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Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban-rural land-use gradient

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Abstract Using reciprocal leaf litter transplants, we investigated the effects of contrasting environments (urban vs. rural) and intraspecific variations in oak leaf litter quality on mass loss rates and nitrogen (N) dynamics along an urban-rural gradient in the New York City metropolitan area. Differences in earthworm abundances and temperature had previously been documented in the stands along this gradient. Red oak leaf litter was collected and returned to its original source stand as native litter to measure decay rates along the gradient. To separate site effects from litter quality effects on decay, reciprocal transplants of litter were also made between stands at the extremes of the environmental gradient (urban and rural stands). Land-use had no effect on mass loss and N dynamics of native litter by the end of the 22-month incubation period. The lack of differences in native litter suggests the factors affecting decay were similar across the stands in this study. However, in the transplant study both environment and litter type strongly affected decay of oak leaf litter. On average urban and rural litter decomposed faster over the incubation period in urban than in rural stands (P=0.016 and P=0.001, respectively, repeated measures ANOVA). Differences in mass loss between urban and rural stands resulted in rural environments having less mass remaining than urban environments at the end of the incubation period (25.6 and 46.2% for urban and rural sites, respectively). Likewise, less N remained in leaf residue in urban sites (71.3%) compared to that in rural sites (115.1%). Litter type also affected mass loss rates during the 22-month incubation period. On average rural litter mass loss rates were faster than urban litter rates in both urban and rural stands (P=0.030 and P=0.026, respectively, repeated measures ANOVA). By the end of the incubation period, rural litter exhibited 43 and 20% greater mass loss and retained 44 and 5% less N than urban litter decomposing in the same urban and rural sites, respectively. These results suggest that different factors were controlling mass loss and N release rates along this urban-rural gradient. In urban stands, exotic earthworms and warmer temperatures may be compensating for what would otherwise be slowly decaying leaf litter because of its lower quality. Likewise, the lower quality litter produced in the urban stands may be decreasing the net release of N from litter despite higher temperatures and earthworm activity. Even though native litter decay rates were similar, the differential importance of the factors affecting decay along this gradient could alter the response of these forests to disturbance and variations in climate.

Keywords Decomposition · Earthworms · Forests · Litterbags · Litter quality

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Introduction

The importance of climate on litter decomposition rate at regional and global scales has been demonstrated by Fox and Van Cleve (1983), Meentemeyer and Berg (1986), and Johansson (1994). At local and regional scales where climatic variation is small, litter chemistry, especially nitrogen and lignin concentrations, becomes a stronger determinant of variations in decay rate of organic materials (Merrill and Cowling 1966; Fogal and Cromack 1977; Melillo et al. 1982; Berg and McClaugherty 1987; Geng et al. 1993).

At local scales, litter quality is primarily determined by plant species composition and the timing and duration of leaf fall. Large variations in leaf litter quality have been measured among a broad range of species (Berg and McClaugherty 1987), whereas variation within species is

less pronounced. In some instances, however, large annual differences in within-species leaf litter quality have been measured (e.g., Taylor and Parkinson 1988). Variation within species occurs because of site quality differences that affect plant growth rates and nutrient use efficiencies (Birk and Vitousek 1986), or stochastic events that affect normal leaf abscission processes, such as prevailing climatic conditions (Carlisle et al. 1966) and wind storms (Sykes and Bunce 1970). Moreover, there is increasing evidence that atmospheric pollutants, such as ozone and acidic compounds, can influence litter quality (Smith 1990; Findlay et al. 1996). These compounds can alter the physical and chemical quality of foliage, directly by mechanisms of wet and dry deposition and stomatal uptake (Schaefer and Reiners 1990), or indirectly through modifications of plant metabolism (Nihlgard 1985), and changes in soil nutrient status (Haines and Carlson 1989).

Forest stands in or near urban areas can be highly polluted (Inman and Parker 1979; Airola and Buchholz 1984; Grodzinski et al. 1984) and therefore plant foliage in these areas may be exposed to O_3, SO_x, and NO_x gases, and to heavy metals. As a result, the quality of litter falling in stands growing in or adjacent to metropolitan areas can differ from that of the same plant species in less densely populated areas that are exposed to less pollution. For example, increased rates of decomposition and N mineralization were reported by Fenn and Dunn (1989) and Fenn (1991) in coniferous stands along an ozone and N deposition gradient in southern California. They attributed the increased decay rates to higher N content of litter in the polluted sites. Kuperman (1999) found similar results in oak-hickory forests along a historic gradient of nitrogen and sulfur deposition in the Ohio River valley. In contrast, Berg et al. (1991) explained decreased rates of coniferous litter decomposition in a heavily polluted site by heavy metal accumulations that occurred in foliage prior to needle drop.

The New York City metropolitan area provides an excellent opportunity for studying the effects of atmospheric pollution on litter quality (Pouyat et al. 1995; Carreiro et al. 1999). In previous studies conducted there, soil properties and soil biota were measured in unmanaged oak stands along an urban-rural transect (Pouyat et al. 1994, 1995). This research indicated that environmental factors with the potential for affecting decomposition rates differed substantially along the transect, including 2–3°C higher temperatures and up to five-fold differences in heavy metal and total salt concentrations measured in the upper 10 cm of soil in the urban than in the suburban and rural stands. Fungal biomass in oak litter was higher in rural than in suburban and urban stands (Pouyat et al. 1994), while abundance of exotic earthworms was higher in urban than in suburban and rural stands (Steinberg et al. 1997). The net result of the changes in soil temperature and soil organism abundances on decomposition was that in situ decay of a single litter type, or reference litter, varied greatly across the transect, with urban stands having higher rates than their suburban and rural counterparts (Pouyat et al. 1997). Moreover, laboratory incubations of red oak (*Quercus rubra* L.) litter collected along the transect demonstrated that senesced oak leaves collected from the rural stands decomposed more rapidly than suburban and urban leaves (Carreiro et al. 1999). These results suggest that while urban conditions tend to accelerate decay, urban litter quality may tend to decrease decay rates.

The purpose of the present study was to determine the net effects of contrasting environmental conditions along this land-use gradient on in situ rates of decomposition of red oak leaf litter. We used reciprocal transplants of red oak leaf litter between urban and rural forest stands to separate the relative importance of environmental factors (litter fungi, exotic species of earthworms, and temperature) versus litter type in controlling mass loss rates along the gradient. By performing a transplant experiment, differences in environmental conditions were detected by comparing mass loss rates within the same litter type placed in both sites; likewise, the contribution of differences in litter quality to decay rates can be assessed by comparing litters from the two different sites decaying in the same stands. Based on the results of Carreiro et al. (1999), we expected that urban litter would decompose at a slower rate than rural litter incubating in the same stands. In addition to the transplant comparisons, we compared native litter mass loss rates among urban, suburban, and rural stands to determine the net effect of the environment associated with contrasting land-use and litter type on decomposing litter. The net effect of the environment and litter type should depend on the relative importance of differences in litter quality, fungal and nonnative earthworm abundances, soil temperature, and other environmental factors along this urban-rural transect. If differences in litter quality as shown by Carreiro et al. (1999) override other environmental factors, then rural stands should have higher decay rates than urban stands with suburban stands having intermediate rates. The reverse should be true if earthworm activity and soil temperature, which were found to be higher in urban than in rural stands (Pouyat et al. 1997; Steinberg et al. 1997), are more important than litter quality in affecting decay rates along this land-use gradient.

