foliage and litter of three tree species at Camp Paivika (CP, high-pollution site) and at Cedar Pines Camp (CPC, moderate-pollution site). Letters above the standard error bars indicate significant differences ($P = 0.05$) between sites, for a given variable, according to Tukey's test for means comparison.

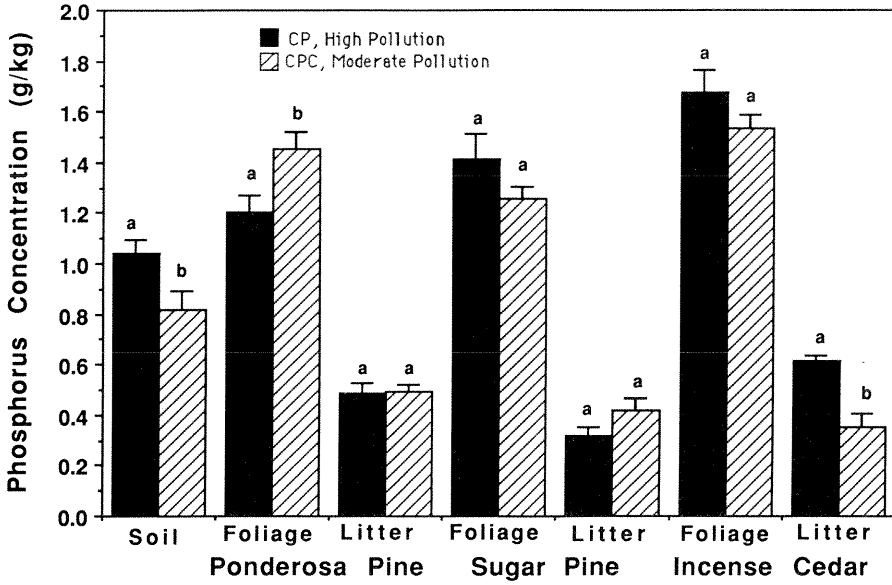

FIGURE 4. Phosphorus concentration in soil, and in foliage and litter of three tree species at Camp Paivika (CP, high-pollution site) and at Cedar Pines Camp (CPC, moderate-pollution site). Letters above the standard error bars indicate significant differences ($P = 0.05$) between sites, for a given variable, according to Tukey's test for means comparison.

concentration of P in foliage of sugar pine and incense cedar did not differ significantly at the two sites, while the P concentration of ponderosa pine foliage was higher at the moderate-pollution site. Phosphorus levels in litter from ponderosa pine and sugar pine were not significantly different at the two sites, but litter from incense cedar was significantly higher in P concentration at the high-pollution site (Figure 4).

Concentration in Foliar-Age Classes of Ponderosa and Jeffrey Pine

Ratios of the concentration of N in litter to the concentration of N in current-year (1988) foliage of ponderosa or Jeffrey pine trees ranged from 0.43 to 0.47 in ten plots of the three gradient location categories. Litter to foliage P ratios ranged from 0.33 to 0.37 in the same plots. Litter to foliar ratios for N and P did not differ significantly among the three gradient location categories.

Ratios of the concentration of N or P in dead needles still attached to a branch versus the concentration of N or P in current-year (1989) needles did not differ significantly at two high-pollution sites (CP and SP) compared with two low-pollution sites (CAO and HB, Table 3). The concentration of N and P in live 1987 foliage at the two high-pollution sites was more than twice that of dead 1987 needles that were still attached to the branch (Figure 5). This same trend also occurred with live and dead 1985 needles at the two low-pollution sites (Figure 5). In all cases, the largest drop in foliar concentration of N or P occurred between the oldest live foliage and the dead needles (Figure 5). The profile of P concentrations in the several age classes were almost identical at the high-pollution plots, as they also were at the low-pollution plots (Figure 5).

No significant differences were found in N concentrations of current year foliage

TABLE 3.

