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Variation in quality and decomposability of red oak leaf litter along an urban-rural gradient

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Abstract This study tested whether urban land use can affect the chemistry and decomposability of *Quercus rubra* L. (red oak) leaf litter in forests within and near a large metropolitan area. Cities may affect the quality of leaf litter directly through foliar uptake of atmospheric pollutants, and indirectly through alterations in local climate and changes in soil fertility caused by pollutant loads and altered nutrient cycling regimes. Using a microbial bioassay, we tested whether red oak leaf litter collected from urban and suburban forests in and near New York City differed in decomposability from litter of the same species collected from rural forests 130 km from the city. We found that oak litter from the urban forests decayed 25% more slowly and supported 50% less cumulative microbial biomass in a laboratory bioassay than rural litter. Rural litter contained less lignin and more labile material than urban litter, and the amounts of these chemical constituents were highly correlated with the decay rate coefficients and integrated microbial growth achieved on the litter. The specific causes of the variation in litter chemistry are not known. The results of this study suggest that decomposer activity and nutrient cycling in forests near large cities may be affected both by altered litter quality and by altered biotic, chemical and physical environments. The sensitivity of the microbial bioassay makes it useful for distinguishing differences in within-species litter quality that result from natural or anthropogenic variation in the environment.

Key words Leaf litter quality · Forest litter decomposition · Urban land use · Microbial bioassay · *Quercus rubra*

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Introduction

Plant litter is an important component of terrestrial ecosystems because it supports diverse decomposer food webs and because it is a reservoir for many nutrients needed to support primary production (Swift et al. 1979; Aber and Melillo 1991). The release rate of these nutrients during decay depends on three factors: climate, the species composition and activity levels of the decomposer community, and the physical and chemical quality of the litter. Cities may affect decomposition processes in natural systems within their boundaries by altering all of these factors. Urban and suburban land use may change the local climate (e.g. urban heat islands; Oke 1995), and may provide foci for the introduction of exotic plant and decomposer species into surrounding natural areas (Sukopp and Hejny 1990; Rapoport 1993; Steinberg et al. 1997). Moreover, urban areas are acknowledged sources of a diverse array of atmospheric pollutants that can affect decomposition and nutrient return rates by changing vegetation abundance and diversity, and by changing decomposer activity by direct pollutant deposition (Bewley and Parkinson 1984; Baath 1989; Francis 1989; Smith 1990). Fewer studies have explored whether air pollutants can also affect litter decay rates and growth of decomposer organisms indirectly by altering the properties of the living leaves that later enter the plant detritus pool (Prescott and Parkinson 1985; Garden and Davies 1988; Findlay et al. 1996). Such changes can occur through foliar uptake of pollutants (Constantinidou and Koz-

lowski 1979; Garten and Hanson 1990; Latus et al. 1990; Jordan et al. 1991), through altered patterns of soil-nutrient uptake (Flanagan and Van Cleve 1983; Haines and Carlson 1989) or through modifications of plant metabolism (Smith 1990).

Urban and suburban areas in the United States have been expanding rapidly since the 1950s (Richards 1990; Douglas 1994). Between 1960 and 1990, 31 million acres of cropland, forest, and pasture in the United States were converted to urban and suburban land use (Frey 1984; Dougherty 1992). This makes it important to evaluate the extent to which urban areas in the United States can affect ecosystem processes in natural systems within and near their boundaries and, where possible, to identify the mechanisms involved. New York City provides an excellent "natural laboratory" for studying the possible cumulative effects of urban environments on ecosystem processes like decomposition, since it has large remnant forests that have been subjected to altered land use, climate, and atmospheric chemistry over many decades. Recently forest stands in New York City have been studied and compared to similar forests in outlying suburban and rural areas to determine whether urban conditions can affect natural communities and ecosystem functions (Pouyat and McDonnell 1991; Pouyat et al. 1994; Pouyat et al. 1995; McDonnell et al. 1997).

The objective of the present study was to determine whether an urban environment can alter the leaf litter quality of a regionally abundant tree species, in this case *Quercus rubra* L. (red oak). We collected red oak leaf litter from forests located along an urban-to-rural land-use gradient in the New York City area and assayed the litter for specific chemical constituents known to influence decay rates (Melillo et al. 1982). We also used a microbial bioassay to detect whether differences in decomposability existed among the urban, suburban and rural litters. Microbial sensitivity to qualitative differences in the litters was assessed by measuring fungal and bacterial biomass responses to the leaf litter incubated in the laboratory, respiratory CO_2 evolution from these microbes, and the decay rates of the litter. We then tested whether these responses significantly correlated with the type of land use surrounding the forest stands where the litter was collected. We also explored whether differences in leaf litter chemistry were related to land use and to differences in litter decay rates.

Materials and methods

Site descriptions

The forest stands selected for this study are located along a 130 km by 20 km belt transect extending from urban Bronx, New York, through suburban Westchester County, New York, and into rural Litchfield County, Connecticut. To minimize variation in site variables not related to surrounding land use, we used the following criteria to select 11 forest stands: (1) domination (40–80% of total basal area) by red oak and/or *Quercus velutina* Lam. (black oak), both in the subgenus *Erythrobalanus*; (2) soils in either of two series (Hollis or Charlton), which are classified in the same soil family (Gonick et al. 1970); (3) stand age of at least 70 years; and (4) no evidence of recent natural or human disturbance (canopy gaps, insect infestations, fire, logging). The urban stands were located in the New York Botanical Garden (N2, N3), Van Cortland Park (V3) and Pelham Bay Park (P1). The suburban stands were located in Saxon Woods Park, N.Y. (S1, S2) and Mountain Lakes Park, N.Y. (M3). The rural stands were located in Mohawk State Forest, Conn. (MF1, MF3) and Housatonic State Forest, Conn. (H1, H3). More information about the land-use gradient and these forest stands can be found in Pouyat et al. (1995), Medley et al. (1995) and McDonnell et al. (1997).

Litter collection and preparation for the bioassay

Leaves were collected in litter traps placed in each of the 11 plots along the urban-rural transect in autumn 1990. Leaves were collected within a few days of falling, air-dried and stored at room temperature. Red oak leaves were selected for this experiment. However, it is possible that some leaves of black oak may have been included in samples from three plots (P1, S1 and S2) where it was present. Leaves of black and red oak are difficult to distinguish, particularly since the two species are in the same subgenus and hybridize (Gleason and Cronquist 1963). As seen in subsequent analyses, where mixing may have occurred there was no tendency for these three plots to group together in any unexpected manner when foliar chemistry and decay parameters were plotted against distance from Central Park. However, data concerning relationships of litter chemistry and decomposability with distance from New York City have been analyzed and reported in two ways: using all 11 plots and using only 8 plots (i.e. excluding P1, S1 and S2).