Materials and methods

Site descriptions

In a previous study (Pouyat 1992), a 20-km-wide by 130-km-long belt transect was established along an urban-rural land-use gradient (Fig. 1). Forest stands were assigned to an urban, suburban, or rural land-use type based on adjacent human population density, road density, urban cover (%), and distance from the urban core (Medley et al. 1995; Pouyat et al. 1995). Forest stands were selected using the following criteria: (1) location on upland sites on either of two soil series (Hollis and Charlton), both of which are classified as well-drained, moderate to shallow, sandy loam inceptisols in the Dystrochrepts group that vary only in depth to bedrock (Gonick et al. 1970; Hill et al. 1980); (2) oak-dominated forest with *Quercus rubra* L. and *Q. velutina* Lam., both of the subgenus *Erythrobalanus*, as major components of the overstory (40–80% of total basal area); (3) minimum stand age of 70 years; and (4) no visual

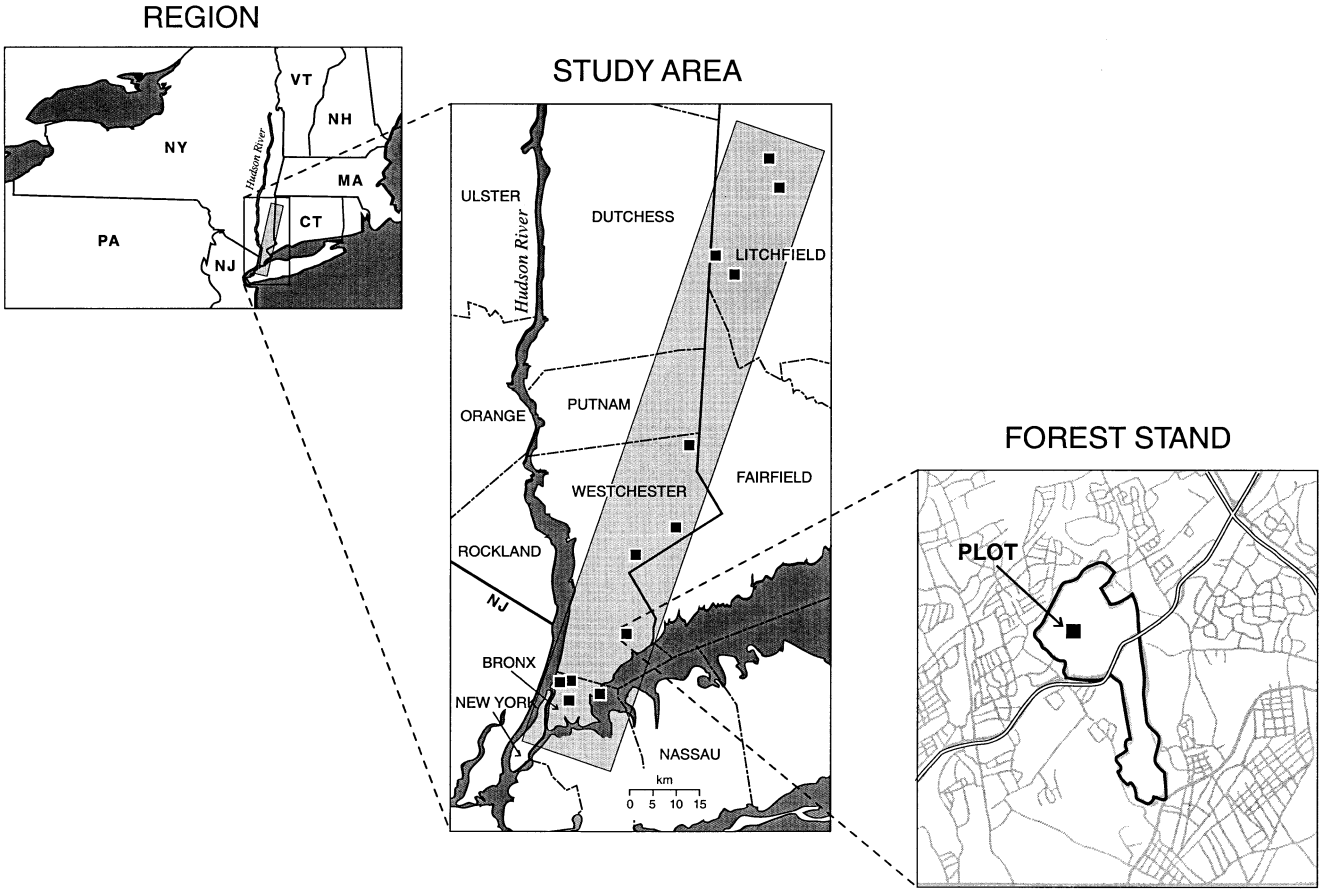

Fig. 1 Location of the urban-rural transect in the New York metropolitan area. Transect runs from highly urbanized Bronx, New York, to rural Litchfield County, Connecticut. Twelve oak plots (*solid squares*) were established along the transect: four urban (Bronx, NY), four suburban (Westchester County, NY), and four rural (Litchfield County, CT) land-use types, respectively. Criteria used to determine the "land use" context for each plot is explained in the text. Description of soils for each stand is presented in Table 1

evidence of natural disturbance and no documented evidence of direct human disturbance (e.g., fire, logging) for at least 70 years. By design, none of the study sites included a significant proportion of non-native tree species. Based on previous measurements, however, there were significant differences in abundances of non-native species of earthworms and soil organic horizon characteristics between plots. The urban, suburban, and rural plots have on average 25.0, 7.0, and 2.5 individuals per m^2 of non-native species of earthworms, respectively (Steinberg et al. 1997). These include individuals of the Megascolecidae (*Amynthas agrestis* and *A. hawayanus*) and Lumbricidae (*Lumbricus rubellus* and *Dendrobaena octoedra*). Moreover, all of the urban plots and a few suburban plots have mull soil organic horizons (Pouyat 1992; Zhu and Carreiro 1999), which are forest soils that do not have well-defined surface organic horizons due to high earthworm activity. A more detailed description of the study area is given in Pouyat (1992), Medley et al. (1995), and Pouyat et al. (1995). Originally, nine oak stands were located along the transect and in each stand, three 20×20-m plots were established (27 total) in which soil characteristics, soil organism abundances and decomposition rates of a reference litter type had been previously measured (Pouyat et al. 1994, 1995, 1997; Steinberg et al. 1997). For this study, a subset of 12 plots was randomly selected from the original 27 (Pouyat 1992). Each plot was divided into sixteen 5×5-m (0.025 ha) quadrats. The urban plots were located in the New York Botanical Garden Forest (N2, N3), Van Cortlandt Park (V3), and Pelham Bay Park (P1) in the Bronx, New York. The suburban plots were located in Saxon Woods Park (S1, S2) and Mountain Lakes Park (M2, M3), both in Westchester County, New York. The rural plots were located in Housatonic State Forest (H1, H3) and Mohawk State Forest (MF1, MF3) in Litchfield County, Connecticut (Table 1).

Litter collection and chemical analyses

Leaves of red oak were collected in eight plastic baskets in late October 1989 at each plot. Ten 4-g subsamples of litter from each plot were oven dried at 60°C to a constant weight to calculate a correction factor for converting air-dry to oven-dry weights. These subsamples were then milled and ashed at 450°C for 4.5 h to determine ash-free dry weights. Total C and N concentrations, reported on a percentage basis, were measured using a Carlo Erba CNS analyzer (Strumentezione, Italy). Mass loss and N concentration data were used to calculate changes in the absolute amount of N (net N immobilization or release) during the incubation period. Lignin was assayed using the acid detergent method of Van Soest et al. (1991) at the laboratories of Agway, Ithaca, N.Y.

