



Land use context and natural soil controls on plant community composition and soil nitrogen and carbon dynamics in urban and rural forests

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Abstract

Forests embedded in an urban matrix are a useful venue for investigating the effects of multiple factors such as climate change, altered disturbance regimes and species invasions on forest ecosystems. Urban forests also represent a significant land area, with potentially important effects on landscape and regional scale nitrogen (N) and carbon (C) storage and flux. We measured forest community composition, litterfall, leaf area index, soil chemical properties, *in situ* net N mineralization and nitrification, soil and soil solution inorganic N pools, and soil:atmosphere fluxes of nitrous oxide (N₂O), carbon dioxide (CO₂) and methane (CH₄) in eight forest stands that differed in their exposure to urban atmospheric conditions and natural soil conditions (high versus low fertility). Our objectives were (1) to compare the influence of urban land use context and natural soil controls on forest composition and C and N cycling processes and (2) to evaluate the importance of “natural” N cycle processes relative to anthropogenic N fluxes in the urban landscape. Forest productivity and N cycling varied more with soil type than with proximity to urban land use, while forest composition and soil:atmosphere fluxes of CO₂ and CH₄ were more strongly influenced by exposure to an urban land use matrix and atmosphere. The magnitude of natural processes was important in the context of urban and suburban landscapes, i.e. production of, and annual variation in, inorganic N in forest patches was large relative to watershed-scale atmospheric deposition, fertilizer use and food/sewage fluxes that have been measured in other studies in these study landscapes.

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1. Introduction

One of the challenges facing ecosystem ecologists is unraveling the effects of multiple factors on the structure and function of ecosystems (Vitousek, 1994; Aber and Driscoll, 1997; Groffman et al., 2004a). Forests in many areas of the world are simultaneously affected by climate change, atmospheric pollution, altered disturbance regimes and species

invasions. Understanding these factors, and how they interact with natural controls such as soil type and ecosystem development to influence nutrient cycling processes requires multiple research approaches, including long-term monitoring, manipulation studies, comparative analyses and simulation modeling (Carpenter, 1998).

Urban land use change produces multiple environmental effects on forests that remain embedded within urban and suburban landscapes (Foley et al., 2005; Pouyat et al., in press). Impervious surfaces now cover over 110,000 km² in the U.S. (Elvidge et al., 2004), and urban land use change affects a much

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larger area through alteration of climate, atmospheric chemistry and water quantity, quality and flow (Oke, 1990; Imhoff et al., 1997; Shepherd and Burian, 2003; Gregg et al., 2003; Ziska et al., 2004; Kaye et al., 2006). Forests embedded in an urban matrix are thus a useful venue for investigating the effects of multiple environmental factors on forest ecosystems (Pouyat et al., 1995; Carreiro and Tripler, 2005). They are particularly useful if comparisons can be made along urban to rural gradients and if variation in natural controls, e.g. soil type, can be compared with variation in exposure to multiple urban effects (McDonnell and Pickett, 1990; McDonnell et al., 1997).

In addition to investigating multi-factor influences on nutrient cycling processes, study of urban forests is important in its own right. On average, urban land in the northeast U.S. has 33% tree canopy cover (Nowak and Crane, 2002) with values up to 80% in older residential areas (Freedman et al., 1996) and significant areas of remnant forest. Urban forests thus represent a significant forest area, with important effects on landscape and regional N and C storage and flux (McPherson, 1998; Jenkins et al., 2001; Jenkins and Riemann, 2003; Pouyat et al., 2006). Urban watersheds have been reported to have surprisingly high capacity for nitrogen retention (Baker et al., 2001; Groffman et al., 2004b; Wollheim et al., 2005), and forests likely play an important role in this important ecosystem service. Urban forests also have socio-cultural significance, influencing human perceptions of environmental quality and well being (Grove et al., 2006). Given that the vast majority of the human population lives in urban areas, there is great interest in the factors regulating urban forest processes that underlie their productivity and dynamics, such as nutrient cycling.

In the Baltimore Ecosystem Study (BES, <http://beslter.org>), one of two urban components of the U.S. National Science Foundation's Long-term Ecological Research (LTER) network, we have established a series of long-term study plots to evaluate the control by urban environment and natural soil type on forest processes. Four plots are located close to the urban core of Baltimore City, and four are located approximately 30 km into the rural/suburban fringe of Baltimore County. In addition to evaluating effects of an urban land use matrix on forest ecosystems, these plots also allow us to compare the major natural soil/vegetation controls in this region as three of the plots are located on relatively fine-textured, fertile soils while five are located on less fertile, more coarse-textured soils.

