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Litter Decomposition Across an Air-Pollution Gradient in the San Bernardino Mountains

Mark E. Fenn* and Paul H. Dunn

ABSTRACT

Air pollution may affect forest ecosystems by altering nutrient cycling rates. The objective of this study was to compare decomposition rates of L-layer litter of ponderosa pine (*Pinus ponderosa* Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) collected from across an air-pollution gradient in the San Bernardino Mountains in southern California. Litter from the more polluted western areas decomposed at a significantly ($P = 0.01$) faster rate than litter from plots in areas exposed to moderate or low pollution levels. The Shannon diversity index values for litter fungi were 1.41, 1.84, and 2.25 for plots in areas exposed to low, moderate, and high pollution levels. Nitrogen content of litter was greatest in the high pollution plots and was positively correlated with litter decomposition rate. Higher N and lower Ca content of litter at the more polluted western sites suggest that litter in the western plots originates from younger foliage than litter at the less polluted sites, possibly because of ozone (O_3)-induced needle abscission. Possible factors contributing to increased decomposition and fungal diversity in the western plots include: higher litter nutrient content because litter originates from younger foliage, higher soil N levels which may result in higher foliar N content, greater input of N from air pollution, and O_3 damage to needles creating favorable sites for microbial decomposers.

THE MIXED CONIFER FOREST of the San Bernardino Mountains, east of Los Angeles is a well-documented case of severe forest damage resulting from exposure to oxidant air pollution (Cobb and Stark, 1970; Miller, 1973, 1983; Taylor, 1974). An O_3 gradient occurs with O_3 concentration decreasing from west to east in the San Bernardino Mountains (Miller, 1983; Miller et al., 1986). Eighteen permanent plots that traverse the extremes of O_3 exposures occurring in the San Bernardino Mountains were established in the early 1970s (McBride and Miller, 1977; Miller, 1983). Ozone injury symptoms of ponderosa pine, i.e., chlorotic mottle of needles, reduced needle length, and low needle retention (Miller, 1973; Pronos et al., 1978) occur more frequently in the high-O_3 plots (Miller, 1983).

Pacific Southwest Forest and Range Exp. Stn., USDA-FS, Forest Fire Lab., 4955 Canyon Crest Drive, Riverside, CA 92507. Received 17 Oct. 1988. *Corresponding author.

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Although N deposition rates have not been determined across the San Bernardino Mountains, it seems likely that a gradient of N deposition is associated with the O_3 gradient. Recent studies indicate high deposition rates for N compounds in mountainous areas of the South Coast (Los Angeles) Air Basin (Bytnerowicz et al., 1987a,b; Riggan et al., 1985). Because pollutants other than O_3 are associated with "smog" (Miller and Ryan, 1977), in this paper the gradient is referred to as an air pollution gradient. Other parameters such as temperature, precipitation, solar radiation, elevation, vegetation, and soil properties also vary across the gradient (Arkley, 1977; Bruhn, 1980).

The litter layer under O_3-damaged trees in the San Bernardino Mountains is deeper than under trees with less O_3 damage (Arkley et al., 1977b; Miller, 1983). A previous field study in the San Bernardino Mountains indicated that litter weight loss was positively correlated with oxidant damage of litter source trees (Bruhn, 1980; Bruhn et al., 1980). Several characteristics of O_3 damage to ponderosa pine needles suggest that litter decomposition could be affected by O_3 exposure. The chemical and physical nature of pine needles could be sufficiently altered to create new habitats for microorganisms or to change the decomposability of the needles. Premature needle abscission results in younger litter needles which have more nutrients available for decomposer organisms (Hom and Oechel, 1983). Premature needle abscission would likely alter the normal microbial community succession on the phylloplane as well (Bruhn, 1980; Bruhn et al., 1980). Ozone could also directly affect the microorganisms inhabiting live needles or needles on the forest floor (Babich and Stotzky, 1974; Rist and Lorbeer, 1981).

The purpose of this study was to compare decomposition rates of L layer needle litter (undecomposed surface litter) from ponderosa and Jeffrey pine collected from across an air-pollution gradient in the San Bernardino Mountains. If litter decomposition in the San Bernardino Mountains is affected by exposure to O_3 and/or other air pollutants this could alter nutrient cycling and possibly add an additional stress to trees already stressed by air pollution, drought, competition, and pests.

Table 1. Descriptive characteristics of nine permanent plots traversing an air-pollution gradient in the San Bernardino Mountains.