Native litter and litter transplant experiment

Decomposition rates and nitrogen dynamics of leaf litter were quantified using bags with an inside area of 15×15 cm constructed of fiberglass window screen material (1.7 mm mesh). This mesh size allows access to most microarthropods, free living nematodes, and small or immature earthworms (Swift et al. 1979). Litterbags were filled with approximately 3 g of air-dried leaves per bag, placed on the mineral soil surface, and covered with leaf litter. To

Table 1 Description of soils in 12 plots along land-use gradient in New York City metropolitan area. Values are the mean of 4 composited samples (10-cm depth) for each plot. Standard errors are given in parentheses. Refer to text for names to plot abbreviations. Adapted from Pouyat (1992) and Zhu and Carreiro (1999)

Land-use Type	Site	Site description	pH	SOM (%)	Organic C (g kg^{-1})	Total N (g kg^{-1})	Sand (%)	Clay (%)
Urban	N2	Mull/mor soil, earthworms present	4.23	10.9 (0.2)	6.8 (0.2)	0.28 (0.01)	71.5 (1.5)	9.9 (0.7)
	N3	Mull soil, mixed by earthworms	4.45	9.4 (0.2)	5.4 (0.4)	0.27 (0.02)	72.9 (0.7)	9.7 (0.9)
	P1	Mull soil, mixed by earthworms	4.40	12.1 (0.3)	9.0 (1.4)	0.36 (0.03)	71.7 (1.1)	9.6 (1.3)
	V3	Mull soil, mixed by earthworms	4.85	8.3 (0.5)	4.8 (0.4)	0.21 (0.02)	74.3 (1.3)	9.0 (0.5)
Suburban	M2	Mor soil, 1–2 cm Oa layer	4.35	8.5 (0.3)	4.9 (0.5)	0.31 (0.04)	71.4 (1.0)	9.9 (0.6)
	M3	Mor/mull soil, earthworms present	4.41	6.5 (0.2)	3.9 (0.7)	0.26 (0.05)	78.1 (0.9)	8.7 (0.6)
	S1	Mor soil, 1–2 cm Oa layer	4.50	9.3 (0.5)	4.6 (0.4)	0.22 (0.02)	70.5 (2.7)	12.6 (0.8)
	S2	Mull/mor soil, earthworms present	4.55	11.4 (0.7)	5.3 (0.6)	0.27 (0.02)	67.0 (1.5)	13.7 (1.0)
Rural	H1	Mor soil, 1–2 cm Oa layer	4.70	7.02 (0.8)	5.7 (1.0)	0.26 (0.04)	71.4 (2.1)	11.0 (0.4)
	H3	Mor soil, 1–2 cm Oa layer	4.52	4.9 (0.2)	2.5 (0.5)	0.11 (0.01)	74.1 (2.7)	7.5 (2.5)
	MF1	Mor soil, 1–2 cm Oa layer	4.52	12.1 (0.7)	6.1 (0.4)	0.27 (0.02)	72.1 (1.0)	10.6 (1.1)
	MF3	Mor/mull soil, few earthworms present	4.75	7.6 (0.4)	6.1 (0.8)	0.25 (0.02)	75.3 (0.5)	9.7 (0.7)

separate site effects from litter quality effects on litter decay, reciprocal transplants of litter (transplant litter) were made between stands at the extreme ends of the environmental gradient (urban and rural stands). In addition, part of the litter collected from each stand was returned to its original source stand for the urban and rural sample locations. We refer to this material as native litter. To allow for a comparison of native litter mass loss rates along the entire urban-rural gradient (including urban, rural and suburban land-use types), litter was also collected in suburban stands and returned to its original source stand. Four litterbags, each of native and transplanted litter, were placed in each of 4 randomly selected quadrats per plot in early November 1989 resulting in a total of 48 sample locations (12 plots x 4 quadrats) along the gradient. Litter bags were collected from each of the quadrats in mid-August and late November 1990 and in late July and late August 1991 (n=4 bags/plot/date). The residual litter from each bag was oven dried; separate subsamples were ashed or analyzed for total C and N as were the initial litter subsamples.

Over the 22-month incubation field period, soil contamination was evident in the litter bags, particularly in bags from the urban plots. Therefore, oven-dried litter mass and N concentration were corrected for soil contamination before litter mass was calculated in all bags using the soil correction equation from Blair (1988). This equation calculates the fraction of litterbag content that is actually litter, based on any reduction in the percentage of ash-free dry mass of the sample from soil contamination. Litter nitrogen concentrations were corrected using the percentage of N that actually is in the residual litter, based on the fraction of the sample that is soil and the percentage of N in that soil (Blair 1988).

Data analysis

The transplant study was designed with two litter types (urban and rural) and two site levels (urban and rural). Four two-way analyses of variance (ANOVA) were performed to determine the treatment level effects of litter type and site environment on litter mass, N content, N concentration, and C-to-N ratios in the residue after the 22-month incubation period among the land-use environments, hereafter referred to as land use (SAS Institute, Cary, N.C.). Hochberg's Method for unequal sample sizes (SAS Institute) was used to test differences between final means of nitrogen variables and litter mass for the different land use and litter types.

Repeated measures ANOVA (SAS Institute) was used to examine differences in mass loss and N release rates for transplanted litter between urban and rural stands and for native litter among urban, suburban, and rural stands. In this procedure, a univariate ANOVA tests for between-subject effects using the average value over time for an unbiased analysis of main effects (SAS Institute 1987). A profile contrast (SAS Institute) was performed along with the repeated measures analysis to determine nth successive differences in collection dates among land-use environments. Reciprocal transformations were performed for percent mass remaining and percent N remaining data prior to statistical analyses to stabilize the variance.

Results

Native litter

Comparing litter decay rate in its site of origin allows us to look at the net effect of both site environment and litter quality on decomposition. There were no statistical differences in native litter mass loss, percentage of original amount of N remaining, N concentration, or C-to-N ratios by the end of the 22-month field incubation period (Fig. 2). Certain trends, however, were evident. After 5 months, mass loss for urban litter was consistently greater (differences of 15–30% on average) than for the suburban and rural native litter (Fig. 2a). Moreover, urban and suburban litter retained from 10 to 15% and 5 to 35% more N than rural litter for the first year of incubation, but by the end of 22 months this relationship had reversed with only the urban litter exhibiting a net loss of N from the litter bags (Fig. 2b). Otherwise, all three native litter types (urban, suburban, and rural) showed no consistent differences in mass loss and N retention along the transect (Fig. 2).

