Forest leaf litter quantity and seedling occurrence along an urban–rural gradient

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Leaf litter, by modifying microenvironmental conditions, can alter plant population distributions and is considered to be a major force in structuring many plant communities. Comparative studies of urban, suburban, and rural forests in the New York City (NYC) metropolitan area have identified numerous biotic and abiotic differences among these forests, including several involved in leaf litter decomposition. These differences in decomposition among the forests could result in differences in litter quantity on the forest floor and hence microenvironmental conditions and safe sites for germination of different plant species. We conducted a survey of forest floor leaf litter quantity in forests located along an urban-to-rural land-use gradient originating in urban NYC and extending to rural Connecticut. Mean litter depth, mass, and density increased significantly with increased distance of the forest from NYC.

We also surveyed woody seedlings and compared the litter depth in which they naturally occurred to the mean litter depth of the surrounding forest. Seedlings of small-seeded species were much more likely to be located in litter shallower than mean forest litter depth than were seedlings of large-seeded species. Taken together, these results suggest that environmental changes associated with urbanization may have profound effects on long-term patterns of forest regeneration.

Keywords: leaf litter; urban-to-rural land-use gradient; New York City metropolitan area; regeneration in forests; safe site

Introduction

Seed and seedling stages are the periods of greatest mortality for most plant species and therefore are critical in determining the distribution of plant populations and the composition of plant communities (Harper, 1977; Grubb, 1977; Cavers, 1983). Recruitment of seedling populations is a function of availability of both seeds and "safe sites" (i.e., sites that provide the specific conditions needed for seed germination and seedling establishment) (Harper, 1977). Conditions favorable for germination and establishment differ among species but typically involve specific light, temperature, and moisture conditions. Plant litter can

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greatly affect all these abiotic conditions as well as other properties of the microenvironment of seeds and seedlings (cf. Facelli and Pickett, 1991). Because of this potential to affect safe site distribution, litter can be a major force in structuring many plant communities (Sydes and Grime, 1981a; Carson and Peterson, 1990; Guzman-Grajales and Walker, 1991; Facelli and Pickett, 1991; Molofsky and Augspurger, 1992, Foster and Gross, 1997).

Experimental studies of herbaceous and woody forest species have shown that litter quantity can strongly affect seed germination and seedling survivorship. Differences in establishment among plant species have been related to litter quantity differences associated with topographic distribution on the forest floor (Beatty and Sholes, 1988) and species successional status (Guzman-Grajales and Walker, 1991). Species germination rates in response to litter quantity also have been related to seedling morphology (Sydes and Grime, 1981b) and seed mass (Tao *et al.*, 1987; Molofsky and Augspurger, 1992; Peterson and Facelli, 1992). Species that are small-seeded and early-successional, have basal shoot extension, and inhabit treefall mounds rather than pits tend to have greater germination and survival on bare ground than on litter-covered ground. Species in which germination and survival are improved or unaffected by litter quantity tend to be large-seeded and mid-to-late-successional, have apical shoot extension, and inhabit treefall pits. While these studies indicate some general trends, they also confirm that species can exhibit highly individualistic responses to leaf litter quantity and distribution.

Recognizing that litter quantity can affect seedling establishment, some researchers have characterized the distribution of litter on a range of temporal and spatial scales. Litter depth, mass, and cover have been shown to differ greatly depending on community successional stage (Persson *et al.*, 1987; Facelli and Carson, 1991), season (Frankland *et al.*, 1963), degree and types of vegetation cover (Shure and Phillips, 1987; Molofsky and Augspurger, 1992), proximity to forest edge (Facelli and Carson, 1991; Matlack, 1993), topography, such as treefall pit and mound complexes (Beatty and Sholes, 1988), and slope and aspect (Dwyer and Merriam, 1981; Orndorff and Lang, 1981). These studies confirm that leaf litter distribution is heterogeneous within and among forest communities. Forest floor microenvironmental conditions affected by leaf litter therefore also are likely to be heterogeneous.

We conducted a survey to determine if differences in litter decompositional processes that have been identified in oak forests along an urban-to-rural land-use gradient in the New York City metropolitan area are paralleled by differences in leaf litter quantity in these forests. This gradient has been the subject of numerous studies over the course of a decade (McDonnell *et al.*, 1997). With increased distance from the urban core along this gradient, there is a decrease in human population density, traffic volume, and the percentage of built-up land, and an increase in the percentage of forest land and the mean size of forest patches (Medley *et al.*, 1995; McDonnell *et al.*, 1997). Mean monthly temperatures are 2–3°C higher and average annual precipitation is 50 mm greater at the urban end of this gradient than at the rural sites (McDonnell *et al.*, 1993). The urban forest soils have elevated concentrations of lead, copper, and nickel (Pouyat and McDonnell, 1991; Pouyat *et al.*, 1994b) and are relatively hydrophobic (White and McDonnell, unpubl. data) compared to the rural forest soils. Pouyat *et al.* (1994a) found that, after nine months of exposure, red oak litter in the rural forests developed twice the total fungal hyphal length of red oak litter in the urban forests. Steinberg *et al.* (1997) found that the urban forests have 12 times the number of earthworms (nonnative species introduced by people) and over 40 times the earthworm biomass of the rural forests. Pouyat *et al.* (1997) found that maple leaf litter placed in litter in the urban forests decomposed at nearly twice the rate of leaf litter in the rural forests.

Based on the faster decomposition rates of single species litter and greater earthworm abundance in the urban forests, we predicted that forest litter quantity would differ along this urban-to-rural gradient. We quantified leaf litter depth, mass, density, and species composition in the forests along this gradient to test the hypothesis that total leaf litter quantity would be lowest in the urban forests and greatest in the rural forests. We also predicted that woody seedling distribution would be related to litter depth in these forests. We surveyed woody seedlings within these forests and the litter depths in which the seedlings naturally

occurred to test the hypothesis that, within a given forest, seedlings of small-seeded woody species would be more restricted to shallower litter than seedlings of large-seeded woody species.