Ratio of N or P concentration in current-year needles (1989) to the N or P concentration of dead needles still attached to the branch, for ponderosa and Jeffrey pine.[a]

Plot	Air-pollution severity	Concentration ratio[b] Dead foliage[c]/current-year foliage	
		Nitrogen	Phosphorus
Camp Paivika	High	0.38	0.19
Strawberry Peak	High	0.37	0.16
Camp Osceola	Low	0.41	0.19
Heart Bar	Low	0.38	0.20

[a] Ponderosa pine trees were sampled at Camp Paivika and Strawberry Peak, and Jeffrey pine trees were sampled at Camp Osceola and Heart Bar.

[b] Ratios for foliage among the four plots were not significantly different for N or P ($P = 0.05$) according to Tukey's test for means comparison.

[c] Dead needles are 1987 needles for the high-pollution plots, and 1985 needles for the low-pollution plots.

from ponderosa pine trees retaining 1 or 2 years of needles at two high-pollution sites (CP and SP, Table 4). At CP the P concentration of the foliage between the two groups did not differ. At SP current year foliage from ponderosa pine trees retaining only the current year's growth contained significantly higher concentrations of P than current-year foliage from trees retaining 2 years of growth (Table 4).

Concentration in Mottled and Unmottled Foliage

Litter from four pairs of ponderosa pine trees (one of a pair with severe chlorotic mottle and one without) at a high-pollution site (SP) both contained 0.9 g P/kg. Nitrogen concentration was higher in the unmottled litter (11.2 g N/kg) compared to 9.3 g N/kg in mottled litter, but the difference was not statistically significant. In another experiment, seven pairs of trees with and without chlorotic mottle were sampled at two high-pollution sites (CP and SP). Once again, P concentration did not differ significantly between mottled (1.2 g/kg) and unmottled foliage (1.1 g/kg) at SP, while the concentration of N in the unmottled foliage (11.8 g/kg) was slightly higher ($P = 0.04$) than the N concentration of mottled foliage (10.9 g/kg) at SP. At CP, which is exposed to higher pollutant levels than SP, no differences were found in N concentrations between mottled (14.2 g/kg) and unmottled foliage (14.4 g/kg). Phosphorus concentration of both mottled and unmottled foliage from CP was 1.4 g/kg.

Rate of Decomposition of Litter from Sites across an Air-Pollution Gradient

Rate for Litter of Three Tree Species at a High and a Moderate Pollution Site

The decomposition rate for litter was significantly greater at the high-pollution site (CP) than at the moderate-pollution site (CPC) for litter of ponderosa pine, sugar pine, and incense cedar (Figure 6). Using the combined data of all three species,