In this paper we present data from the BES long-term forest study plots on several ecosystem N cycle variables including forest community composition, basic soil properties, *in situ* net N mineralization and nitrification, soil and soil solution inorganic N pools, and soil:atmosphere fluxes of nitrous oxide (N₂O). We also measured a series of parameters related to C cycling, and its influence on N dynamics, including leaf area index, litterfall and soil:atmosphere fluxes of carbon dioxide (CO₂) and methane (CH₄). Our objectives were (1) to compare the influence of urban land use context and natural soil controls on forest composition and C and N cycling processes and (2) to evaluate the importance of "natural" N cycle processes (mineralization, nitrification) relative to anthropogenic N

fluxes (atmospheric deposition, fertilizer, food imports, sewage exports) that have been measured in the BES study watersheds.

2. Methods

2.1. Study area

BES research is centered on the Gwynns Falls watershed (76°30', 39°15' and approximately 17,150 ha) in Baltimore City and Baltimore County, MD. Watershed population in the year 2000 was approximately 356,000 people, with sub-watershed densities ranging from 2.2 to 19.4 persons ha⁻¹. Land use varies, with the lower sub-watersheds containing predominantly residential/commercial/industrial and the upper sub-watersheds a mixture of lower density residential areas along with agricultural and forested land use.

The watershed lies in two physiographic provinces, the Piedmont to the northwest and the Atlantic Coastal Plain to the southeast. All BES research is focused on the Piedmont portions of the watershed. The Piedmont Plateau is underlain by old igneous and metamorphic rocks. Differences in these rocks underlie variation in inherent soil fertility, i.e. base saturation, pH and water holding capacity (Froelich et al., 1980). Low fertility soils are found over acid crystalline rocks such as gneiss and micaceous schist, while high fertility soils are found over mixed mafic rocks and material weathered from amphibolite, diabase, or other basic igneous rocks (NRCS, 1998). These soils thus have higher pH and base saturation, as well as better water holding capacity.

The natural forest vegetation of the area (currently approximately 20% of the watershed) consists mostly of tulip poplar (*Liriodendron tulipifera*) and oaks, primarily chestnut (*Quercus prinus*), scarlet (*Quercus coccinea*) and white (*Quercus alba*) in the uplands and red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), river birch (*Betula nigra*) and sycamore (*Platanus occidentalis*) in the lowlands (Brush et al., 1980).

Average annual precipitation is approximately 1060 mm year⁻¹ and stream discharge is approximately 380 mm year⁻¹ (Doheny, 1999). The greatest rainfall intensities occur in the summer and early fall during convective events and occasional tropical depressions.

2.2. Long-term study plot establishment

Due to the complex pattern of land development, long-term study plots could not be located to provide a comprehensive test of the effects of natural soil controls and land use context within the Baltimore metropolitan area. Rather in 1998, eight plots were surveyed into three remnant forests in public parks in the study region. Four "rural" plots were established in Oregon Ridge Park and four "urban" plots were established in Hillsdale and Leakin Parks, two per park. The urban plots were located approximately 5 km from the urban core of Baltimore City and the rural plots were approximately 30 km from the core, in Baltimore County. Data from these plots thus provide

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inference on the population of forest remnants within the Baltimore metropolitan area study region.

Specific sites were selected within the parks to (1) avoid obvious habitat boundaries or edges, (2) have consistent drainage lines within the plot, and (3) maintain at least 80% continuous tree canopy. Plots were surveyed in to correct for slope and to achieve an accuracy of plot side length to within 0.5 cm. Plots were 1600 m² with the exception of the Hillsdale plots which were 900 m².

2.3. Soil characterization

At each plot, a 1.5 m² soil pit was excavated with a back-hoe or by hand to a depth of 1.8 m. Soil horizons were identified and described using NRCS guidelines for describing and sampling soils (NRCS, 2004). A representative sample from each horizon was collected and analyzed for total organic C and N (dry combustion), exchangeable Ca, Mg, K and Na (NH₄OAc extractable), extractable P (resin extraction), extractable heavy metal concentrations (nitric acid), percentage clay, silt and sand (pipet method), and pH (CaCl₂ and H₂O) at the NRCS Lincoln, NE Laboratory (NRCS, 2004). In the field, the 20–75 mm fraction was sieved, weighed, and discarded. Samples taken to the laboratory were sieved and weighed to determine the <2 mm fraction. Weight percentages of the >2 mm fractions were estimated from volume estimates of the >2 mm fractions and weight determinations of the <2 mm fractions. Three undisturbed clods were taken from each horizon for bulk density analysis from the same pit faces as the mixed, representative samples (Blake and Hartge, 1986). Two of the clods were used in the primary analysis, while the third clod was reserved for a rerun, if needed. Amoozometers were used to measure *in situ* saturated hydraulic conductivity (Amoozegar, 1989).