Plot	Pine species†	Elevation, m‡	Estimated O_3 conc. 24-h average ($\mu g\ O_3\ m^{-3}$)§	Annual mean precip., mm¶	Annual mean temperature, °C#
Camp Paivika	PP	1600	235 (0.12 ppm)	580	
Dogwood	PP	1725	196 (0.10 ppm)	1070	
Sky Forest	PP	1720	196 (0.10 ppm)	1110	11.0
Camp Angelus	PP	1830	157 (0.08 ppm)	750	
Schneider Creek	PP	1853	137 (0.07 ppm)	620	
Barton Flats	PP + JP	1946	118 (0.06 ppm)	540	
Camp Osceola	PP + JP	2135	98 (0.05 ppm)	490	
Heart Bar	JP	2160	59 (0.03 ppm)	390	
Holcomb Valley	JP	2225	59 (0.03 ppm)	570	8.8

† PP refers to ponderosa pine and JP to Jeffrey pine.
‡ Elevation values for all plots except Barton Flats are from Arkley, 1977. Value for Barton Flats is from Miller and Ryan, 1977.
§ The 24-h averages of O_3 concentration were measured for 15 to 68 d during July and August of 1974 to 1978 (Miller et al., 1986). A 24-h average consists of hourly O_3 concentrations averaged over a 24-h time period. Values for Dogwood, Schneider Creek, Camp Osceola and Holcomb Valley were estimated based on their location along the O_3 gradient. Ozone concentrations have decreased only slightly or have shown little change in the last 10 yr (Miller et al., 1986).
¶ Long-term annual mean precipitation data are from Arkley, 1977. Precipitation values for Schneider Creek, Barton Flats, and Camp Osceola are estimated from comparisons of winter precipitation data for these three plots and long-term annual precipitation data for nearby plots (Arkley, 1977).
# Annual mean temperature data are not available for the plots. The temperature value for Sky Forest is from Lake Arrowhead which is 2.4 km north of Sky Forest. The temperature value for Holcomb Valley is from Big Bear Lake which is 4.8 km south of Holcomb Valley (Arkley, 1981).

MATERIALS AND METHODS

Study Area

Needle litter from the L layer used in these studies was collected from 9 of 18 permanent plots located along an air-pollution gradient in the San Bernardino Mountains east of Los Angeles, California (Fig. 1; McBride and Miller, 1977; Miller, 1983; Taylor, 1974). The 18 permanent plots were initially selected in 1972 and 1973. Plots selected were relatively homogeneous in regards to tree cover and contained at least 50 ponderosa or Jeffrey pine trees >10 cm DBH (diameter at breast height) (McBride and Miller, 1977). Ozone concentration decreases from west to east and from south to north (Table 1; Miller, 1983; Miller et al., 1986). The area containing the permanent plots spans a west-east distance of 55 km. 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; Fig. 1 and Table 1). Temperature decreases, and pine species shift from ponderosa pine to the closely related Jeffrey pine along the same gradient (Table 1).

The parent material of the soils in the permanent plots is partially weathered or decomposed granitic rock except for Camp Angelus and Heart Bar. Camp Angelus is mainly stony granitic colluvium while Heart Bar is primarily mixed alluvium derived from granitic and metamorphic rock (Arkley et al., 1977a). Soils in the San Bernardino Mountains are sandy with considerable very fine gravel (2–5 mm) (Arkley, 1981). In the three high-pollution plots (Camp Paivaika, Dogwood, and Sky Forest) soils are mainly coarse-loamy, mixed, mesic, Ultic Haploxerolls (Arkley, 1981). In these western plots soils are of the Shaver series, which is dark in