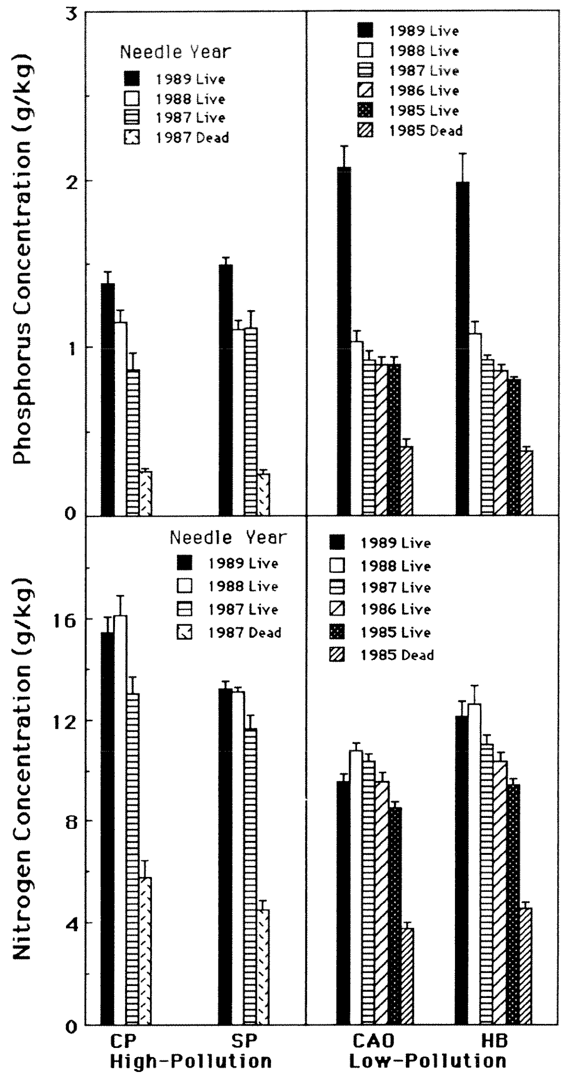

FIGURE 5. Nitrogen and phosphorus concentration in foliage from the various annual whorls of branches collected from Jeffrey pine trees at two low-pollution sites (HB and CAO), and from ponderosa pine trees at two high-pollution sites (CP and SP). The last year shown for each plot represents values for dead needles still attached to the branch. Error bars indicate standard errors. Data are from the same experiment as the data shown in Table 3.

a significant, positive correlation ($r = 0.90$) was found between litter N content and CO_2 evolution from litter needles.

Rate for Unmottled and Mottled Foliage

Litter from four pairs of ponderosa pine trees (one of a pair with severe chlorotic mottle and one without) at SP decomposed at similar rates. Rates of CO_2 evolution were determined 1, 3, 5, and 10 days after wetting the needles with water. Values for CO_2 evolution for unmottled and mottled foliage on the four respective

TABLE 4.

Nitrogen and phosphorus concentration of current-year needles (1989) from ponderosa pine trees retaining one or two years of live needles and growing on high-pollution sites.

	Nitrogen concentration[a] (g/kg)		Phosphorus concentration[a] (g/kg)	
Plot	1-yr retained	2-yr retained	1-yr retained	2-yr retained
Camp Paivika	16.2a	15.4a	1.5a	1.4a
Strawberry Peak	12.7a	13.2a	1.8a	1.5b

[a] Within a given plot, letters compare N or P concentration of current-year foliage from trees with one versus two years of live needles retained. Means with the same letter do not differ significantly according to Tukey's means comparison test ($P = 0.05$).

sampling dates were 49 and 58, 92 and 94, 119 and 115, and 96 and 104 (nmoles CO_2/g/min).

Rate for Litter Amended With NH_4NO_3

Treating litter with 20 mM and 200 mM NH_4NO_3 resulted in a significant ($P = 0.07$ and $P = 0.03$) increase in CO_2 evolution with litter from a high-pollution site (DW), compared with litter treated with water (Figure 7). Treatment of litter from DW with 2 mM NH_4NO_3 had no effect on decomposition rate. Litter from a low-pollution site (HV) decomposed significantly faster ($P = 0.03$) when treated with 20 mM NH_4NO_3 but not when treated with 2 or 200 mM NH_4NO_3, as compared to the rate when treated with water (Figure 7). In a subsequent experiment, treating litter from a high-pollution site (CP) with NH_4NO_3 did not increase the rate of CO_2 evolution, but treating litter from a low-pollution site (HB) with 20 mM NH_4NO_3 resulted in a significant increase ($P = 0.03$, Figure 7).

Cumulative totals of CO_2 evolved over the course of the experiment tended to increase with higher levels of NH_4NO_3. However, only litter from the Dogwood plot treated with 200 mM NH_4NO_3 generated significantly more CO_2 during the experiment than litter treated with water, according to Tukey's test for means comparison (Table 5).

DISCUSSION

Site Fertility, O_3 Sensitivity, and Decomposition Rate

The relatively high levels of N in soil, foliage, and litter of ponderosa pine in several high-pollution sites, and in foliage and litter of three species in a high-pollution site (CP), suggest that a greater supply of soil N in the high-pollution plots leads to higher N levels in foliage and litter. Previous workers have also reported higher N levels in soil in the high-pollution plots than in the low-pollution plots (Arkley et al. 1977).