2.4. Vegetation characterization

For vegetation characterization, each plot was subdivided into four 10 m × 10 m subplots. All vegetation layers were sampled in order to characterize the structure and composition of the plant community. All trees in the plot were identified and their diameter at breast height (dbh) measured. Trees were defined as greater than 8 cm dbh. In each 10 m × 10 m subplot, the height of the tallest tree was measured and the percent open canopy assessed. All other vegetation layers were characterized within a random sampling of 5 m × 5 m subplots stratified by the 10 m × 10 m subplots. There were 16, 5 m × 5 m subplots at each site (except Hillsdale plots which had 9). Within the 5 m × 5 m subplots, all saplings were identified and their diameter measured. Saplings were defined as less than 8 cm dbh and taller than 1 m. The cover of shrubs and vines was quantified along two sides of each 5 m × 5 m subplot for a total of 160 m of transect at each site (90 m at Hillsdale sites). Shrubs and vines were identified, the percent cover for each 1 m segment of the transects determined, and the maximum height measured. Seedling composition, cover, and density and herbaceous species identity and cover were quantified in two

1 m² plots established at a right angle to each other within each 5 m × 5 m subplot.

Litter was collected from each permanent plot during 1999 and 2000. Eight litter baskets were randomly placed in each of the Oregon Ridge and Leakin Park plots. Because Hillsdale plots were smaller, four baskets were randomly placed at each site. Litter was collected each month during leaf-off and leaf-on periods. During the leaf-fall period, litter was collected weekly. Samples were placed in brown paper bags and returned to the lab where they were dried at 65 °C to a constant weight to obtain total dry-weight of litter per plot.

Litter samples were also collected during leaf-fall to obtain leaf-area measurements. Prior to a forecast of dry weather for at least 24 h, baskets were emptied of all litter. After a 24 h period, baskets were again emptied. This sample was placed in brown bags. Upon returning to the lab, samples were pooled by plot and separated by species. A sample of 20 randomly chosen leaves per species was photocopied to obtain leaf areas. Leaf areas were measured using a CI-251 Leaf Area Meter (CID Inc., Vancouver, WA).

2.5. *In situ* net N mineralization and nitrification

Net N mineralization and nitrification were measured using an *in situ* intact core method (Robertson et al., 1999). At each sampling day, ten, 2 cm diameter × 25 cm depth intact cores were removed from each plot. Five of the cores were returned to the laboratory for extraction (2N KCl) of inorganic N (ammonium (NH₄⁺) and nitrate (NO₃⁻)) and five were returned to the plot for *in situ* incubation. During the growing season, cores were incubated for approximately 4 weeks before harvesting and extraction. Cores overwintered from December to March. Inorganic N was quantified colorimetrically using a Perstorp™ 3000 flow injection analyzer. Net N mineralization rates were calculated as the accumulation of total inorganic N over the course of the incubation. Net nitrification rates were calculated as the accumulation of NO₃⁻ over the course of the incubation. Values were converted to an areal basis (g N m⁻²) using bulk density values from the soil characterization described above. Mineralization and nitrification were only measured for 2 years (fall 1998–fall 2000) due to concerns that repeated soil coring would damage our long-term study plots.

2.6. Soil solution chemistry

Zero tension lysimeters (two or three replicates) of the design described by Johnson et al. (2000) were installed at 50 cm depth in two or three subplots at each site in fall 1998. The objective of placing lysimeters at this depth was to be below the root zone to sample water and nutrients exported from the surface ecosystem. Porous cup tension lysimeters (four replicates) were installed at 10 and 50 cm depth in each plot.

Lysimeter samples were collected monthly and stored at 4 °C prior to analysis. To sample tension lysimeters, suction (30 cbar) was applied to each lysimeter on 1 day and samples

were taken the next day. Ammonium and NO_3^- were analyzed as described above.

Estimates of annual leaching losses were produced by multiplying annual runoff measured at the BES forested referenced watershed by the annual volume-weighted mean NO_3^- concentration in tension lysimeters at 50 cm. Runoff from this watershed, which contains the four rural sites, represents water that has passed through the plant canopy and soil profile and is thus a good estimate of soil solution volume, assuming that surface runoff is negligible (Chang, 2006).