Litter transplants

Rate measurements

Site conditions affected mass loss rates during the 22-month incubation period (Tables 2, 3). On the average urban litter decomposed faster over the 22-month field incubation period in urban than in rural stands (P=0.016 by repeated measures ANOVA) (Table 2). A profile contrast in the repeated measures procedure indicated a significant (P=0.050) difference during the 6- to 9-month incubation interval in percentage mass lost from urban

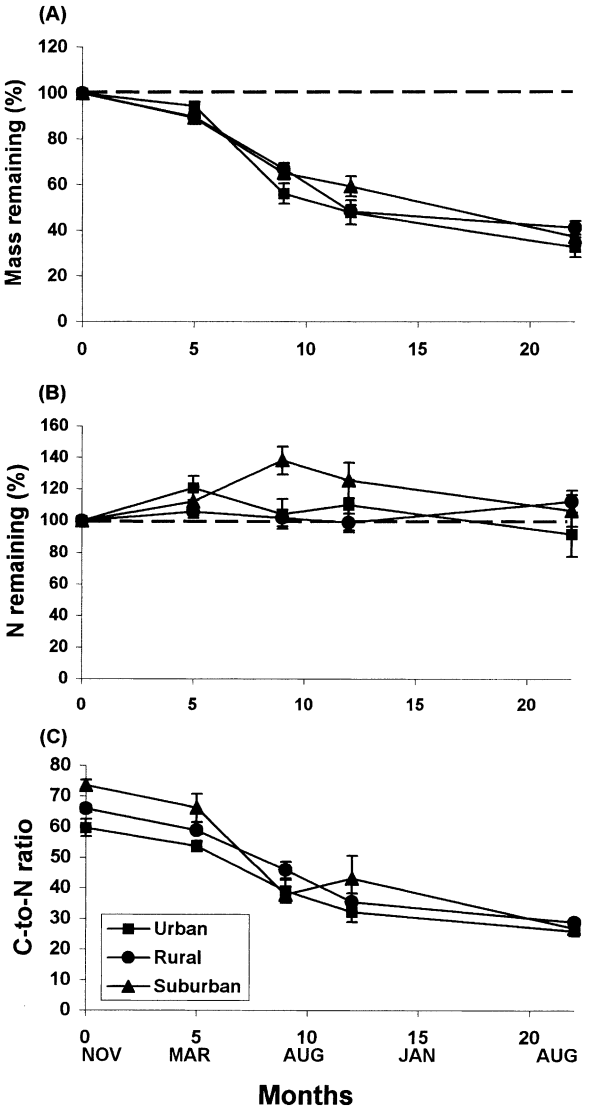

Fig. 2 Changes in mean (±SE) of residual mass (**a**), N content (**b**), and C-to-N ratio (**c**) for native red oak leaves decomposing in litter bags over a 22-month decay period in forest stands along the urban-rural transect; values are the means of four plots per land-use type (16 litter bags per land-use type each sampling period)

litter between urban and rural stands (Fig. 3a). Likewise, a profile contrast detected a difference in mass loss rates of rural litter between urban and rural stands during the 6- to 9-month interval when % mass remaining at both sites decreased from 90% to 70% and 45% in the rural and urban stands, respectively (P=0.030) (Fig. 3b). Similar to the urban litter, rural litter on the average decomposed faster in urban than in rural stands (P=0.001 by repeated measures ANOVA) (Table 3).

Litter type also affected mass loss rates during the 22-month incubation period (Tables 4, 5). On the average rural litter mass loss rates were faster than urban litter rates in both urban and rural stands (P=0.030 and P=0.026, respectively, using repeated measures ANOVA) (Tables 4, 5). In rural stands, a profile contrast in the

Table 2 Repeated measures ANOVA results comparing the residual mass and N content, percent N, and C-to-N ratio of urban red oak litter incubated in the rural and urban stands after 22 months (data are summarized in Figs. 3, 4, 5, 6)

Source	*df*	MSE	*F*	*P*
Mass remaining (%)				
Land-use Type	1	0.69223	12.68	0.016
Error	5	0.05459		
N remaining (%)				
Land-use type	1	0.00003	2.36	0.185
Error	5	0.00002		
N (%)				
Land-use type	1	0.31460	3.85	0.107
Error	5	0.08170		
C-to-N				
Land-use type	1	101.931	1.47	0.279
Error	5	69.260		

Table 3 Repeated measures ANOVA results for residual mass and N content, percent N, and C-to-N ratio of rural red oak litter incubating in the rural and urban stands after 22 months (data are summarized in Figs. 3, 4, 5, 6). Statistical analyses were performed where appropriate on transformed data (reciprocal transformation for percentage mass and N content remaining)

Source	*df*	MSE	*F*	*P*
Mass Remaining (%)				
Land–Use Type	1	1.94182	67.08	0.0004
Error	5	0.02895		
N Remaining (%)				
Land–Use Type	1	0.00017	52.14	0.0008
Error	5	0.00000		
N (%)				
Land–Use Type	1	0.13037	2.14	0.203
Error	5	0.06083		
C–to–N				
Land–Use Type	1	44.6009	0.85	0.399
Error	5	52.39525		

Table 4 Repeated measures ANOVA results for residual mass and N content, percent N, and C-to-N ratio of urban and rural litter incubating in the urban stands after 22 months (data are summarized in Figs. 3, 4, 5, 6). Statistical analyses were performed where appropriate on transformed data (reciprocal transformation for percentage mass and N content remaining)

Source	*df*	MSE	*F*	*P*
Mass remaining (%)				
Litter type	1	0.78693	10.85	0.030
Error	4	0.07256		
N remaining (%)				
Litter type	1	0.00007	5.09	0.087
Error	4	0.00001		
N (%)				
Litter type	1	0.00165	0.06	0.817
Error	4	0.02704		
C-to-N				
Litter type	1	20.34813	0.39	0.565
Error	4	51.87364		

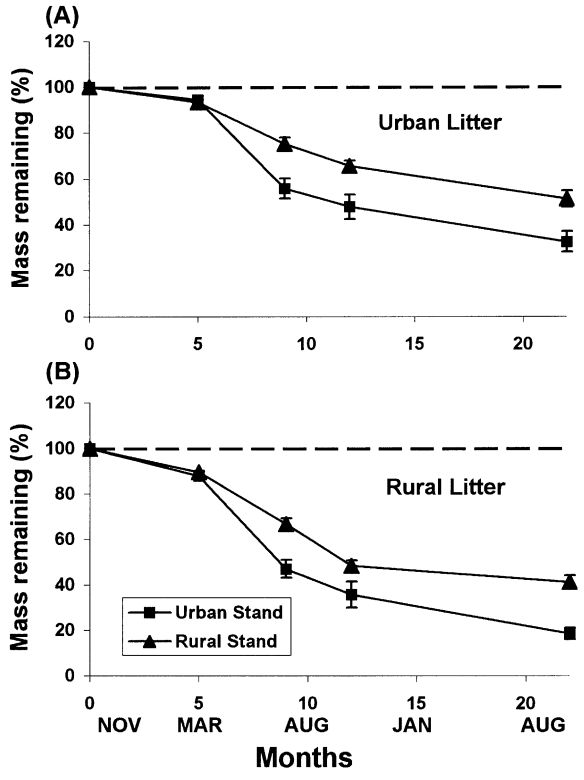

Fig. 3 Changes in mean (±SE) of residual mass of urban oak leaf litter decomposing in urban and rural stands (**a**), and rural oak leaf litter decomposing in urban and rural stands (**b**) over a 22-month decay period; values are the means of four plots per land-use type (16 litter bags per land-use type each sampling period)