In a previous study of ponderosa pine litter decomposition in the San Bernardino Mountains it was suggested that premature needle abscission induced by O_3

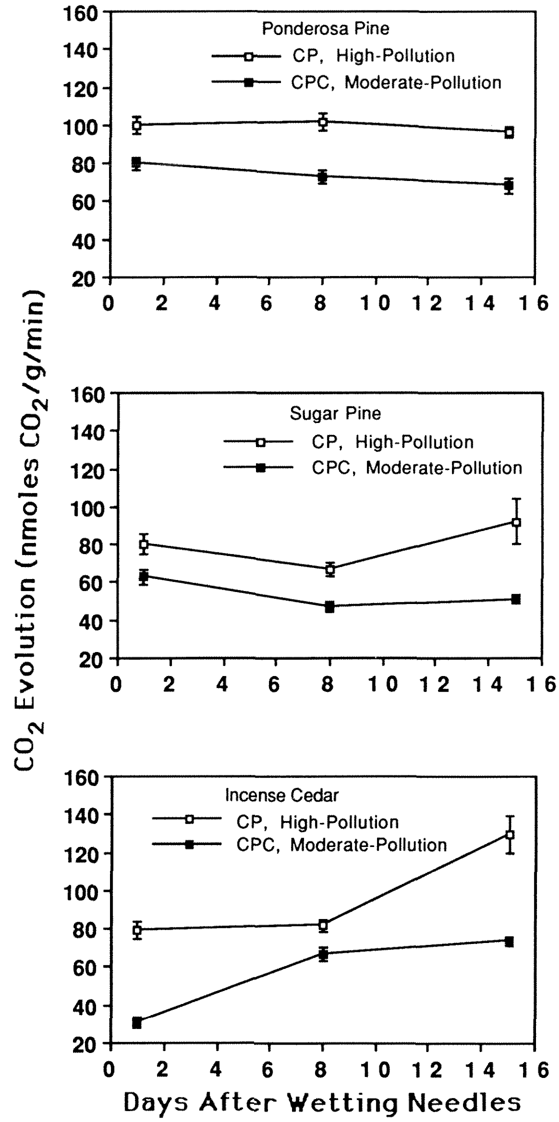

FIGURE 6. Decomposition rate of litter of three tree species collected from Camp Paivika (CP, high-pollution site) and Cedar Pines Camp (CPC, moderate-pollution site). Error bars indicate standard errors.

might also be an important factor leading to more nutrient-rich ponderosa pine litter in the high-pollution plots (Fenn and Dunn 1989). In the present study foliage and litter of sugar pine and incense cedar, which are relatively tolerant to O_3, were also higher in N at a high-pollution site (CP) compared to a moderate-pollution site (CPC). Litter of these ozone-tolerant species also decomposed faster at CP compared to litter from CPC. Thus, the increased rate of litter decomposition in the high-pollution plots does not appear to be related to the O_3 sensitivity or premature needle abscission of ponderosa pine, but rather, due to higher levels of soil N in the high-pollution plots.