2.7. Soil:atmosphere trace gas fluxes

Trace gas fluxes were measured using an *in situ* chamber design identical to that used by Bowden et al. (1990, 1991). Chambers (three per plot) consisted of 287 mm diameter (i.d.) by 40 mm high polyvinyl chloride (PVC) cylinders which were placed on permanently installed PVC base rings immediately prior to measurement. At 0, 10, 20 and 30 min following placement of the chamber on the base, 9 mL gas samples were collected from gas sampling ports in the center of the chamber top using fine-needle polypropylene syringes. Samples were transferred to evacuated glass vials which were stored at room temperature prior to analysis by gas chromatography with electron capture (N_2O), thermal conductivity (CO_2) or flame ionization (CH_4) detection. Fluxes were calculated from the linear rate of change in gas concentration, the chamber internal volume and soil surface area.

2.8. Statistical analysis

Differences among plots and years were evaluated using two-way analysis of variance (with interactions). Plot and annual means were compared using Fisher's protected least significant difference test. The Statistical Analysis System (SAS, 1989) was used for all analyses.

3. Results

3.1. Soils

Soils in the urban plots varied widely in their characteristics and classification. The Legore soil (plots Leakin 1 and Hillsdale 2) was very deep and well drained. This soil was underlain by semibasic and mixed basic and acidic rocks at a depth of 1.5–3 m. The Legore is classified as a fine-loamy, mixed, mesic Ultic Hapludalf. This soil had the highest pH and base saturation of all the soils in this study (Table 1). The Occaquon soil, associated with plot Leakin 2, was an inclusion in a large Legore map unit in the Baltimore City soil survey (NRCS, 1998). Occaquon soil is classified as a loamy-skeletal, mixed subactive, Typic Dystrudept. This soil had the highest percentage of sand and coarse fragments, and in the deeper horizons ranked lowest of all soils in base cation concentrations (Table 1). The Jackland soil associated with Hillsdale 1, was classified as a fine, smectitic, mesic, Typic Hapludalf. This soil had the lowest percentage of sand of all the sites and was

somewhat poorly to moderately well drained. While having relatively high base saturation in the surface horizon, this soil was strongly acidic (pH 5.1–5.5).

Three of the four rural plots had soils of the Glenelg series. These soils developed on mica schist and were classified as fine-loamy, paramicaceous, mesic, Typic Hapludults. The two upper plots consisted of deep, well drained, gently sloping (1–8%) soils, while the lower plots were more strongly sloping (4–16%). These soils were the most acidic of all the soils and were intermediate in base saturation (Table 1). Of all the pedons described, the Glenelg soils had the most well-defined O layer (Oe and Oi horizons, respectively). The highest concentrations of total N were found in the O horizons across all soils; therefore, the Glenelg soils with well-defined O horizons had relatively high total N (Table 1). The fourth rural plot (Oregon mid 2) had Manor soil; a deep, well drained to somewhat excessively drained coarse-loamy, paramicaceous, semiactive, mesic, Typic Hapludult.

A comparison of what we qualitatively defined as “low fertility” soils, i.e. the Glenelg, Manor and Occaquon soils in the four rural and one urban (Leakin 2) plots, with what we qualitatively defined as “high fertility” soils, i.e. the Legore and Jackland soils in the urban Hillsdale and Leakin 1 sites showed that the low fertility soils had significantly higher % sand and C:N ratio, and lower pH and base saturation than the high fertility soils (Table 2).

3.2. Vegetation

Ninety-seven species were found across all plots: 31 species of trees, 17 shrubs, 11 vines, and 38 herbs. Sites ranged in species richness from 35 to 54 (Table 3). The most species rich site was Leakin 2, an urban site on low fertility soil. This high richness relative to other sites was primarily due to high shrub and herbaceous species richness as tree richness in this site was low compared to other sites. All four of the rural plots had similar species richness in the tree, sapling, shrub, and vine layers. Species richness of the herbaceous layer in these plots ranged from 3 to 11 species. The plots in the two urban forests, however, had a greater range of species richness in all vegetation layers. Two of the urban sites had low tree species richness and one of the urban sites had high tree species richness relative to all plots. The vegetation layers in Hillsdale 2 had low species richness except for a species rich vine layer. Leakin 2, had fewer species than average in the tree canopy but more species rich seedling, shrub and herb layers. In contrast, Leakin 1 had high species richness in tree, sapling, and herbaceous layers, but low richness in the shrub and vine layers (Table 3). Only 9 species were non-natives and none were widespread. Six of the non-native species were shrubs (*Ligustrum vulgare*, *Rosa multiflora* and *Rubus phoenicolasius*) and vines (*Celastrus orbiculatus*, *Hedera helix*, *Lonicera japonica*). The non-native tree species were *Acer platanoides* and *Prunus avium*, and *A. platanoides* occurred as a single tree in only one plot, Hillsdale 2. The single non-native herbaceous species (*Amphicarpaea bracteata*) was found only in the two Leakin Park plots.