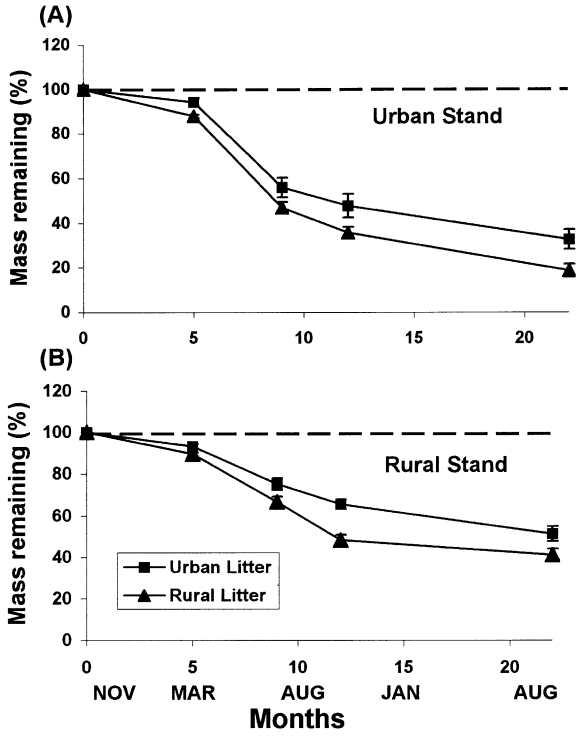

Fig. 4 Changes in mean (±SE) of residual mass of urban and rural oak leaf litter decomposing in urban stands (**a**), and rural stands (**b**) over a 22-month decay period; values are the means of four plots per land-use type (16 litter bags per land-use type each sampling period)

Table 5 Repeated measures ANOVA results for residual mass and N content, percent N, and C-to-N ratio of urban and rural litter incubating in the rural stands after 22 months (data are summarized in Figs. 3, 4, 5, 6). Statistical analyses were performed where appropriate on transformed data (reciprocal transformation for percentage mass and N content remaining)

Source	*df*	MSE	*F*	*P*
Mass remaining (%)				
Litter type	1	0.10439	8.59	0.026
Error	6	0.07284		
N remaining (%)				
Litter type	1	0.00000	1.02	0.352
Error	6	0.00000		
N (%)				
Litter type	1	0.00507	0.06	0.813
Error	6	0.08323		
C-to-N				
Litter type	1	2.60970	0.04	0.845
Error	6	62.56078		

repeated measures procedure detected a statistical difference (P=0.001) in mass loss between urban and rural litter during the 9- to 12-month interval when % mass remaining for urban and rural litter types decreased 75 and 65% to 60 and 50%, respectively (Fig. 4b).

Site environmental conditions had substantial effects on changes in N content for rural litter over the 22-month incubation period (Fig. 5b). The ANOVA repeated measures analysis detected large differences in relative N dynamics of the rural litter decaying in rural and urban stands (P<0.001) (Table 3). A profile contrast of changes in N content of rural litter detected a statistical difference between urban and rural stands during the 9- to 12-month interval (P=0.030) (Fig. 5b). Moreover, by the end of the 22-month period the percentage of original N remaining in the rural litter residue was more than 2 times greater in rural than in urban stands (110 and 50%, respectively), indicating a higher rate of litter N loss from rural litter in the urban than in the rural stands (Fig. 5b).

Litter effects were not statistically detectable for changes in N content in either urban or rural stands (Tables 4, 5). However, on average rural litter lost approximately 25% more N than urban litter in the urban stands (P=0.087) (Table 4). Net N loss from litter occurred for both litter types in the urban stands (Fig. 6a), while in rural stands both litter types accumulated N throughout the field incubation period (Fig. 6b). There were no statistically significant site or litter effects detected for changes in N concentration or C-to-N ratios of remaining litter residue during the entire 22-month incubation period (Tables 2, 3, 4, 5).

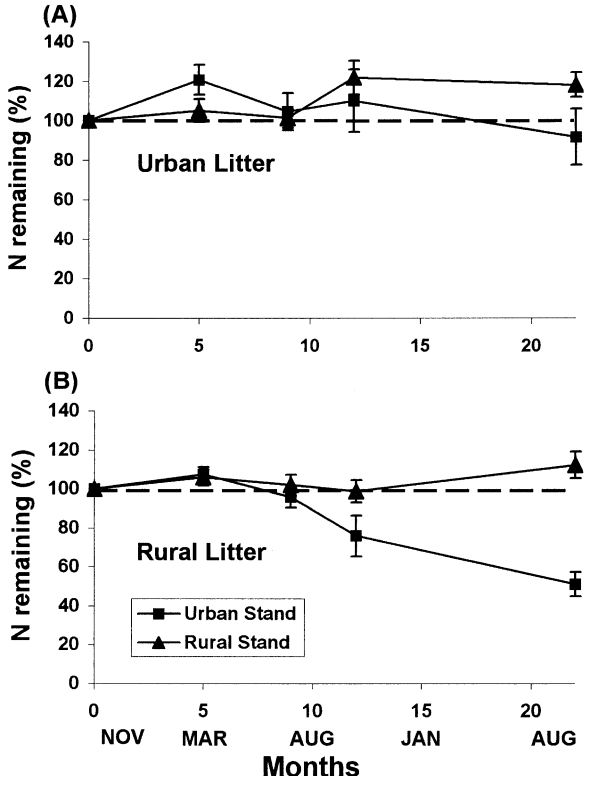

Fig. 5 Changes in mean (±SE) of residual N content of urban oak leaf litter decomposing in urban and rural stands (**a**), and rural oak leaf litter decomposing in urban and rural stands (**b**) over a 22-month decay period; values are the means of four plots per land-use type (16 litter bags per land-use type each sampling period)

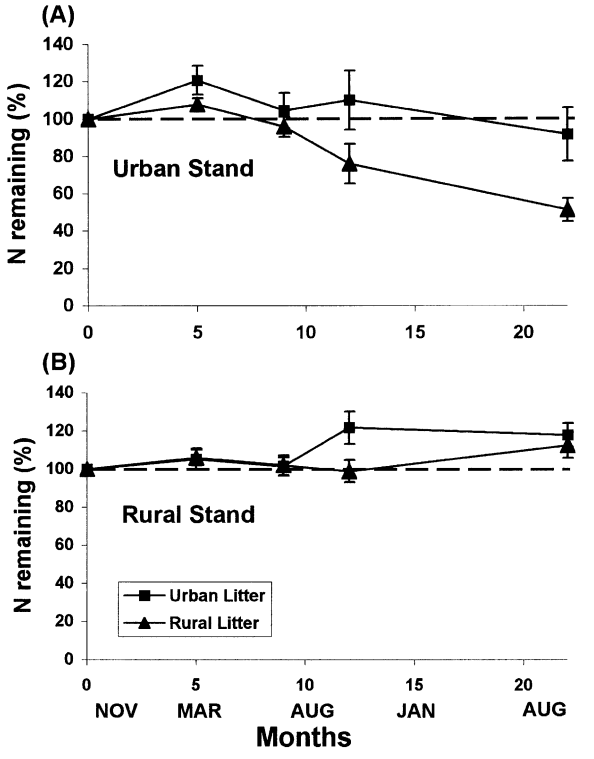

Fig. 6 Changes in mean (±SE) of residual N content of urban and rural oak leaf litter decomposing in urban stands (**a**), and rural stands (**b**) over a 22-month decay period; values are the means of four plots per land-use type (16 litter bags per land-use type each sampling period)

Final collection date measurements

Site-specific environmental factors had consistent effects on mass loss and relative N dynamics by the end of the incubation period (Table 6). Environmental differences associated with land use affected overall mass loss with the average percentage of mass remaining after 22 months being 25.6 and 46.2% for urban and rural sites, respectively (P=0.001 in a two-way ANOVA) (Tables 6, 7). Likewise, the average net N remaining for each land-use type differed greatly with less N retained in urban than in rural sites (71.3 and 115.1% of original N remaining per bag, respectively; P<0.001 in a two-way ANOVA) (Tables 6, 7).