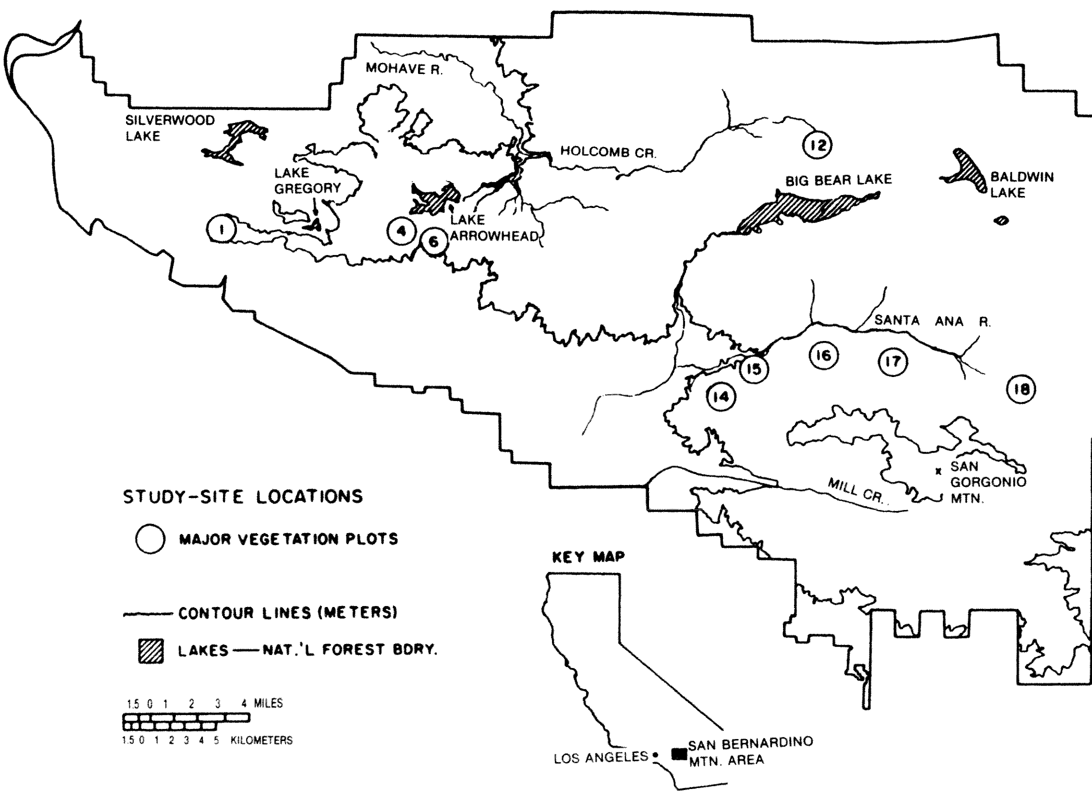

Fig. 1. Locations of the nine permanent plots in the San Bernardino Mountains used in this study. Reproduced from Miller, 1983.

color to a depth of greater than 50 cm with no significant clay accumulation in the subsoil (Arkley et al., 1977a; Lund and Page, 1973). Soil at the Camp Angelus plot (moderate pollution exposure) is a stony, coarse sandy loam. At the Schneider Creek plot (moderate pollution exposure) the soil is sandy-skeletal containing >35% fine gravel (Arkley, 1981). In plots toward the east at elevations >1900 m soils include coarse-loamy, mixed, frigid, Xerumbrepts and Xerochrepts (Arkley, 1981). In the low-pollution site in Holcomb Valley located 4.8 km north of Big Bear Lake, the soil is a sandy clay loam with subsoil clay accumulation at a depth of 25 to 50 cm (fine-loamy Argixeroll). Except for the soil at Holcomb Valley, all soils in the plots sampled in the present study, have weakly developed B horizons and become increasingly coarse textured with depth (Arkley, 1981). Carbon/nitrogen ratios were similar across the gradient and ranged from 21 to 29. In an earlier study the mean value for soil N content in the three high-pollution plots sampled in the present study was 820 mg N kg^{-1} soil, while soil from the three low-pollution sites averaged 440 mg N kg^{-1} soil (Arkley et al., 1977a).

Major overstory species associated with ponderosa or Jeffrey pine in the sampled plots are white fir (*Abies concolor* Gord. & Glend.), incense cedar (*Calocedrus decurrens* (Torr.), Florin.), California black oak (*Quercus kelloggi* Newb.), and sugar pine (*Pinus lambertiana* Dougl.). In the original 18 permanent plots, the average area covered by shrubs was 3.8% for western plots dominated by ponderosa pine, while eastern plots dominated by Jeffrey pine averaged 26% shrub cover (McBride, 1977). Understory fern layers are frequently more dense in the western plots exposed to high pollutant concentrations compared to plots exposed to moderate or low pollutant levels.

Plots were selected for litter collection based on 24-h averages of O_3 concentration measured for 15 to 68 d during July and August of 1974 to 1978 (Miller, 1983; Miller et al., 1986). A 24-h average consists of hourly O_3 concentrations averaged over a 24-h time period. Ozone concentrations have decreased only slightly or shown little change in the last 10 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 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. Three plots were chosen from each of the areas along the gradient classified as receiving low, moderate, or high O_3 concentrations. The Camp Paivika, Dogwood, and Sky Forest plots had 24-h averages of 196 μg O_3 m^{-3} (0.10 ppm) or greater and were considered high. Camp Angelus, Schneider Creek, and Barton Flats had 24-h averages of 118 to 157 μg O_3 m^{-3} (0.06–0.08 ppm) and were classified as moderate. The Camp Osceola, Heart Bar, and Holcomb Valley plots with 24-h average concentrations equal to or less than 98 μg O_3 m^{-3} (0.05 ppm), were classified as receiving a low dose (Miller et al., 1986) (Fig. 1). Although plots were selected based on O_3 concentrations, it is probable that other pollutants, such as N compounds, are associated with O_3 in the San Bernardino Mountains (Bytnerowicz et al., 1987a,b; Miller and Ryan, 1977; Riggan et al., 1985).