Table 1
Soil series, family taxonomic units, characteristics and pedon descriptions to approximately 50 cm

Plot	Horizon	Depth (cm)	Sand (%)	Clay (%)	Total N (g kg ⁻¹)	Total C (g kg ⁻¹)	pH ^a	Sum of all bases ^b (mequiv. 100 g ⁻¹)	Base saturation ^c (%)	Bulk density (g cm ⁻³)
Glenelg (fine-loamy, paramicaceous, mesic Typic Hapludult)										
Oregon upper 1 (rural, low fertility)	Duff	2–0	na	na	17.7	382.7	na	na	na	na
	Oe	0–3	na	na	1.14	207.6	4.5	39.7	49	na
	A	3–10	46.3	17.8	0.315	59.5	4.4	1.9	10	0.74
	AE	10–20	43.4	20.2	0.112	18.2	4.3	0.7	6	1.16
	BE	20–41	41.3	20.9	0.038	3.7	5.4	0.5	6	1.47
Bt1	41–59	44.5	23.7	0.023	2.2	5.1	0.7	9	1.7	
Glenelg (fine-loamy, paramicaceous, mesic Typic Hapludult)										
Oregon mid 1 (rural, low fertility)	Duff	2–0	na	na	1.972	467.6	na	na	na	na
	Oi	0–3	na	na	1.206	301.8	na	na	na	na
	A	3–8	78.5	9.6	na	na	4.9	1.2	20	0.9
	A	8–18	43.3	22.2	0.168	15.9	4.7	1.4	10	1.07
	BE	18–31	42.8	25.3	0.078	5.6	4.3	0.8	9	1.57
Bt1	31–58	43.3	32.7	0.044	2.3	4.8	2.4	25	1.54	
Glenelg (fine-loamy, paramicaceous, mesic Typic Hapludult)										
Oregon upper 2 (rural, low fertility)	Duff	2–0	na	na	16.3	385.8	na	na	na	na
	A1	0–8	39.7	18.3	3.1	46.9	4.4	3.2	15	0.97
	A2	8–20	37.8	19	1.2	16.8	4.6	0.9	8	1.21
	BE	20–31	33.8	23.2	0.7	5.5	4.5	0.5	6	1.52
Bt1	31–58	36.5	27.3	0.3	3	4.7	0.9	10	1.62	
Manor (coarse-loamy, paramicaceous, semiactive, mesic Typic Dystrachrept)										
Oregon mid 2 (rural, low fertility)	Duff	2–0	na	na	23.2	418.7	na	na	na	na
	Ap	0–13	38.3	20.1	2.9	38.1	5	4.1	23	1.09
	EA	13–20	35.7	24.6	0.5	3.7	4.8	1.1	12	1.31
	Bt1	20–38	39.4	20	1	13	4.3	1.1	11	1.45
Bt2	38–56	51.5	23.1	0.5	1.6	4.8	1.9	21	1.52	
Legore (fine-loamy, mixed, mesic, Ultic Hapludalf)										
Leakin 1 (urban, high fertility)	Duff	2–0	33.3	na	10.3	301.4	5.3	na	na	na
	A	0–12	35.3	14.8	2	27.4	5.1	8.4	49	1.12
	EA	12–21	33.1	13.2	0.8	10.4	5	5.3	46	1.52
	BE	21–33	35.8	16.2	0.5	4.4	5.2	5.4	51	1.64
Bt1	33–53	57.4	24.2	0.4	2.9	5.1	14.8	62	1.54	
Occaquon (loamy-skeletal, mixed, subactive Typic Dystrudept)										
Leakin 2 (urban, low fertility)	Duff	2–0	na	na	na	na	na	na	na	na
	A	0–8	53.3	10.1	7.5	na	4.9	6.6	32	1.2
	EA	8–24	57.2	7.9	2.5	na	4.9	0.8	9	na
	Bw1	24–36	60.2	8.1	0.9	na	4.4	0.4	9	1.67
Bw2	36–51	66.7	8.8	0.2	na	4.5	0.5	9	1.81	
Jackland (Fine, smectitic, mesic Typic Hapludalf)										
Hillsdale (urban, high fertility)	Duff	3–0	na	na	16.4	445.1	na	na	na	na
	A	0–8	9.8	14.2	3.6	59.3	5.7	6.4	27	0.89
	A/E	8–14	10.9	14.1	1.7	29.7	4.4	1.8	13	1.1
	BE	14–25	10.9	14.4	0.8	7.3	4.2	0.7	8	1.49
	Bt1	25–46	6.8	22.2	0.5	4.4	4.5	2.0	15	1.54
Bt2	46–69	5.1	37.5	0.4	2.7	4.7	18.7	68	1.15	