Methods

Study area

This study was conducted in ten forests in the New York City metropolitan area during July and August of 1993. These forests are located within a transect 20 km wide by 130 km long, originating in Central Park in Manhattan, NY and extending northeast through urban Bronx and suburban Westchester County, NY to rural Litchfield County, Connecticut (McDonnell *et al.*, 1997). This transect was established in 1988 to study long-term impacts of human activity on forest ecosystems (McDonnell and Pickett, 1990; McDonnell *et al.*, 1993; Pouyat *et al.*, 1994a; McDonnell *et al.*, 1997; Pouyat *et al.*, 1997). To minimize variation in site variables not related to surrounding land use (and improve our ability to detect a possible land-use effect on forests that can be related to urbanization), forest stands were selected based on the following criteria: (1) location on soils in either of two soil series (Hollis or Charlton), Typic or Lithic Dystrochrepts (coarse-loamy, mixed, and mesic subgroups) (Gonick *et al.*, 1970; Hill *et al.*, 1980); (2) domination by oaks, including at least one of the following species: *Quercus rubra*, *Q. velutina*, *Q. alba*, and *Q. coccinea* (basal area of oaks >50% of total basal area); (3) minimum stand age of 60 years; and (4) no evidence of severe natural or human disturbance (fire, canopy gaps, insect infestations, logging). The forests along this transect were classified according to the degree of human impact, as measured by surrounding land-use type (urban, suburban, rural), population density, and vehicular traffic (McDonnell and Pickett, 1990; Pouyat *et al.*, 1994a,b; Medley *et al.*, 1995; McDonnell *et al.*, 1997) (Table 1). These measures of human impact increase along this transect with proximity to New York City and constitute an urban-to-rural land-use gradient.

Leaf litter survey

One stand was sampled within each of the ten forests. Sampling areas (approximately 1000 m^2) within each stand were selected based on the following criteria: (1) location at least 75 m from forest edge, because litter depth has been shown to decrease toward the edge between forest and field within 50 m into the forest (Matlack, 1993) and (2) level topography, to avoid litter redistribution due to slope (Orndorff and Lang,

Table 1. List of forests included in the litter survey along the urban–rural gradient. Included are the categorical designation for each forest based on land-use and the distance of each forest from the origin of the transect in Central Park, New York, NY

Forest	Designation along the transect	Distance from Central Park (km)
New York Botanical Garden, Bronx, NY	Urban 1	10
Van Cortlandt Park, Bronx, NY	Urban 2	13
Pelham Bay Park, Bronx, NY	Urban 3	14
Saxon Woods Park, Scarsdale, NY	Suburban 1	26
Whippoorwill Ridge Park, Armonk, NY	Suburban 2	45
Mianus River Gorge, Bedford, NY	Suburban 3	49
Mountain Lakes Park, North Salem, NY	Transitional	63
Macedonia State Park, Kent, CT	Rural 1	110
Mohawk State Forest, Cornwall, CT	Rural 2	123
Housatonic State Forest, Sharon, CT	Rural 3	128

1981). All sampling within each stand was conducted on a single day. All forest stands were sampled between 20 July and 16 August 1994. Sampling was done at least one full day after a rainstorm to avoid possible compaction of litter due to moisture.

In each forest stand, three 50 m long parallel transects were established approximately 10 m apart. Litter depth was measured at 2 m intervals along each transect for a total of 25 depth measurements per transect and, therefore, 75 per stand. Litter depth was measured by inserting a sharpened wooden dowel (3 mm diameter) into the litter at each 2 m mark. The top of the litter layer was marked along the dowel and the litter was pushed aside until the interface of the litter layer with the humus layer was reached. The difference between these two points was measured to the nearest 0.5 cm. The relative area of ground covered by litter of each 0.5 cm litter depth interval was calculated for each forest stand by dividing the total frequency of each litter depth interval by the total number of depths measured.

Litter mass was measured at 10 random intervals along each transect for a minimum of 30 mass measurements per stand. These included some of the 75 locations at which depth was measured, allowing for the calculation of litter density. However, very shallow litter (≤ 0.5 cm) and very deep litter (≥ 3.5 cm) measurements were seldom encountered. Therefore, when these shallow and deep litter depths were encountered, litter mass also was sampled. This sampling was supplemental to the minimum of 30 randomly collected samples and was done to increase the range of litter depth and mass examined. Litter mass was measured by placing a round 5 cm diameter metal template centered on the point where depth was measured and cutting around the perimeter of the template with a knife. The leaf litter within the area of the template was collected down to, but not including, the humus layer. All samples were oven dried at 105°C for 48 h and weighed. Biomass measurements were then converted to mass per unit area (g/cm^2). Leaf litter density was determined by dividing litter mass per unit area at a sample point by the litter depth at the same point to obtain mass per unit volume (g/cm^3).

Species composition of the litter was determined by sampling at 10 random intervals along each transect, for a total of 30 samples per stand. This allowed us to determine if species composition of the leaf litter was related to litter depth, mass, or density along the gradient. This sampling also was performed at intervals where depth was measured, but because of the destructive nature of the species composition sampling, it had to be done at separate locations from litter mass sampling. To determine species composition, the dowel was inserted into the litter and each leaf and identifiable leaf fragment intercepted by the dowel was identified to species or genus and counted in the field.

Seedling survey

Seedlings younger than 1 year old (based on the presence of cotyledons or seed remains or the absence of bud scale scars) were surveyed along these same transects. At each sampling point (every 2 m), the nearest seedling within 1 m on either side of the transect was identified to species for a maximum of 25 observations per transect and 75 per site, fewer if there were no seedlings within 1 m at each location along the transect. The depth of the litter through which each shoot was growing was measured to the nearest 0.5 cm.