While there were statistical differences of mass loss and N dynamics between urban and rural stands, there were no detectible differences between litter types (Tables 6, 7). The interaction between land-use and litter types, however, was statistically significant for mass loss and the amount of N remaining (P=0.050 and P=0.040, respectively) as the rural litter consistently lost more mass and N than urban litter, and this mass loss was even greater when incubated in urban stands (Fig. 4).

Litter chemistry

Chemical analyses were performed to investigate the potential for differences in chemical constituents in the oak litter along the land-use gradient, and to determine

Table 6 Final means (±SE) after 22-month decay period of residual mass and N content, percent N, and C-to-N ratio of red oak litter by land–use and litter type. Litter was collected in urban and rural forest stands and reciprocally transported to the same urban and rural stands. Values are the mean of 4 plots per land-use type (urban vs. rural); n=4 bags per plot

Property	Treatment levels			
	Land-use type		Litter type	
	Urban	Rural	Urban	Rural
Mass remaining (%)	25.6 (3.5)	46.2 (3.3)	41.7 (4.0)	29.9 (2.8)
N remaining (%)	71.3 (10.2)	115.1 (6.5)	104.7 (10.7)	81.7 (6.5)
N (%)	2.2 (0.11)	2.1 (0.06)	2.1 (0.08)	2.2 (0.09)
C-to-N	26.2 (1.4)	25.9 (0.8)	26.4 (0.9)	25.6 (1.3)

Table 7 Two-way ANOVA results for residual mass and N content, and percent N and C-to-N ratio in residual litter material after 22-month decay period. Statistical analyses were performed where appropriate on transformed data (reciprocal transformation for percentage mass and N content remaining)

Source	*df*	MSE	*F*	*P*
Mass remaining (%)				
Land-use type	1	0.00213	11.83	0.001
Litter type	1	0.00011	0.59	0.447
Land use × litter	1	0.00072	4.03	0.050
N remaining (%)				
Land-use type	1	0.00020	12.70	<0.001
Litter type	1	0.00003	1.59	0.214
Land use × litter	1	0.00007	4.38	0.041
N (%)				
Land-use type	1	0.46521	1.92	0.172
Litter type	1	0.01480	0.06	0.806
Land use × litter	1	0.00420	0.02	0.896
C-to-N				
Land-use type	1	154.2248	0.90	0.346
Litter type	1	3.54270	0.02	0.886
Land use × litter	1	0.00065	0.00	0.999

whether these measurements were correlated with the variation in litter decay rates. Four indicators of litter quality that are known to affect decay rates were quantified for the red oak leaves prior to the field incubation. No consistent patterns existed among litter types for initial concentrations of N and lignin, and ratios of C-to-N and lignin-to-N (Table 8). Urban leaf litter had the highest percentage of N and lignin of the three land-use environments (8.6 and 9.6% higher concentrations than the suburban and rural litter types for N and lignin concentrations, respectively), though these differences were not statistically significant at $P<0.05$. For native litter field incubations, mass loss did not correlate to variations in litter quality, as measured by initial N and lignin concentrations or C-to-N ratio ($r=0.07$, 0.09, and 0.003, and $P=0.40$, 0.34, and 0.86, respectively).

Discussion

Native leaf litter decomposition rate did not differ among sights along the urban-rural land-use gradient (Fig. 2), which suggests the factors affecting mass loss and N dynamics of leaf litter would be similar across the stands included in this study. However, the reciprocal transplant experiment clearly shows that the mechanisms responsible for these patterns differed greatly along this urban-rural gradient (Figs. 3, 4, 5, 6). Comparisons of decay and N release rates between urban vs. rural red oak leaf litter within a land-use type showed that for this species of oak, leaf litter quality is significantly affected by site conditions (Figs. 4, 6a). Likewise, comparisons of mass loss and N release rates between urban vs. rural land-use types showed that site conditions also affected decomposition rates (Figs. 3, 5b).

Determining which aspect of the urban environment caused changes in site condition and litter quality along this urban-rural land-use gradient was not the focus of this study. Measurements made in earlier studies (Pouyat et al. 1994, 1995; Steinberg et al. 1997), along with additional site information collected in this study provide evidence on what specific factors were affecting decomposition and N release rates along the gradient.

Mass loss

The most notable result of the litter transplant manipulations was that rural litter decomposed more rapidly than urban litter regardless of environmental differences (Fig. 4). This was consistent with the Carreiro et al. (1999) study, which showed rural oak litter decomposed more rapidly than urban litter in laboratory incubations. However, unlike the Carreiro et al. (1999) study, which showed that initial lignin concentrations explained 50% of the variation in decay rate among litter types, there were no significant correlations between decay rate and litter quality indices measured in this study.

This discrepancy between laboratory and field incubations was not surprising since field decay rates of the native litter did not differ along the urban-rural gradient

Table 8 Chemical composition before decay of red oak leaf litter collected from forest plots surrounded by urban ($n=4$), suburban ($n=4$), and rural ($n=4$) land-use types. Refer to text for names to plot abbreviations

Plot	Land use	N(%)	C:N	Lignin(%)	Lignin:N
N2	Urban	0.93	55.1	26.8	25.9
N3	Urban	1.03	51.7	27.3	28.1
V3	Urban	0.92	55.0	30.5	30.2
P1	Urban	1.05	51.3	28.5	30.1
S1	Suburban	0.81	65.3	29.0	22.8
S2	Suburban	0.96	55.7	32.2	27.3
M2	Suburban	0.81	63.7	18.5	35.8
M3	Suburban	1.04	50.8	28.4	33.5
MF1	Rural	0.84	61.9	25.4	27.1
MF3	Rural	0.88	58.5	26.5	33.2
H1	Rural	0.97	54.6	25.2	28.8
H3	Rural	0.93	55.5	26.1	26.5
Urban mean (SE)		0.98 (0.03)	53.3 (1.03)	28.3 (0.82)	28.9 (1.50)
Suburban mean (SE)		0.91 (0.06)	58.9 (3.41)	27.0 (2.96)	29.9 (2.95)
Rural mean (SE)		0.91 (0.03)	57.6 (1.65)	25.8 (0.30)	28.6 (1.01)

(Fig. 3). Nevertheless, the lack of correlation between decay rates and initial N and lignin concentrations of litter of the same species contrasts with results reported for comparisons of leaf litter of different species where strong relationships have been found between initial lignin:N ratios and decay rates (Mellilo et al. 1982; Berg and Staaf 1981). As in our study, Johansson (1994) made comparisons of litter of the same species (*Pinus sylvestris*) along an environmental gradient in Sweden and found large differences in litter quality, but did not find strong correlations between initial lignin concentration and mass loss. In ecosystems where soil macroinvertebrate activity is relatively high, lignin and N concentrations may not explain variations in decay rate. The high earthworm activity and fragmentation rates measured in previous studies for these urban stands (Pouyat et al. 1997; Steinberg et al. 1997) may then explain the poor correlations between mass loss and lignin and N concentrations obtained in this study. Staaf (1987) found similar results using beech litter transplants, where lignin and N concentration failed to explain an observed increase in decomposition rate in a mull humus soil, compared to a mor soil, when using litter bags that allowed entry by earthworms. When earthworms were excluded, decay rates were highly correlated with lignin and N concentrations (Staaf 1987). Moreover, earthworm feeding on litter has been shown to increase lignin mineralization while not altering the overall rate of CO_2 production (Scheu 1993), thereby affecting the relationship between initial lignin concentrations and mass loss rate.