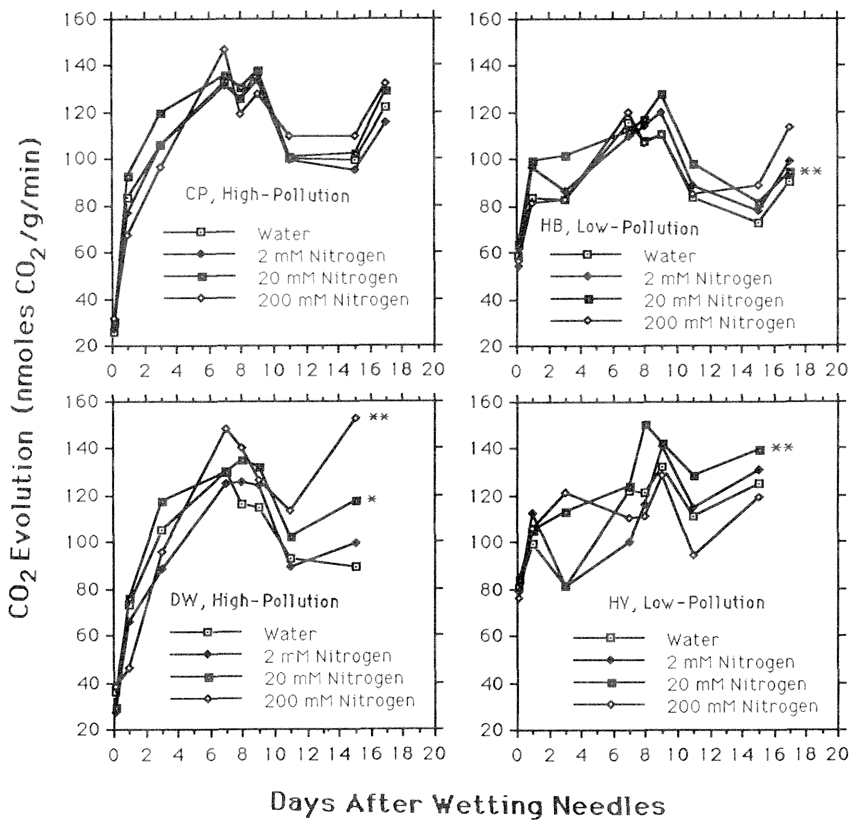

FIGURE 7. Decomposition rate for ponderosa pine (at CP and DW) and Jeffrey pine (at HB and HV) litter treated with water or NH_4NO_3. One asterisk next to line indicates that the decomposition rate was significantly different than litter from the same plot treated with water ($P = 0.1$), and two asterisks indicate significant differences at $P = 0.05$.

The increased rate of litter decomposition in the western plots, as indicated by measurements of CO_2 evolution (Fenn and Dunn 1989, and in the present study) are supported by a long-term field study in the San Bernardino Mountains. Litter weight loss and changes in litter nutrient content were greatest in plots exposed to high air-pollution levels (Bruhn 1980, Bruhn et al. 1980).

RETRANSLOCATION OF N AND P

Ozone injury to ponderosa pine trees could result in more nutrient-rich litter if retranslocation of nutrients from senescing needles to younger needles was reduced. However, the ratio of litter N and P to foliar N and P in ponderosa pine did not differ significantly between plots of the three gradient location categories. Also, the ratio of N and P concentration in dead needles versus the concentration of N and P in current-year needles was equal in two high- and two low-pollution plots.

Even though needles in the high-pollution plots abscissed 2–4 years earlier than those in the low-pollution plots, the greatest drop in foliar concentration of N and P at all the plots occurred just before or during needle senescence and death,

TABLE 5.

Evolution of carbon dioxide from ponderosa and Jeffrey pine litter treated with distilled water or NH_4NO_3.

Litter source plot	No. days	Total CO_2 evolution (mmoles CO_2/g)[a] Concentration of NH_4NO_3 (mmoles/L) 0	2	20	200	F[b]	P[c]
Camp Paivika	17	2.78A	2.71A	2.89A	2.90A	2.0	0.17
Heart Bar	17	2.25A	2.34A	2.45A	2.43A	1.2	0.34
Holcomb Valley	15	2.49A	2.42A	2.79A	2.44A	2.7	0.09
Dogwood	15	2.27A	2.26A	2.55AB	2.79B	7.6	0.004

[a] Within a given plot, letters compare total CO_2 evolution from litter treated with water or NH_4NO_3. Means with the same letter do not differ significantly according to Tukey's means comparison test ($P = 0.05$). Litter from Camp Paivika and Heart Bar was used in one experiment, and litter from Holcomb Valley and Dogwood was used in another experiment.