Data analysis

Data for leaf litter depth and mass were normally distributed in six out of the ten forest stands. The data for the other four stands had slightly skewed distributions that were not significantly improved by transformation. Tests of heteroscedasticity indicated that variances were stable and did not require transformation. Therefore, the data were analyzed in their original form. Regression analysis was performed to determine if mean litter depth, mass, density, and relative ground cover of different litter depth classes varied significantly with distance of the forest from New York City (NYC). This also allowed us to determine if our

method of measuring litter depth could be reliably substituted for the more commonly used method for quantifying leaf litter (i.e., measuring mass), which is slower and more labor-intensive. Conversely, we wanted to know if there was variation in litter mass within forests that was not explained by variation in litter depth.

Percentage species composition of the leaf litter within each forest was calculated by dividing the total frequency of each species of leaf by the total number of leaves identified. Regression analysis was performed for the three most common leaf species, comparing species percentage occurrence with mean litter depth and mass across all forests to determine if species composition of the litter could account for differences in litter quantity.

For the seedling survey, we sought to determine whether seedling emergence in the field was related to its seed size and the litter depth in each forest stand. Mean litter depth was calculated for all seedlings by species for each forest. This was compared with the mean litter depth for the forest stand. The seedlings were separated into two groups based on average seed weight (Young and Young, 1992). "Small-seeded" species were those with average seed weights less than 0.12 g. "Large-seeded" species were those with average seed weights greater than 2.8 g. No seedlings of species with average seed weights greater than 0.11 g and less than 2.9 g were found during our survey, and the large difference in these average seed weights made this an obvious break-point for separating species into seed size classes. A sign test (Sokal and Rohlf, 1987) was performed for both seed mass groups to test whether small-seeded and large- seeded seedlings were found in mean litter depths shallower or deeper than the mean forest litter depth. A Pearson chi-square test (Sokal and Rohlf, 1987) was performed to determine if seed weight class of seedlings was significantly associated with litter depth shallower or deeper than mean forest litter depth.

Effect size was defined as the difference between litter depth where each surveyed seedling was found and the mean litter depth of the forest in which it was located. The mean of this difference for each species was calculated by combining all seedlings of a species across all forests. A positive value indicated that seedlings of that species tended to be located in litter deeper than the mean litter depth of the forest in which they were located. A negative value indicated that seedlings of that species tended to be located in litter shallower than the mean litter depth of the forest in which they were located. For each species, t-tests of the difference of mean effect size (null hypothesis = effect size of zero) were performed. An *a priori* alpha level of 0.05 was used for all analyses.

Results

Leaf litter characteristics

Mean leaf litter depth, mass, and density increased significantly with increased distance from NYC. Mean leaf litter depth in the rural forests was approximately 30% greater than that of the urban forests (Fig. 1a). Although the regression indicated that this increase in litter depth along the gradient was statistically significant ($p < 0.05$), the total depth increase between forests at extreme ends of the gradient was only 0.5 cm. However, litter mass in the rural forests was approximately 2.85 times that of the mean litter mass in the urban forests ($p < 0.001$, Fig. 1b), equivalent to a mean difference of 425 g/m^2 between urban and rural stands. Mean leaf litter density in the rural forests was over 2.5 times that in the urban forests ($p < 0.001$, Fig. 1c).

Mean litter mass was positively related to mean litter depth within forests (minimum $r^2 = 0.188$, $p = 0.017$). Mean litter mass and density were also positively related within forests (minimum $r^2 = 0.229$, $p = 0.006$), except for one (Urban 2, $p = 0.07$). Litter depth and density within forests were not significantly related in any forests except Rural 3 ($p = 0.01$), where the relationship was negative.

Litter cover varied predictably with distance from NYC for each 0.5 cm depth class. Regressions of percentage ground cover for each litter depth class against distance from NYC were negative for each
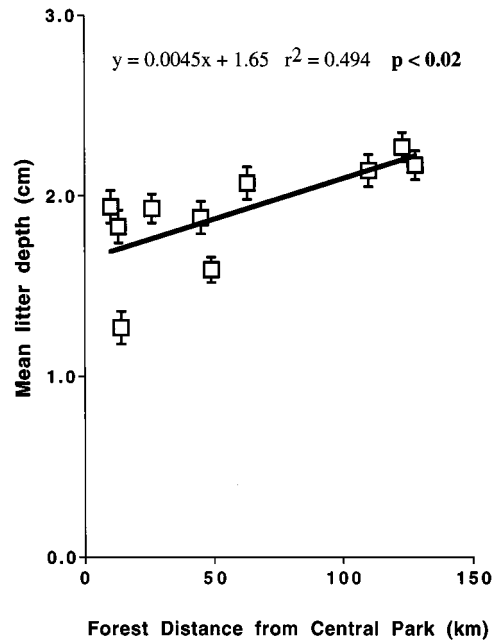
Figure 1a. Regression of mean litter depth (cm) ± standard errors against distance of each forest from Central Park, New York City ($n = 10$). The mean litter depth in each forest is based on 75 measurements.
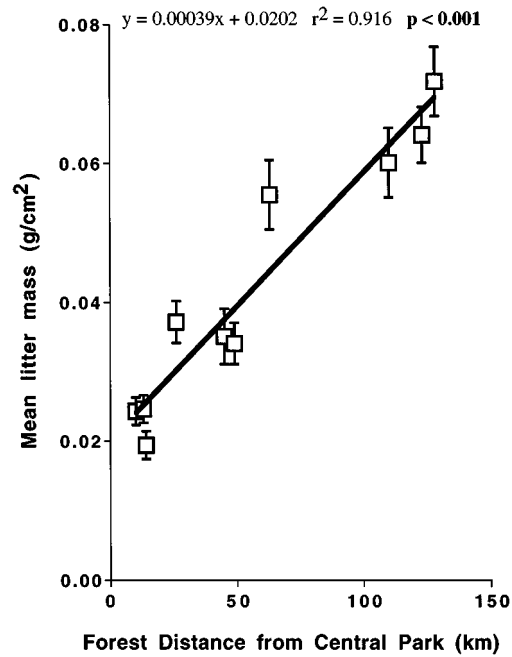