Carbon Dioxide Evolution from Litter

Because of environmental differences in the plots other than oxidant pollutant level, decomposition of litter from plots along the air-pollution gradient in the San Bernardino Mountains was studied under laboratory conditions. Litter decomposition rate was determined in the laboratory by measuring the amount of CO_2 evolved from moistened litter needles. In December 1986, L-layer litter needles were collected from under 10 mature ponderosa pine or Jeffrey pine trees at each of the nine plots. Five trees were randomly selected from each half of the plot. Needles were collected approximately 1 to 2 m from the base of each tree from the two opposing sides which appeared to have the thickest litter layer. Needles from the 10 trees per plot were combined, thoroughly mixed, and air dried at room temperature for 24 h. Four 3.5 g air-dry weight subsamples were taken from each plot sample and placed in a 11.5-cm-long section of PVC tubing (4-cm i.d.). The needles were sprayed with distilled water to runoff, and the ends of the PVC tubing loosely plugged with polyester filter floss to prevent the needles from falling from the tubes. The needles were then incubated at 24°C in the dark for 28 d. The needles were kept moist by spraying with distilled water to runoff twice weekly. The remaining needles were stored in plastic bags and held at 4°C and later sampled for isolation of fungi and for elemental analysis.

To determine CO_2 evolution, rubber plugs with a glass tube in the center were connected to both ends of the PVC tubes. Compressed air, bubbled through water, was pumped through the PVC tubes with a Masterflex[1] pump (model no. 7568, Cole-Parmer Instrument Co., Chicago, IL) at a flow rate of 13.0 mL min^{-1}. Preliminary experiments showed that the concentration of CO_2 from the pine needles had equilibrated after air had been pumped through the cylinders for 10 min. A syringe was used to sample the air stream exiting from the PVC cylinder after the 10-min equilibration period. One milliliter of the sampled air was injected into an infrared gas analyzer for determination of CO_2 content. The concentration of CO_2 was determined from a standard curve created by injection of known concentrations of CO_2. Carbon dioxide evolution was measured eight times over a period of 28 d.

Total N and P content of L-layer litter needles was determined by Kjeldahl digestion of needles and subsequent analysis with a Technicon (Traacs 800) autoanalyzer (Tarryton, NY). Calcium, K, Na, and Mg content of litter needles were determined by atomic absorption spectrophotometry after digestion with perchloric acid.

Species Diversity of Fungi of Decomposing Needles

Ten weeks after needle collection, fungi were isolated from the needles in order to compare fungal populations across the air-pollution gradient. The number of needle sections needed to obtain a representative subsample of the fungal community was determined in a preliminary experiment. Litter samples were cut into 2-cm sections and mixed. Approximately half of these sections were grouped into vials and washed five times with sterile distilled water on a horizontal shaker. Following the washes, 10 needle sections were taken from each of two vials from each plot and placed onto malt agar containing 30 μg mL^{-1} each of streptomycin sulfate and penicillin-G. The plates were incubated at room temperature for 5 d. An agar disk, 5 mm in diameter, was taken near the center and near the two ends of each needle, inverted, and placed onto a fresh plate of malt agar. After incubation, sporulating fungi growing from the inverted agar disks were identified. Nonsporulating fungi with distinctive cultural characteristics were also noted and given a descriptive name.

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

Diversity values of the Shannon index (Shannon and Weaver, 1949) were calculated for litter fungi from each plot sampled along the gradient and for the three combined plots within each of the three gradient location categories. For simplicity only index values computed after combining raw data from the three replicate plots for each category are presented.

Statistical Analysis of Data

Decomposition rates of litter from plots of the three gradient location categories were tested for significant differences by repeated-measures analysis of variance (Milliken and Johnson, 1984). Pairwise comparisons of litter decomposition rates between the three pollution categories along the gradient were tested for significant differences by use of single degree of freedom contrasts. Unless a Type H covariance structure (Huynh and Feldt, 1970) is found, adjustments must be made to attain valid significance levels in a repeated measures analysis. The quoted significance values for time and time × plot location are based on Huynh and Feldt's adjustment for violation of Type H covariances (Huynh and Feldt, 1976), and therefore do not assume a Type H structure. The relationship between litter nutrient content and CO_2 evolution from decomposing needles was tested with the Pearson correlation coefficient, and significance values were calculated using a one-tailed test and Fisher's *Z*-transformation. The numbers of the various fungi isolated from litter needles from plots located within the three gradient location categories were compared by Tukey's means comparison test. Differences in fungal diversity between the three gradient location categories were tested for significance using the *T*-test for comparing diversities based on the Shannon formula (Hutcheson, 1970; Zar, 1974) and the Bonferroni method for simultaneous tests with a familywise error rate of 0.05.

RESULTS

Litter Decomposition Rate

Repeated measures analysis of variance indicated significant differences ($P = 0.007$) in CO_2 evolution rates for litter form plots of the three gradient location categories (Table 2). Throughout the 28-d experiment, litter from the western high-pollution plots decomposed significantly faster than litter collected from plots located in areas exposed to moderate or low pollution levels, according to single degree of freedom contrasts ($P = 0.01$). Litter from all plots located in areas exposed to low or moderate pollution levels decomposed at similar rates (Fig. 2).