Uniform leaf discs (6 mm diameter) were punched from the leaf blades. Leaf petioles and main veins were excluded from this experiment, and no more than 25 discs were cut from any single leaf collected from a stand. Two hundred discs were placed in each of 24 vials (100 × 23 mm) per stand, and their air-dry weights obtained to 0.01 mg. Other leaf discs were weighed to determine the air-dry weight to oven-dry weight correction factor for each stand. Additional leaf discs were ground in a Wiley mill and used for chemical analyses.

On the day before the start of the bioassay, oak leaf litter was collected from the forest floor of each plot in the land-use gradient. Equal fresh weights of leaf litter from each stand were combined as inoculum for the bioassay since microbial diversity in the litter might have differed among stands. A total of 8 g (fresh weight) of combined leaves was blended in 600 ml sterile deionized water, and large particles were removed by filtering through a 250-μm nylon mesh screen. Each vial received 0.5 ml of this prefiltered inoculum and the litter discs were brought up to the same (300%) moisture level with sterile deionized water. The capped vials were placed in racks and covered with plastic bags that contained wet paper toweling to keep the air around the vials humid. The vials were incubated at 20 °C in the dark for up to 150 days.

Litter chemistry

Indices of initial litter quality were obtained as follows. Lignin, cellulose, hemicellulose, neutral detergent fiber (NDF, which includes lignin and structural carbohydrates like cellulose and hemicellulose) and acid detergent fiber (ADF, which includes lignin and cellulose) were assayed using the method of Van Soest et al. (1991). Three one-gram replicates per site were used for these analyses. Percent C and N of the milled leaf litter samples (2–3 replicates per site) were determined using a Carlo-Erba CHN analyzer. Unbound and bound phenolics were assayed using Folin-Denis reagent as described in Findlay et al. (1996). Unbound and bound phenolics were defined as phenolics that were extracted from leaves after mild (5 °C, 18 h) and more stringent (70 °C, 2 h) extraction with 70% CH_3OH, respectively. Tannin was quantified using the method of Dawra et al. (1988).

Mass loss determinations

There were seven sampling dates, 7, 35, 49, 63, 91, 122, 150 days after inoculation, with three vials per plot randomly selected at each date. Vials were processed according to randomized block design, so that each of three blocks consisted of one urban, one suburban and one rural vial. Twenty discs were selected from each vial for measuring CO_2 evolution and microbial biomass. The fresh weight of the remaining 180 discs per vial was obtained to determine the percent moisture content of the litter. Then the vials were placed in a 65 °C oven for 1 week to determine the oven-dry weight of the remaining litter. The oven-dry weight of the 20 destructively sampled discs were estimated based on the mean weight per disc of the remaining 180. This value was added to the weight of the 180 discs, so that litter mass loss for each vial could be estimated, based on the assumption that the mean weight of the 20 discs removed was the same as the mean weight per disc obtained by direct measurement.

CO_2 measurement

As noted above, 20 leaf discs were removed from each vial under sterile conditions and placed in a sterile 20-ml syringe equipped with a stopcock at the tip. The syringe was filled with 20 ml air, closed, and incubated at 20 °C for 1 h. After every second or third syringe was prepared, an air blank was also drawn into a separate syringe to provide information on the ambient CO_2 concentration of the air. Barometric pressure was recorded hourly so that CO_2 partial pressure in the sample volume could be converted to micromoles of CO_2. The CO_2 evolved from the leaf discs was determined by injecting the air in the syringe into a Shimadzu GC-AIT GC equipped with a thermal conductivity detector (110 °C) and a Poropak Q column set at 44 °C. He was used as a carrier gas. The CO_2 concentration $(mg^{-})^{t}$ was converted to micromoles of CO_2 using the following equation:

$$CO_2\ (\mu mol) = \frac{CO_2(\mu g/L) \times (V \times P)}{R \times 10^6 \times T} \quad (1)$$

where V is volume (0.00002 m^3), P is barometric pressure (Pa), T is temperature (=293.16 K) and R, the ideal gas constant, $=8.31 \times 10^{-6}\ m^3 \times Pa \times \mu mol^{-1} \times K$.

Microbial biomass determinations

Microbial biomass was estimated using epifluorescent microscopy [Nikon Optiphot-2 microscope equipped with an exciter filter (450–490 nm) and a barrier filter (515 nm)]. To prepare samples, the same 20 leaf discs used for CO_2 evolution measurements were blended in 100 ml deionized water for 1 min. To determine fluorescein diacetate (FDA)-active fungi and bacteria, 0.5-ml subsamples of the homogenate were incubated with 2 ml FDA working solution (1 ml FDA stock solution in 99 ml PO_4^{3-} buffer, pH 7.6, pre-filtered through a 0.22-μm filter; FDA stock solution: 40 mg FDA dissolved in 20 ml acetone and stored in a freezer) and collected on 0.22-μm pore polycarbonate membrane filters stained with Irgalan black (Poretics, Livermore, Calif.) (Soderstrom 1977). To determine the number and biovolume of total bacteria, another 0.5-ml homogenate subsample was incubated with 2 ml fluorescein isothiocyanate solution (Babiuk and Paul 1970), collected on another Irgalan-black-stained filter (0.22 μm pore), and rinsed with 0.5 M $NaCO_3$ buffer (pH 9.6). Total fungi were quantified by first preserving 9 ml of homogenate in 1 ml of concentrated formalin solution, then staining 0.5 ml of this diluted homogenate with 5 ml water-soluble aniline blue (WSAB) dye (0.1% WSAB in 0.1 M K_2HPO_4) for 30 min and collecting the fungi on 0.45-μm black filters (Millipore, Bedford, Mass.). Sometimes, further dilutions of the preserved homogenate were necessary so as not to clog the filters and to permit better dispersion of the sample on the filters. Two replicate filters were made from each vial for all biomass determinations, and 25 fields from each filter were examined at ×1250 magnification.