Figure 1b. Regression of mean litter mass (g/cm^2) ± standard errors against distance of each forest from Central Park, New York City ($n = 10$). Mass is presented here in units of g/cm^2 to permit comparison with density units (g/cm^3) used in this study. Mass values may be multiplied by 10,000 to obtain units as g/m^2. The mean litter mass in each forest is based on 30–32 measurements.
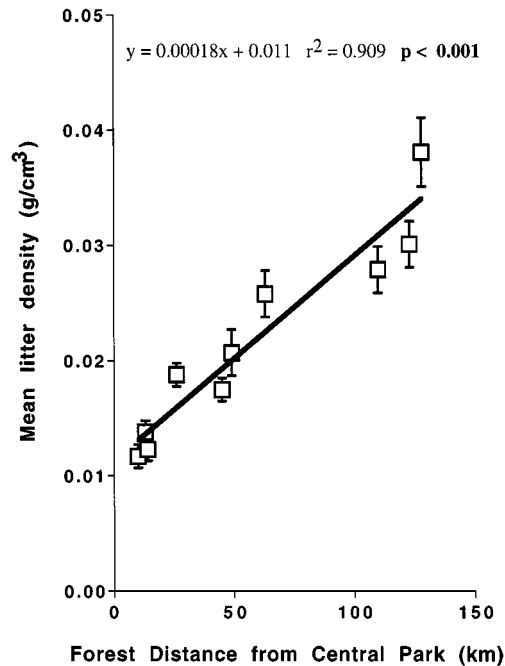
Figure 1c. Regression of mean litter density (g/cm^3) $\pm$ standard errors against distance of each forest from Central Park, New York City ($n = 10$). Mean density was calculated by dividing litter mass by litter depth at each transect point where both measurements were taken (30–32 points per plot).

depth class less than 1.5 cm (Fig. 2). Similarly, the percentage of ground covered by deep litter ($\geq$ 2.0 cm) increased from 43% to 75% with increasing distance from NYC ($r^2 = 0.587$, $p < 0.01$) (Fig. 3). Based on this, we designated litter $\leq$ 1.5 cm as "shallow litter" and litter $\geq$ 2.0 cm as "deep litter."

The forest categorized as "transitional" (63 km from NYC) was generally intermediate between suburban and rural forests for mean litter depth, mass, and density (Figs. 1a–c). However, with regard to percentage ground cover by the different litter depth classes, the transitional forest tended to resemble the suburban forests (Figs. 2 and 3).

The leaves of six tree species accounted for at least 99% of the total leaves collected from the litter in each forest (Fig. 4). Three of these species, *Quercus rubra*, *Fagus grandifolia*, and *Betula lenta*, accounted for > 75% of the leaves in every forest. None of these three species showed a significant relationship between frequency in the leaf litter and leaf litter depth, mass, or density along this gradient (Table 2), and therefore species composition of the litter is not a primary factor responsible for explaining relationships between forest floor litter quantity and distance from NYC.

Seedling occurrence, litter depth, and seed size

Most of the species represented in the seedling survey were classified as small-seeded (11 out of 14 species total), and 67% of the individuals surveyed (340 out of 505 individuals) belonged to these small-seeded species. The mean litter depth for all the seedlings of each species was determined separately for each forest and was shallower than the mean litter depth for each forest in 74% (28 out of 38) of comparisons (Table 3). Among small-seeded species, seedlings were located in microsites with litter shallower on average than the mean litter depth within a forest more frequently than they were located in microsites
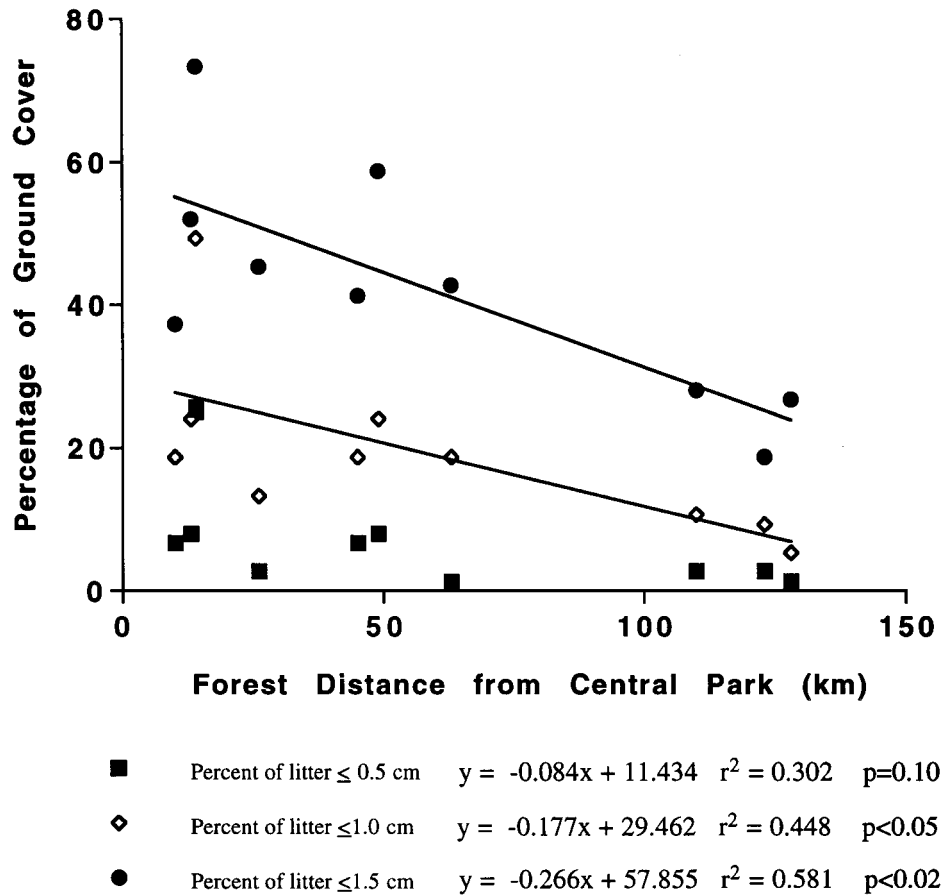
Figure 2. Percent of ground covered by litter $\leq$1.5 cm in each forest (designated "shallow litter" in text) based on regressions of the cumulative frequencies of 0.5 cm litter depth classes against distance of the forest from Central Park, New York City ($n = 10$). Includes only those depth classes with frequencies that are inversely related to distance from New York City.