Elemental Composition of Litter

A significant, positive correlation ($R = 0.91$) was found between needle litter N content and CO_2 evolution from litter needles (Fig. 3). Needles from plots exposed to high levels of air pollution contained an average of 54% more total N than needles from plots exposed to low levels of air pollution. Calcium content of litter needles was negatively correlated ($r = -0.62$) with CO_2 evolution (Fig. 4). Needles from plots exposed to high air-pollutant concentrations contained an average of 46% less Ca than litter needles from plots exposed to low levels of air pollutants. Neither P, K, Na, nor Mg content of litter correlated well with CO_2 evolution rate from decomposing needles.

Table 2. Analysis of variance table for repeated-measures analysis of CO_2 evolution data presented in Fig. 2.

Source	DF†	SS‡	*F* §	*P* ¶
Gradient location category	2	12580.9	12.6	0.007
Error (between sites)	6	2992.5		
Time	7	95134.3	350.9	0.0001
Time × gradient location category	14	2048.1	3.8	0.0004
Error (within site)	42	1626.5		

† DF = degrees of freedom.
‡ SS = sum of squares.
§ *F* = *F* statistic.
¶ *P* = attained significance value.

Fungal Diversity

The Shannon index values for fungal diversity were 1.41, 1.84, and 2.25 for litter from plots exposed to low-, moderate-, and high-pollutant levels. Diversity values of the low and moderate plots were not significantly different ($P = 0.02$). Fungal diversity of litter from the western high-pollution sites was significantly

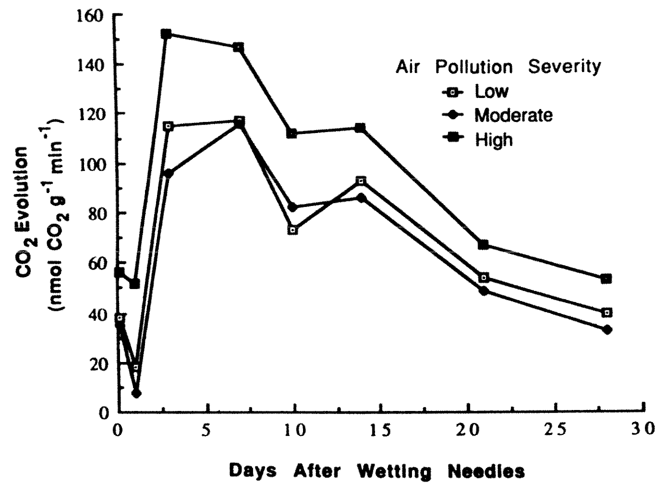

Fig. 2. Carbon dioxide evolution rate over time from decomposing needles of ponderosa and Jeffrey pine. Pairwise contrasts from a repeated-measures analysis of variance indicate that litter from the high-pollution plots had a significantly higher ($P = 0.01$) decomposition rate than litter from plots exposed to low- or moderate-pollutant levels.

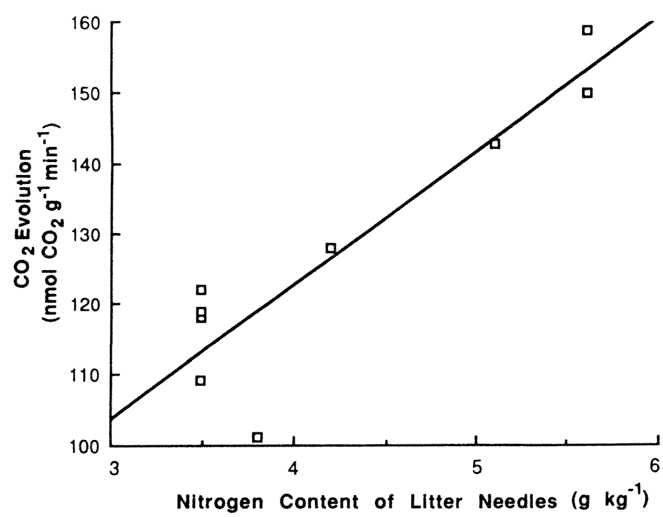

Fig. 3. Relationship between N content of pine needle litter and rate of CO_2 evolution from decomposing needles 1 wk after wetting. Correlation coefficient (r) was 0.91 ($P < 0.001$).