^a Measured at soil/water 1:1 H₂O.

^b NH₄OAc extractable Ca, Mg, Na, and K.

^c Base saturation equals sum of bases divided by sum of cations.

The structure of the forests was well developed with canopy and subcanopy tree layers, shrub and vine layers, and herbaceous cover. The sites differed in the percent openness of their canopies. In general, the urban plots had higher canopy openness than the rural plots (Table 2). Hillsdale 2 had lost approximately 57% of its canopy and standing dead trees were the largest component of the total basal area of the stand. The average height of the tree layer ranged from 24 to 34 m with the rural plots maintaining a taller canopy. The range of average

sapling heights from 5.6 to 7.5 m was much smaller than the range of tree heights. The average height range of shrubs was 1–1.5 m across the sites with the exception of Hillsdale 2, which had a taller shrub layer (3.7 m), and one rural plot with a shorter shrub layer (0.75 m) (Table 3).

Tree density was greatest in the Hillsdale forest while total basal area per hectare was smallest. The plots in Leakin Park and those in the rural forest were similar in both tree density and basal area (Table 3).

Table 2
Soil parameters in low vs. high fertility plots

Parameter	Low fertility	High fertility
% sand	47 (3)*	24 (6)*
% clay	19 (2)	19 (3)
Total C (g kg ⁻¹)	114 (36)	81 (45)
Total N (g kg ⁻¹)	3.3 (1.2)	3.4 (1.6)
C:N	75 (18)**	14 (2.3)**
pH	4.7 (0.1)***	4.9 (0.2)****
Sum of bases (mequiv. 100 g ⁻¹)	3.4 (1.8)	7.1 (2.0)
% base saturation	15 (2.3)*	38 (7.4)*
Bulk density (g cm ⁻³)	1.3 (0.1)	1.3 (0.1)

Values are means (with standard error) of all horizons sampled from soil pits in the five low fertility and two high fertility sites described in Table 1. *, **, *** indicate statistically significant differences at $p < 0.01$, 0.05 and 0.10, respectively.

The urban plots had higher ($p < 0.05$) leaf area index (LAI) than the rural plots and the plots on high fertility soils had higher ($p < 0.10$) LAI than the plots on low fertility soils (Table 4). Leakin plot 2, the urban plot located on a low fertility soil type had the lowest LAI of the urban plots.

Twenty-one of the tree species occurred as canopy trees and all sites were dominated by *L. tulipifera*, and several species of *Quercus* (*Q. velutina*, *Q. alba*, *Q. rubra*, and *Q. prinus*). *Q. alba* was the only species to occur across all sites. *A. rubrum*, *Carya tomentosa*, *L. tulipifera*, *Q. rubra* and *Q. velutina* were found in all sites except Hillsdale 2. Six other species each occurred in only one site. Litterfall was dominated by oak species, followed by tulip poplar, except at the Hillsdale sites, which had very little tulip poplar (Table 4).

Twenty-nine species of saplings were found across all sites. The dominant species in the sapling layer were not the same species that dominated the canopy layer and, in fact, *Quercus* spp. and *L. tulipifera* saplings were rarely found in the sapling layer. The sapling layers of the rural sites were all dominated by *Nyssa sylvatica*, *A. rubrum*, and *Cornus florida*. The sapling layers in the Leakin Park sites were dominated by *C. florida*, *Sassafras albidum*, and *A. rubrum*. The two plots in Hillsdale Park represented the two extremes of the sapling density gradient. Hillsdale 1, with 6044 stems ha⁻¹, was dominated by *F. americana* and *C. florida* and Hillsdale 2, with 1244 stems ha⁻¹, by *Viburnum prunifolium*. *V. prunifolium* was sampled as a sapling because of its single stem and tall