with litter deeper than the forest mean (sign test, 22 out of 24 comparisons, $p < 0.001$; Table 3). Among large-seeded species, there were no significant differences between the mean microsite litter depth and the forest average ($p = 0.791$; Table 3). Overall, seedlings of small-seeded species were much more likely to be located in litter shallower than mean forest litter than were seedlings of large-seeded species (Fisher's Exact Test, two-tail; $p = 0.002$).

The analysis of mean effect size of litter depth on all 14 seedling species across all forests indicated that 7 out of 11 species of small-seeded seedlings were located in litter shallower than the average litter depth of the surrounding forest (Fig. 5). All three large-seeded species had positive but nonsignificant mean effect sizes (Fig. 5).

Discussion

Leaf litter differences along the urban-to-rural land-use gradient

The results support our hypothesis that leaf litter quantity increases along this gradient. The increase in mean leaf litter depth along the gradient (30%, or 0.5 cm over a 130 km distance) is less substantial than the
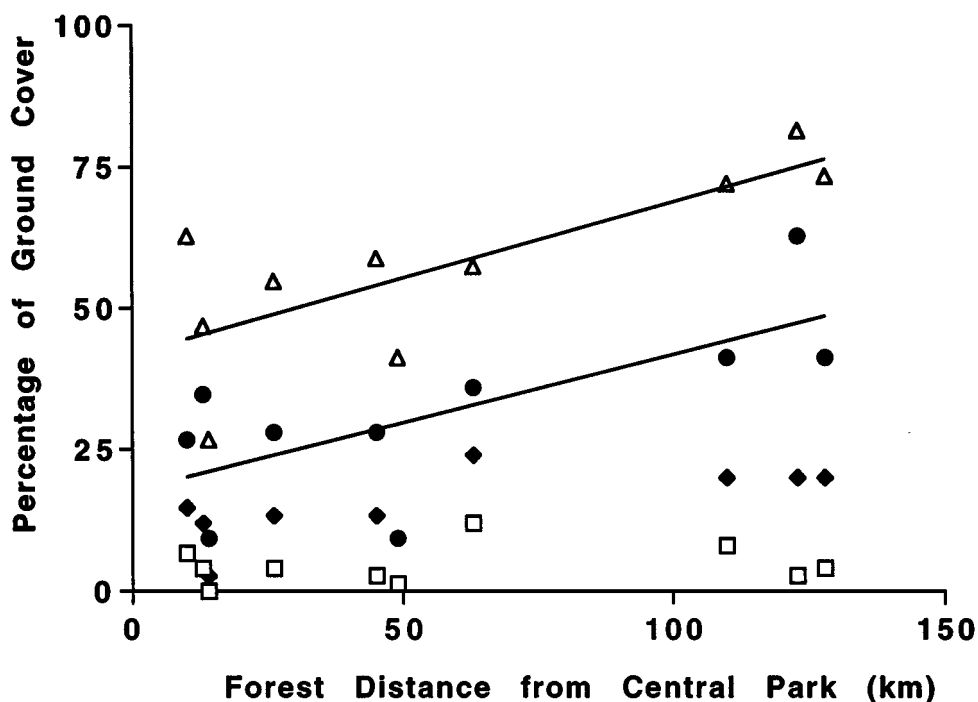
Figure 3. Percentage of ground covered by litter ≥ 2.0 cm in each forest (designated "deep litter" in text) based on regressions of the cumulative frequencies of 0.5 cm litter depth classes against distance of the forest from Central Park, New York City ($n = 10$). Includes only those depth classes with frequencies that are directly related to distance from New York City.

2.5-fold and greater increases in mean litter mass and density; microsites with shallow litter are more than twice as abundant at the urban end of the gradient. The increase in litter density with increasing distance along the gradient demonstrates that leaf litter quantity may best be characterized by measuring both depth and mass rather than either of these alone.