[b] F = F statistic.

[c] P = attained significance value.

regardless of needle age or severity of oxidant injury symptoms. The low concentrations of N and P in dead foliage attached to branches could have been partly due to leaching, but leaching is not likely to be highly significant as needles were harvested before the rainy season. The results of this study indicate that the higher levels of N in litter of the western high-pollution plots is due to factors other than reduced retranslocation of N from senescing foliage.

N Concentration and Decomposition of Mottled Foliage

Ozone injury to foliage does not appear to cause the increased N concentration of litter in the high-pollution sites, nor does ozone injury predispose litter to an increased rate of decomposition. The following results support these conclusions: (1) the concentration of N in mottled foliage was either equal to or slightly lower than in unmottled foliage at two high-pollution plots (CP and SP); (2) mottled and unmottled foliage from a high-pollution plot (SP) decomposed at the same rate; and (3) litter of ozone-tolerant species was also higher in N and decomposed faster in a high-pollution site.

In an earlier study in the San Bernardino Mountains it was reported that oxidant injury score of ponderosa and Jeffrey pine trees was correlated with litter needle size and concentration of N, P, and K (Arkley 1980, Arkley and Glauser 1980). Freshly fallen needles from ponderosa and Jeffrey pine trees with ozone injury were reduced in size and were higher in concentration of N, P, and K than needles from trees with little or no ozone injury. An inverse-dilution effect was suggested as the mechanism leading to higher concentrations of N, P, and K in ozone-damaged litter (Arkley 1980, Arkley and Glauser 1980). However, litter samples in this earlier study were collected from widely separated plots in the San Bernardino Mountains. The results may reflect the effects of significant variability across the pollution gradient in primary factors affecting plant growth, litter production, and litter nutrient content (e.g., rainfall, temperature, and soil characteristics). To reduce confounding effects of site variability in the present study, paired trees (one of which had severely mottled foliage and one of which did not) located adjacent to each other were sampled and compared for N and P concentration, and rate of decomposition.

N Deposition and Litter Decomposition

High levels of ammonium and nitrate are deposited in dry form to chaparral and coniferous forests in the (Los Angeles) South Coast Air Basin (Bytnerowicz et al. 1987a,b, Riggan et al. 1985). Litter in the high-pollution plots accumulate higher concentrations of N onto litter surfaces compared with the low- and moderate-pollution plots (Fenn and Bytnerowicz[1]). In the dry Mediterranean climate of southern California, summer rain events are frequently sporadic and few in number. During dry periods, moisture limits the rate of litter decomposition, and N compounds, and to a lesser extent S compounds, accumulate on plant and litter surfaces as a result of dry deposition. When precipitation falls, and if temperatures are favorable, litter decomposers and plants are stimulated by the newly available moisture. Nutrient uptake and other physiological processes of plants and decomposer organisms are probably further stimulated by nutrients in rain and throughfall, including nutrients from dry deposition dissolved by rain.

Treating litter from four plots with water or one of three concentrations of NH_4NO_3 yielded mixed results. In three plots the rate of decomposition was significantly increased by treatment with one or two levels of NH_4NO_3. The total amount of CO_2 generated during the course of the experiment increased with N amendment in most cases, but was significantly higher only with litter from Dogwood treated with 200 mM NH_4NO_3. While it is difficult to extrapolate results from short-term laboratory incubations to *in situ* litter decomposition, responses of litter to treatment with solutions of NH_4NO_3 may indicate short-term fluctuations in decomposition rate due to wetting and solubilization of pollutants on litter surfaces. The long-term, ecologically significant effects of N deposition on litter decomposition will depend on complex interacting factors such as dynamics and chemistry of throughfall and atmospheric deposition (wet and dry); duration and intensity of rainfall or snowmelt; the presence of other rate-limiting factors; and the amounts, residence time, and availability of nutrients on litter.