In addition to macroinvertebrate activity, secondary metabolites other than lignin (e.g., other polyphenolic compounds such as tannins) may override the effects of lignin and N concentrations on decay rate (Horner et al. 1988). In urban areas tissue damage from air pollution, such as ozone, can result in the polymerization of carbon-based and N-containing secondary metabolites in plant foliage (Jordan et al. 1991; Findlay et al. 1996). Since our study makes an intraspecific comparison of leaf decay, a secondary factor affecting litter quality may be the cause of differences in decay rate between urban and rural derived red oak litter. Our repeated measures analysis suggested that the greatest differences in mass loss rates between the two litter types occurred during the first year when differences in plant secondary metabolites are expected to have the greatest effect on decay (Horner et al. 1988) (Fig. 4). However, results from our earlier laboratory incubations of urban, suburban, and rural oak litter did not show significant relationships between bound and unbound polyphenolic compounds and decay rate even though the early separation between decay curves of rural and urban oak litter also occurred in these laboratory incubations (Carreiro et al. 1999).

In addition to the effect of litter type, a site effect on mass loss was detected since litter, particularly rural litter, placed in the urban stands decayed faster than those placed in the rural stands (Fig. 3). Mean soil temperature (2 cm depth, averaged over the year) was 2°C higher in the urban than in the rural stands (Pouyat 1992). This can account for as much as 20% of the difference in mass loss rate between urban and rural sites, assuming a doubling of decay rate with a 10°C increase in temperature (Pouyat et al. 1997).

Besides site differences in temperature, the rapid mass loss measured in the urban stands can be partly attributed to fragmentation by earthworms (Pouyat et al. 1997). Although the mesh size of the litterbags (1.7 mm) is relatively small for most earthworm species (Swift et al. 1979), small and immature earthworms were found in bags upon collection, and leaf skeletonization, a characteristic of earthworm activity (Lee 1985), was observed primarily in litterbags collected from the urban stands. In addition, a previous study found that earthworm abundance and biomass along the transect was an order of magnitude higher in urban than in rural stands (Steinberg et al. 1997). Otherwise, a higher rate of decomposition would not be expected since Pouyat et al. (1994) found reduced litter fungal biomass and densities of mycophagous soil fauna in urban stands. The fact that the rural litter exhibited a larger response than the urban litter to the effect of site suggests that the macrofauna, of which earthworms are a significant component in urban stands, were feeding more easily on the rural litter. This is consistent with studies of earthworm feeding preferences, which have shown that worms selectively feed on higher quality litter (Luxton 1982).

There were no differences between the urban, rural, and suburban stands in mass loss and N dynamics of native litter (Fig. 2) even though differences in leaf litter quality (Carreiro et al. 1999), site environment (Pouyat and McDonnell 1991; Pouyat et al. 1995), and soil biota (Pouyat et al. 1994; Steinberg et al. 1997) were measured in these stands in previous studies. If we compare, however, the rural litter incubating in both urban and rural sites, a situation where no differences in litter quality should exist, we find significantly higher mass loss rates in the urban than in rural stands (Fig. 3). This indicates that site factors in the urban stands promote more rapid decay than those in the rural stands. A separate litterbag experiment using a single litter type (*Acer saccharum*) revealed the same trend (Pouyat et al. 1997). Since the transplant experiment showed that urban oak litter decomposed more slowly than rural oak litter, it is also probable that without earthworms or warmer soil temperatures, rates of mass loss of native oak litter would have been slower in the urban than in the rural stands.

N dynamics

Not only did mass loss rates differ between urban and rural litter, but N dynamics did as well (Figs. 5b, 6a). In this study, both urban and rural litters accumulated N during most of the 22-month incubation period (N immobilization phase). By the end of the study, however, a net release of N was observed only in rural litter placed in the urban stands (Fig. 5b). The net release of N from the rural litter bags in the urban stands coincided with a

large loss of mass between 5 and 10 months, suggesting that this released N is part of the labile fraction of this litter. This is consistent with our previous findings that rural litter had a greater labile fraction than urban litter (Carreiro et al. 1999). In contrast, rural litter decomposing in rural stands continued to accumulate N in leaf litter residue during the 22-month period (Fig. 6b). This net accumulation of N in rural litter placed in the rural stands may be related to greater fungal colonization (and hence fungal N retention) of native oak litter in rural stands compared with native oak litter in urban stands that was reported in a previous study (Pouyat et al. 1994). Moreover, in another study the percentage of original N remaining after 6 months in sugar maple litter was strongly affected by leaf litter loss due to fragmentation in the urban stands (Pouyat et al. 1997). This finding suggests that at least part of the N release from the rural litter bags incubating in urban stands was due to fragmentation loss and ingestion by earthworms and other invertebrates, and not necessarily due solely to net mineralization losses by microbes.

Since mass loss rates of a reference litter were higher (Pouyat et al. 1997) and earthworm's more abundant (Steinberg et al. 1997) in urban than in rural stands, the N release rates from oak litter decaying in urban stands would be much higher, if the urban oak litter responded as the rural litter (Fig. 5b). The results of this study, therefore, suggest that urban litter, with its' tendency for having relatively slow N release rates, may offset the tendency for urban site factors (such as higher earthworm abundances and warmer temperatures) to stimulate N loss rates from litter.

Differential effects of factors on mass loss and N dynamics

The relative contribution of site conditions and litter origin (litter type) on litter decomposition were separately quantified in this study by reciprocally transplanting leaf litter of the same species between forest stands that are differentially affected by urban environmental factors. By performing a transplant experiment, differences in site conditions were detected by comparing response variables within the same litter type placed in both sites; likewise, the potential contribution of differences in litter quality to decay rates can be assessed by comparing litters from the two different sites decaying in the same stands. We also compared the net effects of site environment and litter type on litter decomposition by comparing mass loss and N release rates of native litter among urban, suburban, and rural stands.

Although the net effects of site and litter type factors resulted in litter decay rates being similar in urban, suburban, and rural stands, opposing mechanisms (earthworm fragmentation vs. microbial mineralization; warmer vs. cooler temperatures) may result in very different ecosystem responses to environmental stress and disturbance along the urban-rural gradient. As an example, a reduction in earthworm activity due to drought could result in a disproportionate decrease in decomposition rates in the urban than in the rural forest stands. This disproportionate response could occur because earthworm activity appears to compensate for the lower fungal densities measured in the urban stands. Likewise, if the native litter in the urban stands was of the same quality as rural oak leaves and decay rates remained high, N release from the litter layer may increase substantially.

In conclusion, results from this study indicate that both environmental conditions and litter type had important effects on mass loss rates and N dynamics in litter residue along the urban-rural gradient. Oak litter produced in urban stands decomposed more slowly than oak litter produced in rural stands. This was consistent with results from laboratory bioassays that showed that the urban oak litter decayed more slowly than the rural oak litter (Carreiro et al. 1999). These results are particularly compelling since litter was collected for each study in different years (1989 vs. 1990, respectively) indicating that inter-annual variation in litter decomposability was small, and perhaps occurs consistently across years at these sites. We also found a poor relationship between mass loss rates and indices typically used to measure litter quality (e.g., N and lignin concentrations) in our field incubations in contrast to the laboratory incubations in Carreiro et al. (1999). These results suggest that under field conditions where factors affecting decomposition differ spatially these indices may be inadequate to predict the outcome of within-species incubations.