Litter quantity might differ along this gradient because of differences in (1) on-site litter production, (2) litter deposition from outside the system, (3) litter destruction, and/or (4) litter removal (Facelli and Pickett, 1991). Regressions of litter input in these forest stands (Pouyat and Carreiro, unpublished data) indicate that there is an opposite trend toward slightly greater litter input in the urban forests (mean = 362 g/m^2, SE $\pm$ 15.2) than in the suburban forests (330 $\pm$ 14.4 g/m^2) or the rural forests (310 $\pm$ 18.1 g/m^2) (r^2 for the regression = 0.3, $p = 0.04$). We found no significant pattern in species composition of litter along this gradient as related to litter depth, mass, or density. Net import and export of litter to or from these stands has not been measured but should have been minimized based on our selection of sites on
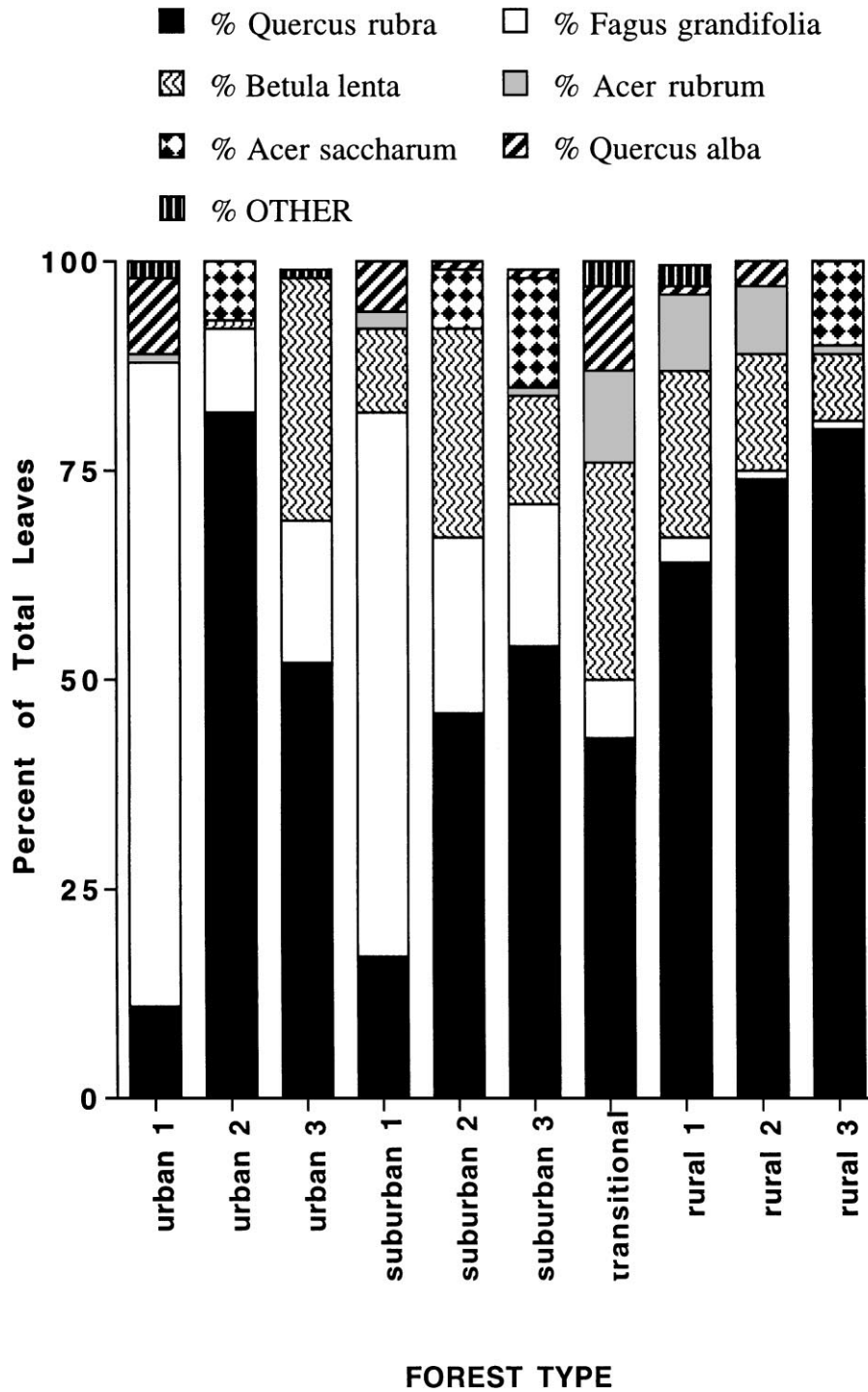
Figure 4. Percent composition of the six tree species comprising 99% of the leaf litter surveyed in each of the ten forests along the urban–rural transect in the New York metropolitan area. Percent species composition was surveyed at 30 transect points in each forest. See Table 1 for key to forest designations.

Table 2. Correlation matrix between measures of leaf quantity (depth, mass, and density) and percent composition of the three predominant tree species in the leaf litter for ten forests along an urban-to-rural land-use gradient in the New York City metropolitan area. Correlation coefficients followed by *p* values in parentheses

Variable	*n*	% *Quercus rubra*	% *Fagus grandifolia*	% *Betula lenta*
Depth	10	0.180 (0.619)	0.164 (0.652)	0.268 (0.455)
Mass	10	0.442 (0.200)	0.544 (0.104)	0.101 (0.781)
Density	10	0.518 (0.125)	0.590 (0.073)	0.072 (0.844)

level ground (Orndorff and Lang, 1981) and more than 50 m from the forest edge (Facelli and Carson, 1991; Matlack, 1993).

Litter destruction is caused by physical, chemical, and biotic agents; decomposition is considered to be the most important and best understood process by which litter is destroyed (Facelli and Pickett, 1991). Using a microbial bioassay, Carreiro *et al.* (in press) found that rural oak leaf litter actually decomposes more readily than urban oak leaf litter. So, based on litter chemistry differences, we would expect litter quantity to be greater in the oak stands of these urban forests. It is likely that the trend in decreased litter depth and mass with proximity to NYC is partly related to (1) the urban heat island effect and (2) the abundance of earthworms in these urban forests, but not in these rural forests (Steinberg *et al.*, 1997). Because temperatures in NYC forests are on average 2.5°C warmer than the rural stands in Connecticut year round, temperature is estimated to account for about 25% of the difference in decay rate between these stand types (based on a Q10 effect that would double the rate of decay for every 10°C increase in temperature). Therefore, despite other factors that could act to decrease decay rate of urban litter (e.g., heavy metals), we suggest that these nonnative earthworms in the urban forests may be the primary agents responsible for the differences in litter quantity documented in this study.