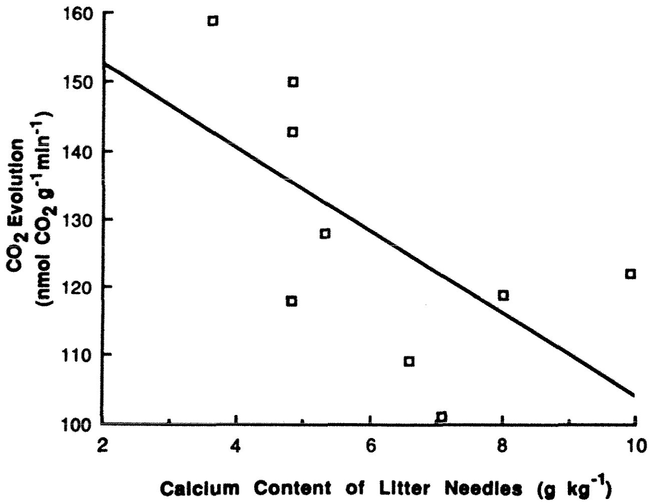

Fig. 4. Relationship between Ca content of pine needle litter and rate of CO_2 evolution from decomposing needles 1 wk after wetting. Correlation coefficient (r) was -0.62 ($P < 0.04$).

higher than diversity of litter from plots exposed to low and moderate pollutant levels ($P < 0.001$).

Decomposer Fungi

Aureobasidium pullulans (deBary) Arn. var. *pullulans* and *A. pullulans* (deBary) Arn. var. *melanigenum* Hermanides-Nijhof, var. nov. comprised 74% of the fungi isolated from the low-pollution plots, 61% of the fungi from the moderate plots, and only 11% of the fungi from the high-pollution plots (Table 3). An unidentified fungus with dark, sterile, knobby mycelium (DSK) constituted 32% of the fungi isolated from needles of the high-pollution plots, and was isolated consistently from needles of all three of the high-pollution plots. This fungus was isolated from litter collected at Schneider Creek but not from the other two moderate-pollution plots. The DSK fungus was not isolated from needles of the low-pollution plots (Table 3). *Alternaria alternata* (Fr.) Keissler was isolated from 4 to 7% of the needles from the low, moderate, or high plots. Nineteen other fungi were isolated from <5% of litter needles (Table 3).

Table 3. Isolation frequency of fungi from Jeffrey and ponderosa pine L layer litter collected from permanent plots traversing an air-pollution gradient in the San Bernardino Mountains.

Fungus	Mean number of fungal isolations per plot from plots of the three gradient location categories†			Minimum significant difference‡
	Low	Moderate	High	
Aureobasidium pullulans (deBary) Arn. var. *pullulans*	20.7	25.3	6.0	21.1
Aureobasidium pullulans (deBary) Arn. var. *melanigenum* Hermanides-Nijhof, var. nov.	31.3a	15.3b	2.7b	15.0
Dark septate knobby	0.0a	9.3ab	24.7b	19.2
Alternaria alternata (Fr.) Keissler	4.3	2.7	5.0	11.5
Gray crusty	1.7	2.0	3.7	11.3
White fuzzy sterile	0.0	2.3	3.0	8.6
Rhodotorula spp.	0.0	0.3	1.0	2.6
Dark green pycnidia former	0.0	0.0	2.7	4.4
Penicillium spp.	2.0	1.0	2.0	3.5
Cryptococcus spp.	0.7	0.7	0.7	2.5
Epicoccum purpurascens Ehrenb. ex Schlecht.	0.0	1.0	0.0	2.5
Amorphous mycelium	0.0	0.7	1.7	2.8
Sterile burnt olive	0.0	0.0	3.3	7.1
Sulcate white, yellow pigment	0.0	0.0	3.7	9.2
Greenish brown sterile	0.7	0.0	2.3	6.1
White, apricot reverse	0.0	0.0	1.7	4.2
White compact, sterile	0.0	1.0	0.7	1.7
Cladosporium cladosporioides (Fres.) de Vries	0.3	0.7	0.0	1.2
Cladosporium herbarum (Pers.) Link ex Gray	0.3	0.0	0.0	0.8
Tan concentric circle	0.0	1.7	0.0	4.2
Phoma spp.	0.0	0.3	0.0	0.8
Rubbery	1.0	0.0	0.0	2.5
Verrucobotrys spp.	1.7	0.0	0.0	4.2

† According to Tukey's test for mean comparison ($P = 0.05$), there were no significant differences in occurrence of individual fungi between the gradient location categories, except for those fungi whose data values are followed by one or more letters. Means with the same letter are not significantly different.

‡ According to Tukey's test for mean comparison ($P = 0.05$).