Fungal lengths (L) were estimated using the intersection method of Olson (1950) and hyphal widths (w) were measured with an ocular micrometer. Fungal biovolume was estimated using the formula for a cylinder $[v = \pi \times (0.5w)^2 \times L]$. Bacterial biovolume was estimated from images projected onto a television screen using a CCTV video camera with sensitivity at 0.08 lx at F 1.4 (Panasonic wvBP504, Visitrak Corp., Pleasantville, N.Y.), and based on the lengths and widths of 50 cells/plot. The average bacterial cell biovolume ($\pi w^3/6$ for spherical cells; $\pi w^2 L/6$ for ellipsoidal cells) was calculated and multiplied by total cell number to obtain the bacterial biovolume for each sample. Control solutions without homogenate for both FDA and total microbial biovolume determinations were simultaneously prepared and filtered. Any microbial cells observed in the control solutions were counted and the number subtracted from the microbial biomass estimates in the samples to provide final biomass values.

Data analysis and statistics

First-order decay rate coefficients (k) from the exponential mass loss equation:

$$M_t = M_0 e^{-kt} \quad (2)$$

where M_t is mass at time t and $M\emptyset$ is mass at $t = \emptyset$, were estimated using the nonlinear regression function in Systat (Systat, Evanston, Ill.). A two-component exponential mass loss model:

$$M_t = M_L\ e^{-k_L t} + M_R\ e^{-k_R t} \quad (3)$$

was also fitted to the mass loss curves, again using Systat software. This permitted estimation of two decay rate coefficients, one, k_L, for the more labile litter fraction that is rapidly broken down and absorbed by microbes, and another, k_R, for a more recalcitrant litter fraction that is broken down more slowly. The two-component model also permitted estimation of the initial mass of the labile (M_L) and recalcitrant (M_R) fractions. Differences among measured variables were analyzed using one-way ANOVA and two-way ANOVA (by land-use type and date), and relationships between these coefficients and litter chemistry or stand distance from Central Park NY, NY, were also explored using regression analysis. The Fisher PLSD test was used to determine the significance (95% level) among the three land-use types. When necessary, data were either log-transformed (for continuous variables) or square-root-transformed (bacterial count data) to stabilize the variances. Although such transformations can sometimes change the directions of comparisons (Zhou et al. 1997), they did not do so for any of our data. To provide summary information on microbial biomass responses to litter type, the areas under the curves of biomass vs incubation time were calculated using trapezoidal integration to provide a cumulative microbial response index (microbial biomass × day). The curves of CO_2 evolution vs time were also integrated to provide a similar index (μmol CO_2 × day).

Results

Litter mass loss and relationships with distance from the city

Oak leaves collected from the rural stands decayed more rapidly than those from the urban stands, with those from suburban stands being intermediate (Table 1, Fig. 1). After 150 days of incubation, the percent mass remaining (±1 SE) for litter from the 11 plots was 65.7±0.9% (rural), 68.9±1.0% (suburban), and 74.1±1.3% (urban; ANOVA $P = 0.001$). When only eight plots were analyzed the percent mass remaining for litter was 65.7±0.9% (rural), 67.2% (suburban) and

Table 1 First-order oak litter decay rate coefficients (k), decay rate coefficients for labile (k_L) and recalcitrant (k_R) litter fractions, estimated fractions of labile (M_L) and recalcitrant material (M_R), and density of litter collected from oak stands at increasing distances from Central Park, New York City. ANOVA probabilities refer to differences in means among the three land-use types using data from 11 stands. Means in the *same column* with the *same superscript* are not statistically different at $P=0.05$ [Fisher (PLSD)]. *adj* Adjusted; *N2, N3, V3, P1* urban stands; *S1, S2, M3* suburban stands; *MFI, MF3; HI, H3* rural stands

Stand	Distance (km)	k [a] %/day	adj. R^2 [a]	k_L [b] %/day	k_R [b] %/day	adj. R^2 [b]	M_L [b] (%)	M_R [b] (%)	Leaf density (mg/cm^3)
N2	10.3	0.211	0.951	7.01	0.157	0.998	8.6	91.4	8.17
N3	10.3	0.224	0.948	2.94	0.122	0.998	13.7	85.9	8.38
V3	13.7	0.166	0.907	6.08	0.105	0.992	9.7	90.4	9.41
P1 [c]	13.9	0.171	0.912	7.70	0.113	0.998	9.5	90.5	9.34
S1 [c]	26	0.233	0.944	20.46	0.190	0.993	8.4	91.6	10.04
S2 [c]	26	0.214	0.938	16.49	0.167	0.999	9.0	91.0	10.12
M3	64	0.254	0.955	10.20	0.198	0.999	9.2	90.8	10.08
MF1	123	0.268	0.873	7.00	0.147	0.998	17.3	82.7	9.30
MF3	123	0.286	0.889	8.79	0.178	0.994	16.1	83.9	9.83
H1	128	0.247	0.865	7.96	0.138	0.998	16.3	83.6	9.80
H3	128	0.259	0.881	12.6	0.172	0.988	14.5	85.5	10.22
Urban mean		0.193 [d]		5.93 [d]	0.124 [d]		10.36 [d]	89.5 [d]	8.83 [d]
(SE)		(0.014)		(1.05)	(0.012)		(1.16)	(1.2)	(0.32)
Suburban mean		0.234 [e]		15.72 [e]	0.185 [e]		8.87 [d]	91.1 [d]	10.08 [e]
(SE)		(0.012)		(2.98)	(0.009)		(0.25)	(0.3)	(0.023)
Rural mean		0.265 [e]		9.08 [d]	0.159 [e]		16.02 [e]	83.9 [e]	9.79 [e]
(SE)		(0.008)		(1.22)	(0.010)		(0.59)	(0.6)	(0.38)
ANOVA P		0.006		0.013	0.012		0.0007	0.001	0.014

[a] Based on fitting the data to the exponential decay model; $M_t = M_0 e^{-kt}$, where M_t is mass at time t and Mø is mass at $t = ø$

[b] Based on fitting the data to the two-component decay model: $M_t = M_L e_L^{-kt} + M_R e^{-k_R t}$

[c] Plots where some *Quercus velutina* leaves may have been mixed with *Quercus rubra* leaves

73.4 ± 1.5% (urban; ANOVA $P=0.01$). Mean values of k for all 11 rural, suburban, and urban litters were 0.265 ± 0.01%, 0.234 ± 0.01% and 0.193 ± 0.01%/day, respectively (ANOVA $P=0.006$; Table 1). Mean k values when only eight plots were considered were 0.265 ± 0.01% (rural), 0.254% (suburban) and 0.200 ± 0.02% (urban; ANOVA $P=0.036$). To determine whether a relationship existed between proximity to the city and litter decay rate, the k values for litter from each plot were plotted against stand distance from Central Park. Using the 11 plots, distance from Central Park was associated with 62% of the variation in litter k values ($P=0.003$; Table 2). Using only eight plots, distance from Central Park was associated with 60% of the variation in k ($P=0.01$).