Another property that differed along the urban–rural gradient was the cohesiveness of the leaf litter. Leaves of rural forest litter were bound together fairly tightly and were hard to peel apart (F. Kostel-Hughes, personal observation). This contrasted with leaves of urban forest litter, which exhibited no cohesion and separated readily. This cohesion may be due to the greater amount of fungal hyphae in the rural forest litter. Oak litter in the rural forest developed an average of 2741 ± 332 m of fungal hyphae (per g dry mass of litter) compared to oak litter in urban forests, which develops only 1344 ± 396 m of fungal hyphae (per g dry mass of litter) over a 9 month period (Pouyat *et al.*, 1994a). Fungal hyphae are minute filaments that derive nourishment from the leaves and, in so doing, tend to bind leaves together. Fungi, the predominant decomposers in these rural forests (Pouyat *et al.*, 1994a), decompose the litter more slowly than the nonnative earthworms, the predominant decomposer in these urban forests (Pouyat *et al.*, 1994a; Facelli and Pickett, 1991; also see the review on earthworms by Lee, 1985). The much greater density of the rural litter is likely due to fungal hyphae binding and weaving the leaves together, producing a more compact and continuous litter mat. The litter of the urban and suburban forests, lacking this cohesiveness, tends to be looser and have a lower density and also is more likely to be redistributed by the wind.

Another way to evaluate differences in litter quantity among these forests is the relative area of the forest floor covered by litter of different depths. This relative ground cover of litter depth classes is probably more indicative of the availability of safe sites for seedlings than is the overall mean litter depth of the forest. The percent ground cover of shallow litter (≤1.5 cm) decreased by 60% (and deep litter [≥2.0 cm] similarly increased) in the forests with increased distance from NYC. If a species is constrained to establish in litter depths above or below a certain threshold depth (see Fig. 5 and Table 3), then the availability of such safe sites differs substantially between the urban and rural forests.

Table 3. Seedling species surveyed in each of ten forests along an urban–rural transect in the New York City metropolitan area. Species are in order of increasing seed size based on average seed weight (Young and Young, 1992). A "neg" indicates that the species has a mean litter depth shallower than the mean litter depth of the corresponding forest. A "pos" indicates that the species has a mean litter depth deeper than the mean litter depth of the corresponding forest. A "—" indicates that seedlings of the species were not recorded in the corresponding forest. The numbers in parentheses are the total number of seedlings of each species recorded along the transects at each site

	Small-seeded											Large-seeded		
Species	LIST	ACRU	AIAL	LITU	PAQU	FRAM	ACPE	HAVI	ACSA	SAAL	PRSE	CACO	QURU	QUAL
Avg. seed weight (g)	0.006	0.02	0.03	0.03	0.03	0.03	0.04	0.05	0.06	0.08	0.11	2.94	3.57	3.85
Forest type														
Urban 1	neg (4)	—	—	—	—	—	—	—	—	—	—	—	—	—
Urban 2	neg (1)	—	neg (10)	neg (6)	neg (44)	—	—	—	—	—	—	neg (1)	neg (1)	—
Urban 3	—	—	—	—	neg (1)	—	—	—	—	—	—	neg (8)	pos (5)	—
Suburban 1	—	—	—	—	—	—	—	—	—	—	—	—	neg (14)	—
Suburban 2	—	—	—	—	—	neg (4)	—	—	—	pos (4)	—	pos (6)	neg (26)	—
Suburban 3	—	—	—	neg (2)	—	neg (26)	—	—	—	—	—	pos (5)	pos (20)	—
Transitional	—	neg (29)	—	—	—	neg (81)	—	—	neg (2)	—	neg (3)	—	pos (33)	—
Rural 1	—	neg (23)	—	—	—	neg (3)	neg (28)	—	—	—	—	—	pos (2)	—
Rural 2	—	neg (16)	—	—	—	—	neg (8)	—	—	—	—	—	pos (42)	pos (1)
Rural 3	—	neg (4)	—	neg (3)	—	pos (28)	—	neg (7)	—	—	—	neg (1)	—	—

LIST = Liquidambar styraciflua, ACRU = Acer rubrum, AIAL = Ailanthus altissima, LITU = Liriodendron tulipifera, PAQU = Parthenocissus quinquefolia, FRAM = Fraxinus americana, ACPE = Acer pensylvanicum, HAVI = Hamamelis virginiana, ACSA = Acer saccharum, SAAL = Sassafras albidum, PRSE = Prunus serotina, CACO = Carya cordiformis, QURU = Quercus rubra, QUAL = Quercus alba.
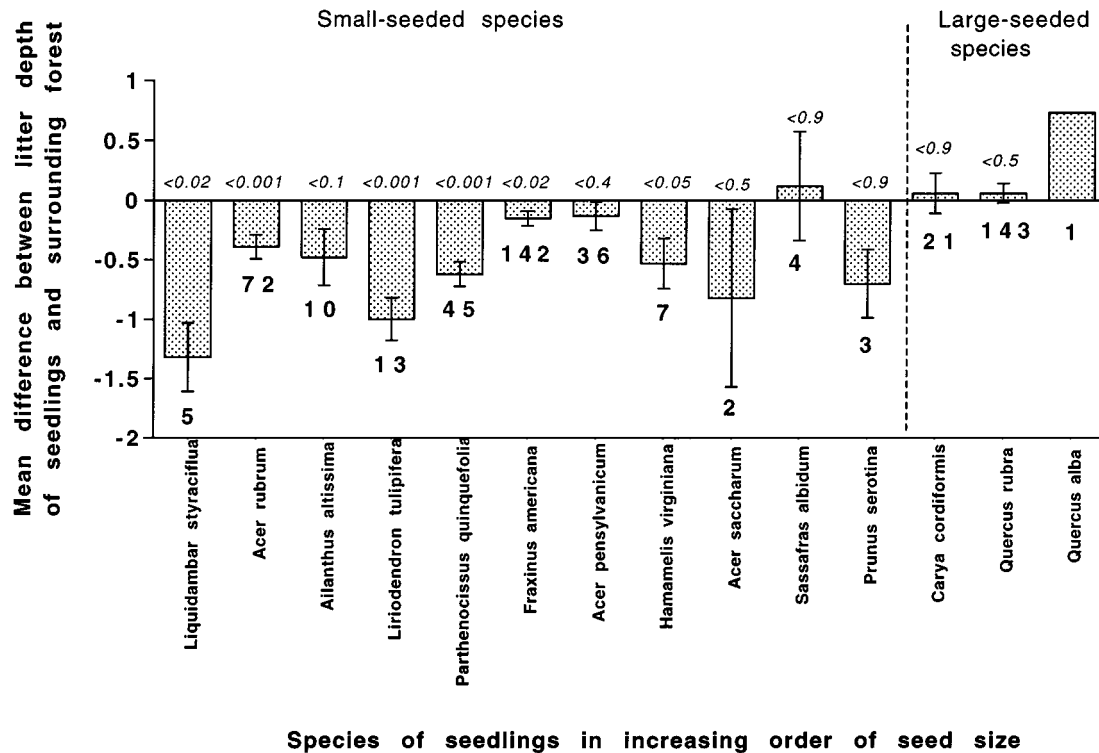
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Figure 5. Mean differences ± standard errors between litter depth of seedlings and that of the surrounding forest across all ten forests for each woody species (mean effect size). Negative values indicate that seedlings were found in litter shallower than the mean litter depth of the forest. Positive values indicate that seedlings were found in litter deeper than the mean litter depth of the forest. Numbers in bold below the x-axis represent *n* for each species. Numbers in italics above the x-axis represent the *p* values for the *t*-tests of the mean litter depth differences and zero for each species. Species are ordered according to increasing mean seed mass based on values from Young and Young (1992).