Table 3
Vegetation composition and structure in eight forest plots arrayed along an urban rural gradient and a soil fertility gradient

Land use context	Urban				Rural			
	Hillsdale 1 ^a	Hillsdale 2 ^a	Leakin 1 ^a	Leakin 2 ^b	Oregon Ridge upper 1 ^b	Oregon Ridge upper 2 ^a	Oregon Ridge mid 1 ^a	Oregon Ridge mid 2 ^a
Area (m ²)	900	900	1600	1600	1600	1600	1600	1600
No. of tree species	12	7	16	8	12	10	11	10
No. of sapling species	14	8	17	12	13	13	12	7
No. of seedling species	10	6	10	17	13	14	15	14
No. of shrub species	10	4	4	12	8	10	8	8
No. of vine species	9	10	6	8	6	7	6	3
No. of herbaceous species	12	8	14	16	3	8	4	11
Total vascular plants ^c	49	35	45	54	37	42	35	39
No. of non-native species	5	5	3	7	0	3	0	0
% canopy gap	19	57	1	14	1	3	6	1
Average maximum tree height (m)	25.16	24.22	29.48	30.40	28.91	33.95	33.17	32.68
Average maximum sapling height (m)	7.53	5.67	5.95	6.27	6.00	6.03	7.36	6.85
Average maximum shrub height (m)	1.04	3.69	0.95	1.12	0.96	1.46	0.76	0.95
Trees ha ⁻¹	84	63	37	39	38	38	46	43
B.A. ha (cm ² × 1000)	156.16	199.24	331.38	338.55	224.79	376.82	349.79	352.98
Saplings ha ⁻¹	6044	1244	3100	5575	1425	1175	1925	1400
B.A. ha (cm ² × 1000)	32.93	13.30	16.31	36.80	16.40	13.94	26.34	19.71
Seedling ha ⁻¹ (×1000)	77.78	8.89	102.81	36.25	41.25	18.44	34.38	38.75
% seedling frequency	94.44	27.78	100.00	90.63	100.00	71.88	9.38	6.25
Shrub cover (cm m ⁻¹)	9.24	81.67	16.83	16.39	50.29	61.64	30.88	38.85
% shrub frequency	78	100	62.5	93.75	100	100	100	100
Vine cover (cm m ⁻¹)	5.26	57.10	4.98	5.01	2.74	2.31	1.11	0.39
% vine frequency	78.00	100.00	87.50	75.00	56.25	62.50	68.75	37.50
Understory plant cover (%)	39.28	92.03	47.56	42.83	47.66	62.78	32.72	30.89
Herbaceous cover (%)	11.06	15.11	6.64	4.97	0.84	1.91	0.34	2.91

^a High fertility soil.

^b Low fertility soil.

^c Total vascular plants is not additive because a single species can exist in more than one lifeform, e.g. tree and sapling.

Table 4
Leaf area index and litterfall mass and % oak and tulip poplar in eight urban and rural forest sites from fall 1998 to fall 2000

Site	Land use context	Soil fertility	Leaf area index	Litterfall		
				Mass (kg ha ⁻¹)	% oak ^a	% tulip poplar ^b
Hillsdale 1	Urban	High	10.6	4845	77	1
Hillsdale 2	Urban	High	10.7	5840	48	8
Leakin 1	Urban	High	9.7	4122	25	52
Leakin 2	Urban	Low	8.5	4670	42	15
Oregon upper 1	Rural	Low	6.9	4605	73	21
Oregon upper 2	Rural	Low	6.9	4188	56	33
Oregon mid 1	Rural	Low	5.8	4665	42	14
Oregon mid 2	Rural	Low	5.4	4889	68	32

Hillsdale plots 1 and 2 and Leakin plot 1 are located on high fertility soil types while the other plots are located on low fertility soil types. In a two-way analysis of variance with “land use context” and “soil fertility” as main effects, leaf area index was significantly higher in urban than in rural plots ($p < 0.05$) and on high fertility soils than on low fertility soils ($p < 0.10$).

^a *Quercus alba* (white oak), *Quercus rubra* (red oak), *Quercus prinus* (chestnut oak), *Quercus velutina* (black oak).