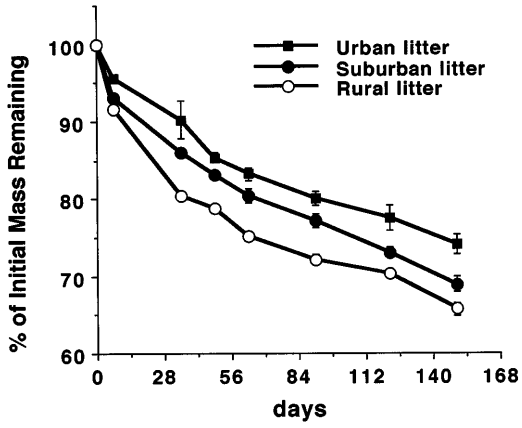

Fig. 1 Mass/oss curves for oak litter collected from 11 forest plots surrounded by urban, suburban and rural land use, incubated at 20 °C for 150 days. Mean ± SE ($n=4$) for urban and rural litter, $n=3$ for suburban litter

A visual comparison of the slopes of the percent-mass-remaining curves for rural, suburban and urban leaves (Fig. 1) revealed that the greatest difference among sites in fractional mass loss rates occurred during the first 35 days of decay. Therefore, Eq. 3 was fitted to the data to obtain separate decay rate coefficients (k_L and k_R) for the rapidly decomposing, labile, and slowly decomposing, recalcitrant (R) fractions of the litter from each plot. The values of k for both labile and recalcitrant litter components (Table 1) were highest for the suburban litter (15.7% and 0.185%/day, respectively), followed by rural (9.0% and 0.159%/day) and urban litter (5.9% and 0.124%/day). These differences were statistically significant (ANOVA $P=0.01$). Since relationships between these coefficients by plot and distance from the city were neither linear nor monotonic, linear regression of these values against distance from the city was not performed. Note (Table 1) that the two-component model (Eq. 2) provided a better fit (as measured by the adjusted R^2) than the simpler one-component model (Eq. 3) for the decay of litter from the 11 sites.

Initial litter quality and relationships with land use and decay rate

Equation 3 also permitted estimation of M_L and M_R (Table 1). When all 11 plots were considered, rural lit-

Table 2 Results of regressing each litter variable (k, M_L, M_R) against stand distance (km) from Central Park (refer to Table 1). Column *A* ahows results when all 11 stands were included in the linear regression. Column *B* shows results when stands P1, S1 and S2 were excluded from the linear regression. For abbreviations, see Table 1

Regression parameters	k[a]		M_L[b]		M_R[b]	
	A	B	A	B	A	B
Slope	5.74×10^{-4}	5.41×10^{-4}	0.055	0.049	–0.054	–0.048
y-Intercept	0.195	0.199	8.71	9.53	91.2	90.4
Adjusted R^2	0.615	0.602	0.654	0.556	0.629	0.521
P value	0.003	0.015	0.002	0.021	0.002	0.026

[a] Estimated from the first-order decay model: $M_t = M_0 e^{-kt}$
[b] Estimated from the two-component decay model: $M_t = M_L e^{-k_L t} + M_R e^{-k_R t}$

ter contained on average the greatest M_L (16.1% of total mass), suburban litter contained the lowest M_L (8.9%), and urban litter was intermediate (10.4%; ANOVA $P = 0.0006$). When only eight plots were examined, for the suburban stands, the mean M_L was 9.2% and for the urban stands was 10.7% (ANOVA $P = 0.02$). Distance from Central Park accounted for 65% of the variation in the estimated M_L in the litter ($P = 0.002$; Table 2) when all 11 sites were considered, and for 56% of the variation ($P = 0.02$) when only eight sites were included in the regression. M_L in the litter explained 44.2% of the variation in k ($P = 0.03$).

The estimated M_R was greatest for the suburban stands (91.1%) and lowest for the rural stands (83.9%). The large amount of recalcitrant material in the suburban litter relative to the rural litter could explain why suburban litter had a greater percent mass remaining after 150 days, despite it having the highest k_L and k_R of the three litter categories. Percent M_R in litter was negatively correlated with distance from the city (Table 2) and explained 43.7% of the variation in k ($P = 0.03$).

The initial density of the leaves also varied with land use (Table 1), with urban litter having the lowest (8.83 ± 0.32 mg/cm^2), suburban litter having the highest (10.08 ± 0.02 mg/cm^2), and rural litter having intermediate (9.79 ± 0.38 mg/cm^{-2}) densities when all 11 plots were included in the analysis. These differences among land-use means were statistically significant overall (ANOVA $P = 0.01$), but the suburban and rural means were not statistically separable at $P = 0.05$ (Fisher PLSD test). Using eight plots, mean urban litter density was 8.65 ± 0.38 mg/cm^2 and suburban litter density was 10.08 mg/cm^2 (ANOVA $P = 0.06$). The variation in litter density by plot was positively correlated with the decay rate of the labile fraction ($R^2 = 0.472$, $P = 0.02$) but did not correlate strongly with any other litter property.

Chemical analyses were performed to identify any chemical constituents in the oak litter that differed along the land-use gradient, and to determine whether these were correlated with the variation in litter decay rates. Eleven indicators of litter quality that are known to affect litter decay rates were quantified for the oak leaves collected from each plot (Table 3); these included structural components, chemical modifiers of decay, and concentration ratios of certain constituents. Using ANOVA we found statistically significant differences in the lignin:N ratio, and concentrations of hemicellulose and unbound phenolics with land use (Table 3). Rural litter had the lowest amounts of hemicellulose and unbound phenolics, and the lowest lignin:N ratio. Suburban litter had the highest amounts of unbound phenolics and the highest lignin:N ratio.

Regression analyses were also performed to explore whether the concentrations of any litter constituents varied linearly with distance from Central Park. Statistically significant relationships were found for only 5 of the 11 indices of litter quality (Table 4). When all 11 plots were included in the analysis, these were lignin:N ratio, percent lignin, and percent NDF. When only eight plots were included these were lignin:N ratio, percent hemicellulose and percent cellulose. We recognize that P values lose some of their meaning when multiple tests are performed. However, if all null hypotheses were true (an unlikely scenario), the probability of obtaining three or more statistically significant results with $P = 0.05$ in 11 independent tests would be less than 2%. Although these tests were not independent, e.g. with percent lignin and lignin:N ratio, we considered that the results of the exploratory analyses in Table 4 most likely indicated some real relationships. Confirmation of this would require further studies.