DISCUSSION

Increased Decomposition Rate

Fungal diversity and L-layer litter decomposition rate, measured as CO_2 evolution under controlled conditions, were greatest for litter from the western San Bernardino Mountains. This region of the San Bernardino Mountains is closer to Los Angeles and nearby cities and has higher air-pollution levels than areas to the east (Miller, 1983; Miller et al., 1986). In a previous field study using litter bags in the San Bernardino Mountains, litter weight loss and changes in litter nutrient content were also greater in plots exposed to high air-pollution levels (Bruhn, 1980; Bruhn et al., 1980). No definitive conclusions can be made regarding the mechanism(s) causing increased L-layer litter decomposition rate and fungal diversity in the western plots. Precipitation, temperature, elevation, soil properties, solar radiation, plant community composition, and probably pollutants other than O_3 also vary across the gradient. The litter decomposition studies reported here were done under controlled conditions to reduce environmental variation during the analysis. The differences in CO_2 evolution rate of needles collected across the gradient must therefore be due to conditions prevailing at the site of litter collection.

In the dry Mediterranean climate of southern California, moisture and litter N content are probably the main factors limiting decomposition of the exposed L layer. Litter from Camp Paivika decomposed faster than litter from any other site in this study, although Camp Paivika averages less precipitation than four of the other plots and approximately the same amount as two of the plots. Apparently factors other than precipitation levels are the main cause(s) of increased decomposition rate at the western sites. Litter from the western plots was highest in N content, suggesting that differences in litter decomposition rates may be determined primarily by the amount of available N in litter needles.

Tree species did not appear to be a major factor in determining litter decomposition rate. Decomposition was significantly faster with litter from the western high-pollution plots compared to the moderate-pollution plots, although pine species composition was nearly equal. Ponderosa pine was the predominant species in all three of the plots exposed to high-pollutant levels and in two of the three plots exposed to moderate-pollutant concentrations. The third moderate plot (Barton Flats) was a mixed stand of ponderosa and Jeffrey pine.

Soil Properties and Associated Vegetation

Differences in physical and chemical characteristics of soils across the air-pollution gradient may affect live needle nutrient content and subsequent litter quality. Except for the Holcomb Valley plot, soil in the three western high-pollution plots is of a finer texture than soils in the moderate- and low-pollution plots. Nitrogen content of soil in the high-pollution plots (820 mg N kg^{-1}) was nearly twice as great as in soil from the low-pollution plots (440 mg N kg^{-1}) (Arkley et al., 1977a). Greater N content of soils in the high-pollution plots may be contributing to the greater N content of live needles and subsequently of litter in the high-pollution plots.

Quantitative information on biological N fixation in the San Bernardino Mountains is not available. Nitrogen fixing plants such as *Lupinus* species and shrubs such as *Ceanothus* and *Cercocarpus* species, some of which are known to fix N (Hellmers and Kelleher, 1959), are found in the San Bernardino Mountains (McBride and Miller, 1977; Ohmart, 1980). However, it seems unlikely that biological N fixation is a major factor contributing to the higher soil and litter N levels found in the plots exposed to high-pollutant levels. Dense fern layers often dominate the understory in the high-pollution sites, while shrub cover, which probably includes N fixing species, is more prominent in the areas dominated by Jeffrey pine and exposed to lower pollutant concentrations (McBride, 1977).

Reduced Needle Retention and Altered Nutrient Content

An important factor, related to the increased N content and decomposition rate of litter in plots exposed to high O_3 concentrations, is that pine trees damaged by O_3 drop their foliage prematurely (Arkley and Glauser, 1980; Miller and Van Doren, 1982). Consequently, litter in high O_3 areas is likely to originate from younger foliage compared to litter in low O_3 areas. Younger needles are higher in N content than older needles (Bruhn, 1980; Hom and Oechel, 1983; Zinke and Stangenberger, 1981). Thus, litter in areas exposed to high levels of O_3 may contain more N. In fact, Arkley et al. found a higher rate of litter fall, more litter accumulation, and higher N content of litter needles under trees severely impacted by O_3 in the San Bernardino Mountains (Arkley, 1980; Arkley et al., 1977b).

In previous studies (Arkley, 1980; Arkley and Glauser, 1980; Bruhn, 1980) and in the present study, litter needles from trees exposed to O_3 contained less Ca than those from trees not exposed to high levels of O_3. Younger needles on a living branch of ponderosa or Jeffrey pine (Bruhn, 1980; Zinke and Stangenberger, 1981), or younger litter needles (Klemmedson et al., 1985), were lower in Ca content than older needles. The lower Ca and higher N contents of litter from the western plots indicate that litter in the western plots is from more recent annual needle whorls compared to litter from areas of low or moderate pollutant exposure. Needle age at the time of abscission is probably an important variable contributing to enhanced L-layer litter decomposition in areas of high pollutant exposure.

Increased Atmospheric Nitrogen Deposition

Chronic deposition of nitrogenous pollutants in the western plots provides an additional source of N for decomposer organisms via deposition of N directly onto litter or in throughfall. Bytnerowicz et al. (1987a,b) found a high input of nitrate (NO_3^-) and ammonium (NH_4^+) from dry deposition in the San Gabriel Mountains near Los Angeles, CA. Inorganic N in canopy throughfall in the San Dimas Exp. For. in Los Angeles County, CA was 2.5 to 16 times that reported for forests nationally (Riggan et al., 1985).