The depth, density, and cohesiveness differences in leaf litter along this urban-to-rural gradient may have important implications for the plant community and forest regeneration. The denser litter layer in the rural forests may present a much more formidable barrier to emerging seedlings (especially of small-seeded species) than the looser urban litter. Litter can also protect seeds, especially large ones, from being found by seed predators (Shaw, 1968; Sydes and Grime, 1981b). This refuge effect may be more prominent in the denser rural litter. The tightly "woven" rural litter mat may have a more pronounced effect on soil moisture levels either by reducing evaporation of water from the soil or by retaining water and preventing it from percolating down to the soil when rain events are light (McCarthy and Facelli, 1990; Facelli and Pickett, 1991; Liechty *et al.*, 1992). Although any leaf litter could be expected to reduce soil temperature fluctuation (MacKinney, 1929; Beatty and Sholes, 1988), the denser rural litter should do so to a greater extent than the urban litter. Combinations of these different light, moisture, and temperature conditions could differentially enhance or reduce germination or foster the growth of pathogens and result in greater seed mortality (Facelli and Pickett, 1991). All of these possible differences in microenvironmental conditions need empirical confirmation but are likely to affect the availability of safe sites among the forests along this gradient and result in different patterns of seedling recruitment.

Seedling survey

In the forests surveyed here, small-seeded species tended to occur in litter shallower than the mean litter depth of the forest, whereas the litter depth of the large-seeded species differed little from the rest of the forest. Several experimental studies have shown that germination and seedling emergence of small-seeded species tends to be inhibited more greatly by ground cover than that of the relatively larger-seeded species (Gross and Werner, 1982; Winn, 1985; Tao *et al.*, 1987; Molofsky and Augspurger, 1992; Peterson and Facelli, 1992; Reader, 1993; Kostel-Hughes, 1995).

In a field study to determine the microhabitat preferences of seedlings in an oak–pine forest in the New Jersey Pine Barrens, Collins and Good (1987) measured densities of 1-year-old seedlings and the physical environment (including litter depth) immediately surrounding each seedling. They found that while random points in the forest stands tended to be concentrated in areas with deep litter, most seedlings grew in areas with shallow litter (Collins and Good, 1987). Also, seedling density was lowest in the forest stand with the significantly deepest litter (Collins and Good, 1987). Because Collins and Good (1987) studied 1-year-old seedlings, their results may be indicative of seedling survivorship, as well as initial emergence. In contrast, we studied seedlings younger than one year to focus specifically on seedling emergence in response to litter depth.

Based on our findings that seedlings of small-seeded species tend to be located in shallow litter and that the urban forests tend to have a higher incidence of shallow litter cover, one might expect a higher frequency of small-seeded seedlings at the urban end of the gradient. This was not apparent in our survey (Table 3). While three of the small-seeded species (*Liquidambar styraciflua, Ailanthus altissima*, and *Parthenocissus quinquefolia*) were found only in urban forests, this may be due to additional factors affecting safe site availability or it may reflect seed availability. To make further comparisons of seedling species composition among forests, information on seed availability such as seed rain and/or seed bank data would be required. These data were not gathered in this study. We recognize the importance of these other factors in determining recruitment but, preliminarily, the consistency between our field results in this study and the findings of other experimental studies (Kostel-Hughes, 1995) suggests that litter depth may be one of the forces influencing germination and establishment of species in these forests.

Also worth noting is that *A. altissima*, a nonnative species, was one of the minority of small-seeded species whose mean litter depth did not differ significantly from the surrounding forest. This supports the findings of two lab experiments in which the mean percentage germination of *A. altissima* did not differ among bare, shallow litter, and deep litter treatments (Kostel-Hughes, 1995).

Conclusions

Many biotic and abiotic factors that vary in these forests have been related to surrounding land use (White and McDonnell, 1988; McDonnell *et al.*, 1990; Pouyat and McDonnell, 1991; Pouyat *et al.*, 1994a,b; McDonnell *et al.*, 1997). The difference in forest floor litter quantity along this gradient, in combination with patterns of seedling establishment relative to litter depth, suggests that plant regeneration in these forests may be directly and indirectly affected by human land use. In addition, the differences in leaf litter characteristics along this gradient could have implications not only for the plant community but also for other organisms. Litter structure (based on litter depth and the amount of interstitial space) may also affect habitat availability and therefore the diversity and size of invertebrate communities (Uetz, 1974), which could have cascading effects throughout the food webs in these ecosystems.

Acknowledgments

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