Linear regression was also used to explore relationships between litter chemistry and litter decay rate. Initial percent lignin and percent NDF proved to be the best predictors of k for the litter from each stand, based on the simple model with a single, overall k ($R^2 = 0.505$, $P = 0.01$ and $R^2 = 0.573$, $P = 0.007$, respectively). Both indices were negatively correlated with k, indicating that litter containing more of these fibrous, structural components decayed more slowly. Since tannins and other phenolic compounds are known to modify litter decay rates during early stages of decomposition (Swift et al. 1979), regression analysis was used to search for possible relationships between the k_L and these two chemical fractions. As shown in Fig. 2, k_L declined rapidly as tannin concentration increased from about 110 to 140 mg/g (dry weight) litter and then more or less stabilized at higher concentrations. Because this relationship was non-linear, we computed the Spearman

Table 3 Chemical composition before decay of red oak leaf litter collected from forest plots surrounded by urban ($n=4$), suburban ($n=3$) and rural ($n=4$) land use. ANOVA probabilities refer to differences in means among the three land-use types using data from all 11 stands. Means in the *same column* with the *same superscript* are not statistically different at $P=0.05$ (Fisher PLSD test). NDF Neutral detergent fiber, ADF acid detergent fiber; for other abbreviations, see Table 1

Plot	Land use	N (%)	C:N	Lignin (%)	Lignin:N	NDF (%)	ADF (%)	Hemicellulose (%)	Cellulose (%)	Tannin (mg/g)	Total phenolics (mg/g)	Unbound phenolics (mg/g)
N2	Urban	0.69	72.8	24.2	35.0	52.7	38.5	14.2	14.8	128	2.02	1.41
N3	Urban	0.76	67.4	24.0	31.7	49.7	33.4	16.3	11.1	211	2.12	1.45
V3	Urban	0.80	63.7	28.4	35.8	59.2	42.3	16.9	14.1	136	2.37	1.52
P1	Urban	0.89	56.9	26.6	29.8	55.4	39.1	16.3	14.3	132	2.39	1.56
S1	Suburban	0.73	70.1	27.4	37.9	52.3	40.0	12.3	14.8	121	2.42	1.61
S2	Suburban	0.72	70.2	26.2	36.4	56.6	44.8	11.7	20.4	107	2.61	1.76
M3	Suburban	0.71	71.3	23.2	32.6	50.3	33.8	16.5	13.3	203	2.45	1.80
MF1	Rural	0.83	60.5	24.3	29.2	51.7	39.2	12.4	15.6	158	2.44	1.65
MF3	Rural	0.79	62.6	23.6	29.7	50.9	37.3	13.6	14.4	129	1.94	1.23
H1	Rural	0.77	64.7	21.6	27.9	47.4	36.2	11.2	16.2	174	2.03	1.40
H3	Rural	0.76	66.1	22.1	29.2	49.7	36.9	12.8	16.6	112	1.96	1.34
Urban mean		0.78	65.2	25.8	33.1[a]	54.3	38.3	15.9[a]	13.6	151.6	2.2	1.48[a]
(SE)		(0.04)		(1.05)		(2.0)	(1.8)	(0.6)	(0.8)	(19.9)	(0.09)	(0.03)
Suburban mean		0.72	70.5	25.6	35.6[a]	53.1	39.6	13.5[ab]	16.2	145.9	2.5	1.72[b]
(SE)		(0.004)		(1.27)		(1.8)	(3.2)	(1.5)	(2.1)	(21.3)	(0.06)	(0.06)
Rural mean		0.79	63.5	22.9	29.0[b]	49.9	37.4	12.5[b]	15.7	143.2	2.1	1.40[a]
(SE)		(0.64)		(0.02)		(0.93)	(0.6)	(0.5)	(0.5)	(14.0)	(0.12)	(0.09)
ANOVA *P*		0.25	0.16	0.11	0.01	0.19	0.75	0.04	0.29	0.95	0.06	0.03

Table 4 Results of regressing each chemical component of oak litter against stand distance from Central Park (refer to Table 3). Column *A* shows results when all 11 stands were included in the linear regression. Column *B* shows results when stands P1, S1 and S2 were excluded from the linear regression

Chemical Component	Slope		y-Intercept		Adj R^2		*P* value	
	A	B	A	B	A	B	A	B
N (%)	1.94×10^{-4}	3.85×10^{-4}	0.756	0.735	–0.076	0.095	0.60	0.24
C:N	2.74×10^{-2}	4.17×10^{-2}	67.7	69.3	–0.012	0.201	0.37	0.15
Lignin (%)	2.88×10^{-2}	2.24×10^{-2}	26.4	25.6	0.444	0.278	**0.02**	0.10
Lignin:N	4.68×10^{-2}	4.54×10^{-2}	35.1	34.8	0.475	0.763	**0.01**	**0.003**
NDF (%)	3.99×10^{-2}	3.35×10^{-2}	54.8	54.0	0.318	0.179	**0.04**	0.16
ADF (%)	1.82×10^{-2}	3.50×10^{-3}	39.4	37.5	–0.018	–0.161	0.39	0.87
Hemicellulose (%)	2.13×10^{-2}	2.98×10^{-2}	15.3	16.9	0.218	0.584	0.08	**0.02**
Cellulose (%)	1.00×10^{-2}	2.16×10^{-2}	14.4	12.9	–0.053	0.402	0.49	**0.05**
Tannin (mg/g)	1.40×10^{-2}	1.59×10^{-1}	145.6	168.2	–0.111	–0.097	0.95	0.56
Total phenolics (mg/g)	1.86×10^{-3}	8.50×10^{-4}	2.36	2.23	0.088	–0.109	0.20	0.60
Unbound phenolics (mg/g)	1.17×10^{-3}	6.70×10^{-4}	1.59	1.53	0.027	–0.114	0.28	0.61

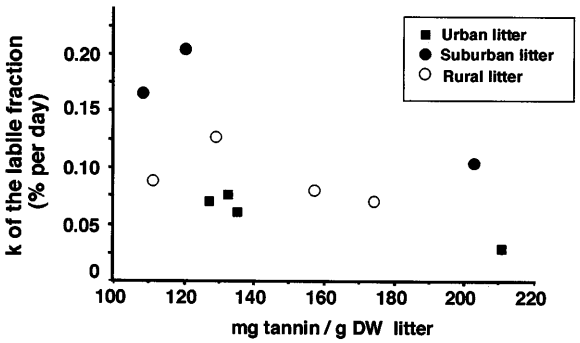

Fig. 2 The decay rates (k) of the labile fraction of litter, collected from 11 forest plots along an urban-rural transect, in relation to the respective tannin content. *DW* Dry weight

rank correlation coefficient between these variables ($r=-0.618$, $P=0.05$). However, since litter tannin content varied greatly even for stands close to each other (see values for the rural stands in Fig. 2), it consequently did not correlate well with distance from New York City. No relationships were apparent between k_L and unbound, bound or total (bound plus unbound) phenolics.