Possibly the most significant mechanism whereby chronic N deposition could affect the rate of litter decomposition is by increasing plant uptake of N, and thus the concentration of N in foliage and litter. It is not known to what extent atmospheric deposition of N pollutants in the San Bernardino Mountains affects site fertility, and thus N concentration of foliage and litter. Litter from high-pollution plots in this and in a previous study (Fenn and Dunn 1989) was higher in N, and decomposed faster than litter from moderate- and low-pollution plots. In a long-term field study in the San Bernardino Mountains, litter weight loss was greatest in plots exposed to high air-pollution levels, but the possible effects of chronic N deposition in the San Bernardino Mountains on litter decomposition was not investigated (Bruhn 1980, Bruhn et al. 1980).

Camp Paivika is located on the extreme western end of the pollution gradient and is exposed to higher levels of pollution than any of the other plots. Litter from CP decomposed at similar rates following treatment with water or 2, 20, or 200

[1] Fenn, M.E., and A. Bytnerowicz. Dry deposition of nitrogen and sulfur in the San Bernardino Mountains in Southern California. Submitted to the Journal of Environmental Quality.

mM NH_4NO_3, which may indicate that N is not rate-limiting for L-layer litter decomposition. The higher internal N concentration of litter from CP may have provided sufficient N so that treatment with NH_4NO_3 did not cause further stimulation of litter decomposition. It is also possible that the high levels of N, accumulated from dry deposition onto litter at CP (Fenn and Bytnerowicz[2]), contributed enough N upon wetting with water that treating the litter with additional N did not stimulate decomposition further.

Nitrogen from atmospheric deposition in some areas with elevated pollution loads has been shown to supply significant quantities of N in terms of the N budget of a forest (Aber et al. 1989, Lindberg et al. 1986, Swank 1984). The high atmospheric input of N in the western portion of the San Bernardino Mountains may supply N in sufficient amounts to increase foliar and litter N levels above that supplied by the normal processes of nutrient cycling in the absence of anthropogenic emissions. Zinke (1980) reported that the N concentration of foliage of big cone Douglas-fir (*Pseudotsuga macrocarpa* [Vasey] Mayr.) increased concurrently with air-pollution concentration along air-pollution gradients in the San Bernardino and San Gabriel Mountains near Los Angeles. The ratio of N to P in foliage of big cone Douglas-fir was an especially sensitive indicator of differences in nutrient concentrations across the air-pollution gradients (Zinke 1980). In the present study, concentrations of P in soil, foliage, and litter did not change as consistently or as dramatically as N concentrations across the air-pollution gradient in the San Bernardino Mountains. This suggests that atmospheric deposition of N may be an important factor contributing to higher concentrations of N in soil, foliage, and litter in the high-pollution sites.

CONCLUSIONS

The primary factor causing enhanced decomposition of L-layer litter of ponderosa pine, sugar pine, and incense cedar in the high-pollution plots seems to be greater site fertility, leading to the production of foliage and litter that is higher in concentration of N than foliage and litter in the moderate- and low-pollution plots. Chronic deposition of high levels of N may contribute to increased site fertility in the high-pollution plots. Litter decomposition may be further stimulated when N accumulated from dry deposition onto plant and litter surfaces is wetted by precipitation. Ozone damage to ponderosa pine foliage has no major effect on the rate of litter decomposition, and retranslocation of N and P is not inhibited in the high-pollution plots. The higher rate of litter decomposition in the high-pollution sites is expected to result in more efficient nutrient cycling in the high-pollution sites as nutrient release rates are also increased.

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[2] See footnote 1.

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AUTHOR AND ACKNOWLEDGMENTS

Mark E. Fenn is Research Plant Pathologist, USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Forest Fire Laboratory, 4955 Canyon Crest Drive, Riverside, CA 92507. The author thanks the Electric Power Research Institute who partially supported this work, and also Thomas Lawson, Joseph Johnson, and Donald Ferrin for technical reviews, David Randall for statistical review, and Roberta Burzynski for editorial review of the manuscript. Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.