Elevated levels of atmospheric N in the more polluted mountainous regions of the Los Angeles Air Basin may also result in higher N content of live and litter needles compared to needles in areas further from urban pollution sources. Zinke (1980) harvested foliage of various age classes of big-cone Douglas fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) from across air-pollution gradients in the San Gabriel, San Bernardino, and San Jacinto Mountains in southern California. Foliar N content was highest in the most heavily polluted sites. The gradients in foliar N content were especially apparent when expressed as a N/P ratio (Zinke, 1980). Lindberg et al. (1986) reported that atmospheric deposition supplied 40% of the N requirement and 100% of the S requirement for annual woody increment of an oak-hickory forest in Tennessee. The extent to which N from atmospheric deposition contributes to the greater N content of big-cone Douglas fir foliage and ponderosa pine litter in highly polluted mountainous areas in southern California warrants further investigation.

Increased Fungal Diversity and Altered Species Composition

The diversity and composition of the L-layer fungal community differed significantly between plots located at the western and eastern regions of the San Bernardino Mountains. Younger, more nutrient-rich litter from trees exposed to elevated pollution levels in the western plots may provide a more favorable substrate for a wider variety of fungal decomposers, compared to litter needles originating from older foliage of trees not exposed to high-pollution levels. Premature needle abscission may alter normal development of the successional phylloplane communities, which could in turn affect the fungal community and the rate of decomposition (Bruhn, 1980; Bruhn et al., 1980). The predominant fungi from litter in plots exposed to low and high air-pollution levels were also different. *Aureobasidium pollulans* was the predominant fungus of litter in plots exposed to low and moderate pollutant levels, while an unidentified fungus with characteristic dark, sterile, knobby mycelium (DSK) was isolated most commonly from litter needles of all three western high-pollution plots.

The DSK fungus and a diverse community of fungi colonized litter needles in the western plots very effectively despite the chronic air-pollution exposure. In a previous field study in the San Bernardino Mountains the rate of litter decomposition was highest in the plots exposed to high O_3 levels (Bruhn, 1980; Bruhn et al., 1980). Fumigation with 392 $\mu g\ O_3\ m^{-3}$ (0.2 ppm) for 8 h d^{-1} for 14 wk did not significantly affect weight loss of litter needles (Bruhn, 1980). Apparently, the physiological activity of decomposer fungi is not seriously inhibited by exposure to O_3 concentrations as high or higher than the hourly averages normally occurring in polluted areas of the San Bernardino Mountains. Wilcox and Oldham (1981) isolated a species of *Phanerochaete* from the San Bernardino Mountains which under controlled fumigation actually caused a significantly greater weight loss in decaying wood when exposed to 392 $\mu g\ O_3\ m^{-3}$ (0.2 ppm) than when exposed to filtered air. Decomposition by most decay fungi was reduced by treatment with 392 $\mu g\ O_3\ m^{-3}$ (0.2 ppm), but the differences were usually not statistically significant (Wilcox and Oldham, 1981). Furthermore, high O_3 concentrations occur in the San Bernardino Mountains during the summer when the physiological activity of decomposer fungi is severely limited by lack of moisture. In summary, factor(s) causing an increase in fungal diversity and litter decomposition rate in the western plots are operative notwithstanding the high O_3 concentrations which occur in the San Bernardino Mountains during the summer.

Increased Rate of Nutrient Release

In the San Bernardino Mountains where fires are suppressed because of heavy residential and recreational use of the forest, nutrient release from litter is due predominantly to biological decomposition. Increased rates of decomposition in areas exposed to high-pollution levels may result in a more rapid release of N and other nutrients from litter, compared to the low-pollution sites. If fires were allowed to burn in the San Bernardino Mountains, the amount of N released from litter by periodic fires would probably be orders of magnitude greater than the amount of N released by litter decomposition (Covington and Sackett, 1986; Ryan and Covington, 1986). Thus, if fires were not suppressed, increased rates of nutrient release from biological decomposition in the western regions would probably be of little significance compared to the amount of nutrients released by fire.

CONCLUSIONS

Fungal diversity, N content and decomposition rate of L-layer litter were highest in the plots located on the western end of the air-pollution gradient. Possible factors contributing to greater decomposition rate and fungal diversity in the western plots include higher soil N levels, greater input of available N in the form of dry deposition, and a greater proportion of litter originating from younger foliage because of O_3-induced needle abscission. Additional contributing factors might include O_3 damage to needles creating favorable sites for microbial decomposers, and the activity of fungi which are efficient decomposers despite the chronic air-pollution exposure. More definitive studies will be required to elucidate the relative importance of the factors mentioned or other factors that may increase litter decomposition rates in areas of high air-pollution exposure in the San Bernardino Mountains.

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