Microbial biomass responses to litter and relationships with decay rate

Rural litter contained greater total and FDA-active fungal lengths and biovolume than did either urban or

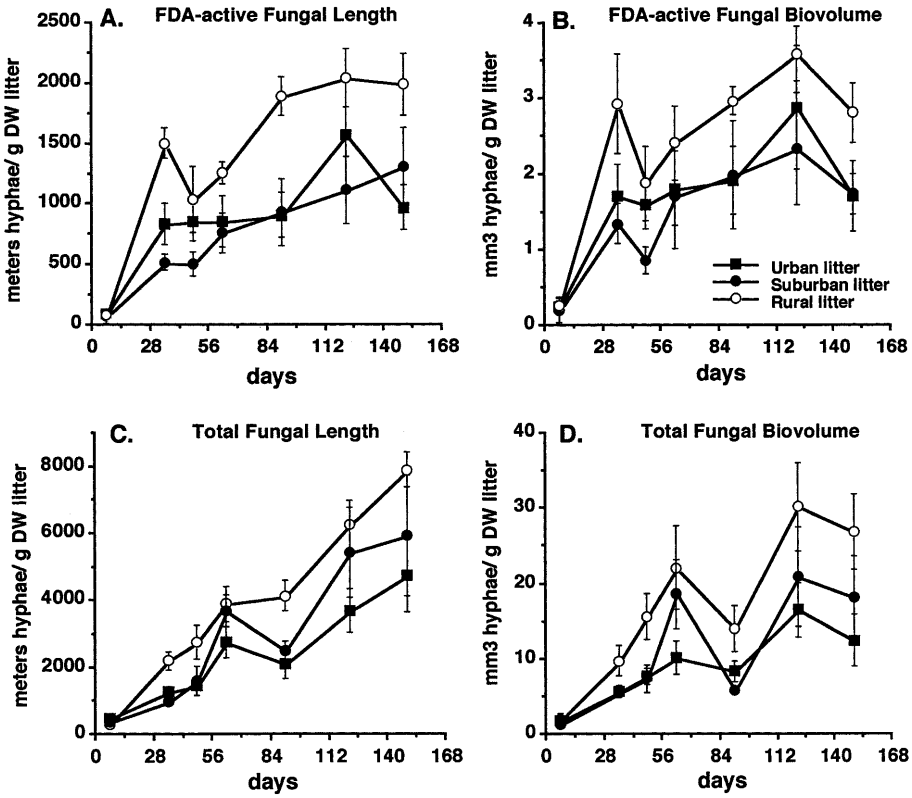

Fig. 3 A–D Fungal responses (mean ± SE) to litter collected from four rural, three suburban, and four urban forest plots and incubated in the laboratory at 20 °C over a 150-day period

suburban litters (Fig. 3 A–D). Except for total fungal length (Fig. 3C), the latter two litter types did not differ consistently. Length of fungal hyphae, number of bacterial cells, fungal biovolume, and bacterial biovolume differed with land-use category at $P < 0.001$ in two-way ANOVA based on land-use and date. Total fungal length/g (dry weight) litter integrated over the entire incubation period was 69% and 33% greater in rural litter than in urban and suburban litter, respectively (Table 5). Integrated fungal biovolume in rural litter was 89% and 55% greater than in urban and suburban litter. However, the integrated biomass measures differed much less between the latter two litter types (Table 5).

Table 5 Mean cumulative total microbial biomass growing on oak litter from urban, suburban and rural forests integrated over a 150-day laboratory incubation period. Means in the *same column* with the *same superscript* are not statistically different at $P = 0.05$ (Fisher PLSD). *CTFL* Cumulative total fungal length, *CTFBV* cumulative total fungal biovolume, *CTBN* cumulative total bacterial cells, and *CTBBV* cumulative total bacterial biovolume

Land-use	CTFL (m × days)	CTFBV (mm^3 × days)	CTBN (cells × days)	CTBBV (mm^3 × days)
Urban	347509[a]	1368[a]	65.1×10^{10}	84
(SE)	48913	230	4.5×10^{10}	7.1
Suburban	442218[ab]	1670[a]	57.6×10^{10}	79
(SE)	81317	252	9.3×10^{10}	17.4
Rural	586639[b]	2589[b]	87.4×10^{10}	117
(SE)	38558	242	9.3×10^{10}	16.2
ANOVA *P*	0.03	0.02	0.07	0.15

Responses of bacteria to the different litter types were not as pronounced or consistent as those of fungi, but the total biomass measures were similar to those for the fungal responses (Fig. 4 A–D). Over most dates, rural litter contained greater total bacterial biomass than urban and suburban litters (Fig. 4C, D). These differences were also statistically significant as determined by two-way ANOVA for the effect of litter origin on bacterial number ($P \leq 0.0001$). Integrated total bacterial cell number/g (dry weight) rural litter was 34% and 52% greater than integrated total cell numbers in urban and suburban samples (Table 5). There was also 40% and 49% more integrated total bacterial biovolume in rural than in urban and suburban litters. For the first two sampling dates, FDA-active bacterial number was highest in rural litter, but this difference was not maintained as decay progressed. FDA-active bacterial biovolume did not differ greatly among land-use types (Fig. 4B).