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References

Airola TM, Buchholz K (1984) Species structure and soil characteristics of five urban sites along the New Jersey Palisades. Urban Ecol 8:149–164

Berg B, McClaugherty C (1987) Nitrogen release from litter in relation to disappearance of lignin. Biogeochemistry 4:219–224

Berg B, Staaf H (1981) Leaching, accumulation, and release of nitrogen in decomposing forest litter. In: Persson T (ed.) Structure and function of northern coniferous forests: an ecosystem study. Ecol Bull 32:163–178

Berg B, Ekbohm G, Soderstromm B, Staaf H (1991) Reduction of decomposition rates of Scots pine needle litter due to heavy-metal pollution. Water Air Soil Pollut 59:165–177

Birk EM, Vitousek PM (1986) Nitrogen availability and nitrogen use efficiency in loblolly pine stands. Ecology 67:69–79

Blair JM (1988) Litter decomposition, nitrogen dynamics and litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. J Appl Ecol 25:683–698

Carreiro MM, Howe K, Parkhurst DF, Pouyat RV (1999) Variations in quality and decomposability of red oak leaf litter along an urban-rural gradient. Biol Fert Soils 30:258–268

Carsile A, Brown AHF, White EJ (1966) Litter fall, leaf production and the effects of defoliation by *Tortrix viridana* in a sessile oak (*Quercus petraea*) woodland. J Ecol 54:65–85

Fenn ME (1991) Increased site fertility and litter decomposition rate in high pollution sites in the San Bernardino Mountains. For Sci 37:1163–1181

Fenn ME, Dunn, PH (1989) Litter decomposition across an air-pollution gradient in the San Bernardino Mountains. Soil Sci Soc Am J 53:1560–1567

Findlay S, Carreiro M, Krischik V, Jones CG (1996) Effects of damage to living plants on leaf litter quality. Ecol Appl 6:269–275

Fogal R, Cromack K Jr. (1977) Effect of habitat and substrate quality on Douglas Fir litter decomposition in Western Oregon. Can J Bot 55:1632–1640

Fox JF, Van Cleve K (1983) Relationship between cellulose decomposition, forest floor nitrogen, and soil temperature in Alaskan U.S.A. Taiga forests. Can J For Res 13:789–794

Geng X, Pastor J, Dewey B (1993) Decay and nitrogen dynamics of litter from disjunct congeneric tree species in old-growth stands in northeastern China and Wisconsin. Can J Bot 71:693–699

Gonick WN, Shearin AE, Hill DE (1970) Soil survey of Litchfield County. USDA Soil Conservation Service, Washington, DC.

Grodzinski W, Weiner J, Maycock PF (1984) Forest ecosystems in industrial regions. Springer, Berlin Heidelberg New York

Haines BL, Carlson CL (1989) Effects of acid precipitation on trees. In: Adriano PC, Johnson AH (eds) Acid precipitation, vol 2: biological and ecological effects. Springer, Berlin Heidelberg New York, pp 1–27

Hill DE, Sauter EH, Gonick WN (1980) Soils of Connecticut. Conn Agric Exp St Bull 787

Horner JD, Gosz JR and Cates RG (1988) The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. Am Nat 132:869–883

Inman, JC, Parker GR (1978) Decomposition and heavy metal dynamics of forest litter in northwestern Indania. Env Pollut 17:34–51

Johansson MB (1994) Decomposition rates of Scots pine needle litter related to site properties, litter quality, and climate. Can J For Res 24:1771–1781

Jordan DN, Green TH, Chappelka AH, Lockaby BG, Meldahl RS, Gjerstad DH (1991) Response of total tannins and phenolics in loblolly pine foliage exposed to ozone and acid rain. J Chem Ecol 17:505–513

Kuperman RG (1999) Litter decomposition and nutrient dynamics in oak-hickory forests along a historic gradient of nitrogen and sulfur deposition. Soil Biol Biochem 31:237–244

Lee KE (1985) Earthworms: their ecology and relationships with soils and land use. Academic Press, Sydney, Australia

Luxton M (1982) Substrate utilization by the soil fauna. Oikos 39:340–341

Meentemeyer V, Berg B (1986) Regional variation in rate of mass loss of Pinus-Sylvestris needle litter in Swedish pine forests as influenced by climate and litter quality. J For Res 1:167–180

Medley KE, McDonnell MJ, Pickett STA (1995) Forest-landscape structure along an urban-to-rural gradient. Prof Geogr 47:159–168

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Merrill W, Cowling EB (1966) Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. Can J Bot 44:1555–1580

Nihlgard B (1985) The ammonium hypothesis – an additional explanation to the forest dieback in Europe. Ambio 14:2–8

Pouyat RV, McDonnell MJ (1991) Heavy metal accumulation in forest soils along an urban-rural gradient in Southern New York, U.S.A. Water Air Soil Pollut 57–58:797–807

Pouyat RV (1992) Soil characteristics and litter dynamics in mixed deciduous forests along an urban-rural gradient. PhD Dissertation, Rutgers University, New Brunswick, N.J.

Pouyat RV, Parmelee RW, Carreiro MM (1994) Environmental effects of forest soil-invertebrate and fungal densities in oak stands along an urban-rural land use gradient. Pedobiologia 38:385–399

Pouyat RV, McDonnell MJ, Pickett STA (1995) Soil characteristics of oak stands along an urban-rural land use gradient. J Environ Qual 24:516–526

Pouyat RV, McDonnell MJ, Pickett STA (1997) Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land-use gradient. Urban Ecosys 1:117–131

SAS Institute (1987) SAS Statistics User's Guide. SAS Institute, Cary, N.C.

Schaefer DA, Reiners WA (1990) Throughfall chemistry and canopy processing mechanisms. In: Lindberg SE, Page AL, Norton SA (eds) Acid precipitation, vol. 3: sources, deposition and canopy interactions. Springer, Berlin Heidelberg New York, pp 241–284

Scheu S (1993) Litter microflora-soil macrofauna interactions in lignin decomposition: a laboratory experiment with 14C-labelled lignin. Soil Biol Biochem 25:1703–1711

Smith WH (1990) Air pollution and forests: interaction between air contaminants and forest ecosystems, 2nd edn. Springer, Berlin Heidelberg New York

Staaf H (1987) Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. Oecologia 72:58–6

Steinberg DA, Pouyat RV, Parmelee RW, Groffman PM (1997) Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. Soil Biol Biochem 29:427–430

Swift MJ, Heal OW, Anderson JM (1979) Studies in ecology, vol 5: decomposition in terrestrial ecosystems. Blackwell, Oxford

Sykes JM, Bunce RGH (1970) Fluctuations in litter-fall in a mixed deciduous woodland over a three-year period. Oikos 21:326–329

Taylor BR, Parkinson D (1988) Annual differences in quality of leaf litter of aspen (*Populus tremuloides*) affecting rates of decomposition. Can J Bot 66:1940–1947

Van Soest PJ, Robertson RB, Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. J Dairy Sci 74:3583–3597

Zhu W, Carreiro MM (1999) Chemoautotrophic nitrification in acidic forest soils along an urban-to-rural transect. Soil Biol Biochem 31:1091–1100