Litter contained a greater proportion of fungal compared to bacterial biomass. Total fungal biovolume ranged from 72% to 98% of total microbial biovolume between 35 and 150 days of incubation, while 92–99.5% of FDA-active microbial biovolume consisted of fungal biovolume over the same period. There were no trends apparent in the fungal fraction of total or FDA-active microbial biomass over time or on the different litters. Net fungal growth occurred in all litter types over time (Fig. 3A–D), while total bacterial numbers and biovo-

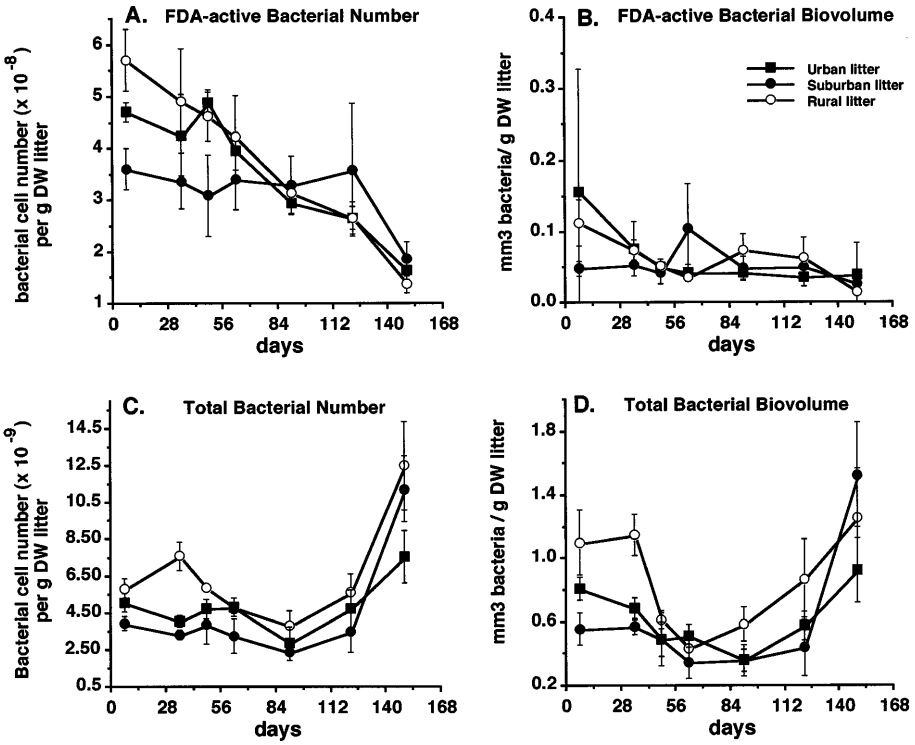

Fig. 4 A–D Bacterial responses (mean ± SE) to litter collected from four rural, three suburban, and four urban forest plots and incubated in the laboratory at 20 °C over a 150-day period

lume were highest at the beginning and end of the incubation period (Fig. 4C, D). FDA-active bacterial number and biovolume declined steadily in all litter types as decay progressed (Fig. 4A, B).

To determine the strength of the relationship between the amount of microbial biomass on the litter and litter decay rates, the total microbial biovolume (fungal and bacterial)/g (dry weight) litter was integrated over the 150-day incubation period for each of the litter types from the 11 plots along the land-use gradient. The values of k for litter from each plot (Table 1), which also represented a time-integrated effect, were then regressed against the cumulative microbial biovolume estimates. For cumulative total microbial biovolume (CTMBV) the relationship was strong, with k nearly doubling over the range of CTMBV (Fig. 5, $r^2 = 0.76$, $P = 0.0005$). The analogous relationship for cumulative FDA-active biovolume was slightly weaker, with k increasing by more than 50% over the range of this variable ($r^2 = 0.51$, $P = 0.01$; data not shown).

The steepest drop in litter mass occurred during the first 35 days of decay, indicating that the fraction of labile material in the litter may have accounted for the most important difference in litter quality observed along the land-use gradient. The amount of this labile fraction was estimated using Eq. 3. To increase confidence in these mathematically derived estimates of labile material, we regressed the total microbial biovolume cumulated over the first 35 days of decay on the estimated labile fraction in the litters from each of the 11 plots. The assumption here was that greater amounts of labile material would support a greater microbial biomass during early decay. The microbial biovolume integrated over the period when most of the labile leaf material was lost approximately doubled over the observed range of the labile fraction ($r^2 = 0.82$; $P = 0.0001$; Fig. 6).

CO_2 production during decomposition

Integrated CO_2 production from rural litter over the incubation period was 20% and 15% greater than from the urban and suburban litters, although these differ-

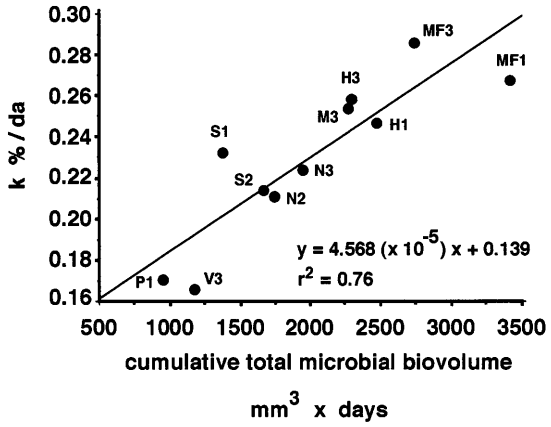

Fig. 5 Relationship between the first-order decay coefficient (k) for oak litter collected from 11 plots along an urban-to-rural gradient and total microbial biovolume (sum of fungal and bacterial biovolume) integrated over 150 days of incubation. *N2, N3, V3, P1* Urban stands; *S1, S2, M3* Suburban stands; *MFI, MF3, HI, H3* rural stands, *da* day

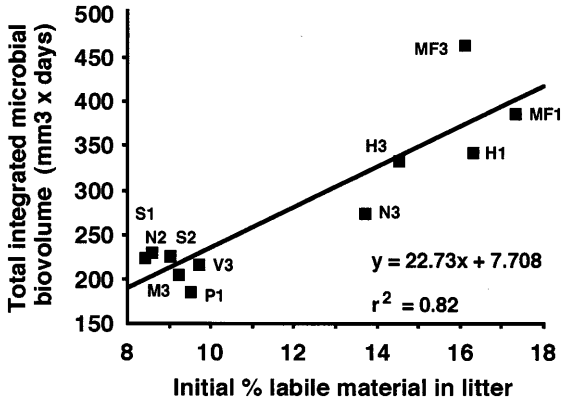

Fig. 6 Relationship between estimated amount of labile material in litter and the total microbial biovolume integrated over the first 35 days of incubation when labile material was most rapidly decayed. For abbreviations, see Fig. 5

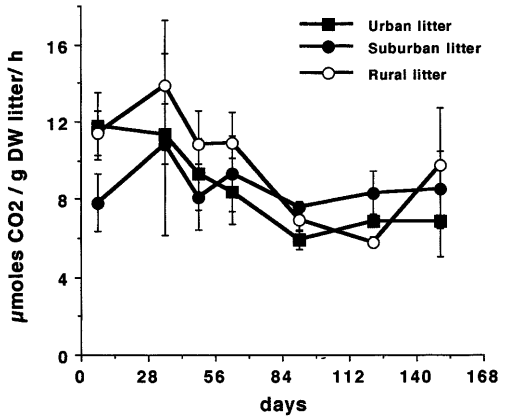

Fig. 7 Rate of CO_2 evolution/g dry weight (*DW*) litter/h. Litter collected from four rural, three suburban, and four urban forest plots and incubated in the laboratory at 20 °C over a 150-day period

ences were not statistically significant as determined by two-way ANOVA ($P=0.36$ for the effect of land use). For all litter types there was a tendency for CO_2 evolution to decrease over the incubation period (Fig. 7). There were no obvious relationships between CO_2 evolution and overall decay rate, total microbial biovolume, or FDA-active microbial biovolume. The large within-group variation in the CO_2 measurements suggested that: (1) either the error of the method used was too high to allow detection of trends over time or among litter types, or (2) microbial C-use efficiencies varied greatly as the microbial communities adapted to changing litter chemistry as decay progressed. In either case, CO_2 evolution was not significantly correlated with microbial growth responses to litter in this experiment.

Discussion

The microbial bioassay used detected differences in decomposibility of oak litter that varied with the type of land use (urban, suburban and rural) surrounding the forests. Rural oak litter contained more readily decomposable material, supported more microbial biomass, and decayed faster than urban or suburban oak litter. Some structural components of the litter (percent lignin, percent NDF) correlated well with both distance from the city and subsequent decay rate, and provided potential explanations for the trends observed in decay rate. Lignin and NDF content were negatively correlated with decay rate, while the estimated percent labile material correlated highly and positively with decay rate. The integrated microbial biomass for the first 35 days of incubation correlated strongly with the estimated percent labile fraction, thereby providing further independent validation that the mass loss differences detected among these litter types were due more to differences in amount of labile material than to microbial suppression by recalcitrant materials like lignin, or chemical modifiers like bound or unbound phenolics. The chemical composition of this labile fraction was not determined, however, since its importance was an unanticipated finding of this study.

One of the objectives of our study was to determine whether urban conditions involving combined differences in atmospheric chemistry, soil fertility, and local climate might alter the properties of senescent leaves enough that their subsequent decay rates may be affected. We do not know which specific factors caused the differences in litter quality and decomposability observed in this study. However, since surrounding land use was highly correlated with variation in oak litter quality and decay rates, future research could benefit from appraising factors that are known to affect litter quality in the directions observed.

Both soil N status and atmospheric pollutants varies along the land-use gradient studied (NYDEC 1990, Pouyat et al. 1995, Pouyat et al. 1997), and both factors are known to affect the chemical composition of living and senescing leaves. Forests in the urban end of this transect exhibit faster N mineralization and nitrification rates than the rural forests (Pouyat et al. 1997), and receive greater inputs of NO_3 and NH_4 during the growing season (Lovett et al., unpublished data). However, the percent N of the oak litter was not higher in the urban stands, as would be expected from results of N fertilization experiments (Flanagan and Van Cleeve 1983, Aber et al. 1995) and experiments involving direct foliar uptake of atmospheric N compounds (Garten and Hanson 1990; Latus et al. 1990). In fact, percent N and C:N ratios in oak litter did not vary predictably along this particular land-use gradient and could not explain the differences in decay rates observed. These urban forests are also exposed to higher concentrations of atmospheric SOx and H_2SO_4 (NYDEC 1990). H_2SO_4 is known to alter litter quality by reducing foliar N concentrations and raising C:N ratios (Garden and

Davies 1988). However, as mentioned above, the litter along this gradient did not vary substantially in either percent N or C:N ratio. O_3 concentrations are also higher in New York City than in the rural end of the land-use gradient (NYDEC 1990). Findlay et al. (1996) performed a microbial bioassay of decaying cottonwood (*Populus deltoides*) litter from plants exposed to a single dose of O_3 (200 mg L^{-1} for 5 h) in a greenhouse. The bioassay showed that the O_3–treated litter decayed 50% more slowly than unexposed controls. In addition, the amount of recalcitrant residual material (R) calculated from an asymptotic mass-loss model ($M_t = R + (M_t - R) \times e^{-kt}$) was more than 50% greater in O_3–treated cottonwood litter than in controls. These litter-decay responses to O_3 are similar to the decay rate variation observed along our urban-rural gradient where urban oak litter decayed most slowly and was estimated to contain high amounts of M_R.

All of the above factors are known to work both singly and synergistically to affect the foliar quality of vegetation (Smith 1990; MacKenzie and El-Ashrie 1989), and hence can potentially, and indirectly, affect decomposer microbial populations and decay processes once the foliage drops to the forest floor. Of course, it is possible that if these simultaneously occurring factors interacted antagonistically, their net effects on litter quality could mask the effects of any one factor. The relative importance of these factors could also vary from year to year at any one location, causing net effects on litter quality to vary annually. In the present study, urban conditions had the overall net effect of reducing oak litter decomposability for that year's cohort of red oak litter.

A shortcoming of this bioassay approach is its short duration and probable limitation with respect to the broad microbial diversity occurring in the field. For example, white rot fungi, which can decompose lignin completely (Dix and Webster 1995), probably did not grow under the laboratory conditions employed. Therefore, it was not possible to determine whether the decay rate of the most recalcitrant litter fraction may have varied between litter types. However, while the bioassay approach to testing litter quality variation does not provide decay rate coefficients applicable to the field, it may discriminate between subtle differences in litter chemistry, important to microbes, that might not be detected by standard chemical analyses and that might be masked when litters are decomposed under variable and heterogenous field conditions. Because temperature and moisture were held constant, decay rates were limited only by resource quality and the enzymatic potential of the microbes introduced into the system. In addition, the microbes that competed in this simple system were forced to rely solely on the energy and mineral sources provided by the litter without nutrient supplementation from throughfall, other litter species, or soil. The resultant decay curves thus reflected the chemical and physical characteristics of only the litter. If the sampling intervals during the bioassay are short, two-component models of decay can be applied to the data to estimate the abundance of labile and recalcitrant fractions as determined by the microbial decomposers in the bioassay system. The microbial bioassay approach may then be particularly useful in detecting differences in within-species litter quality caused by natural or anthropogenical variation in the environment.

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