^b *Liriodendron tulipifera*.

growth form. The four urban plots ranged from 1244 to 6044 stems ha⁻¹, and the density of saplings in the four rural plots varied between 1175 and 1925 stems ha⁻¹. Sites with greater sapling density also had greater total sapling basal area (Table 3). The only non-native species in the sapling layer was *A. platanooides* which was found in Hillsdale 2. *N. sylvatica* and *C. florida* were the only two sapling species to be found in all sites and *A. rubrum* was found in all sites except Hillsdale 2. Sapling mortality, measured as standing dead stems, was consistent across sites ranging from 12 to 20% of the total sapling community. One rural site had a higher mortality of 29%. No standing dead saplings were found at Hillsdale 2.

Seedling density was highest in two of the urban plots, Hillsdale 1 and Leakin 1. Hillsdale 2 contained the fewest seedlings. The variation of seedling density among plots was again greatest among the urban sites (9–102 seedlings ha⁻¹ ($\times 1000$)). Seedling density in the rural plots varied between 18 and 41 seedlings ha⁻¹ ($\times 1000$) (Table 3). The most abundant seedlings across all sites were *A. rubrum*, *F. americana*, and *Prunus serotina*. *P. serotina* was the only species found across all sites. Unlike the sapling layer, *Quercus* spp. comprised 18% of the seedling layer. The most abundant seedling species across sites was *A. rubrum* but this species was not found in the seedling layer at Hillsdale 2. Of the 27 seedling species recorded, only two were non-native, *A. platanooides* and *P. avium*. One individual of each of these species was recorded in Leakin 2.

The shrub layer was well developed in all of the sites. In the rural sites, shrubs were found on all 16 of the sampled transects and they were frequent in the urban plots as well (Table 3). Though there were 17 shrub species identified, few contributed substantially to the vegetation. The rural plots were heavily dominated by *Viburnum acerifolium* and the urban plots by *Lindera benzoin* and *V. acerifolium*. *V. acerifolium* was not

found in the Hillsdale plots. Two non-native species were found on the shrub transects; one in Hillsdale 1 (*R. multiflora*) and one in Hillsdale 2 (*L. vulgare*). Six of the 15 shrub species were only found in one plot.

Vines were a relatively minor component of the vegetation in all plots except Hillsdale 2. Vines were frequently present but their cover was minimal. More than 50% of the total sampled transect was intersected by vines in Hillsdale 2 (Table 3). There were seven species of vines in this plot and the dominant species was *H. helix*, a non-native species. The other two non-native vine species, *L. japonica* and *C. orbiculatus*, were also found in Hillsdale 2. All three non-native vines were only found in the urban plots. *Toxicodendron radicans*, *Dioscorea quaternata* and *Glechoma hederacea* were also only in the urban plots. The most widely distributed vine species was *Parthenocissus quinquefolia*, which was found in all sites except Hillsdale 1.

Herbaceous species contributed little to the vegetation community cover. Though some plots had high average cover in the ground layer, most of the cover was due to woody plants or vines. The greatest average ground layer cover was in Hillsdale 2 and the herbaceous cover in these plots was also highest (Table 3). The proportion of the ground layer made up of herbaceous species was higher in the urban than the rural plots, with the greatest proportion in Hillsdale 1 at 28%. The other urban plots ranged from 12 to 16% and the rural plots ranged between 1 and 9%. Urban plots were more species rich than rural plots in the herbaceous layer and 25 of the 38 total herbaceous species were found only in the urban plots. Only one herbaceous species was non-native and this species, *A. bracteata* was found only in the Leakin Park plots.

3.3. Soil N cycle processes

There was no difference in net N mineralization and nitrification rates (Fig. 1) nor in soil NO₃⁻ levels (data not shown) between urban and rural forest sites. However, all three variables were significantly ($p < 0.05$) higher on sites with high fertility soil types than on sites with low fertility soil types (Fig. 1). Soil NH₄⁺ levels did not differ among sites. Hillsdale plot 2 had notably high levels of mineralization, nitrification and soil NO₃⁻.

Net nitrification showed significant annual variation, with higher ($p < 0.10$) rates in 2000 than in 1999 (Fig. 2, Table 5). These patterns were correlated with precipitation which was higher in 2000 than in 1999. Precipitation at Baltimore-Washington airport, approximately 25 km from our urban sites, in water year 2000 (October 1999–September 2000) was 120% of normal, while precipitation in water year 1999 was 71% of normal. Fall 1999 was particularly dry, with 34% of normal precipitation. Mineralization showed less annual variation than nitrification.

Soil solution concentrations of NO₃⁻ were consistent with patterns of soil N cycling, with higher ($p < 0.05$ in an analysis over all years) concentrations in plots on high fertility soil types, no land use effect, and particularly high concentrations at Hillsdale plot 2 (Fig. 3). Patterns were more marked at 10 cm

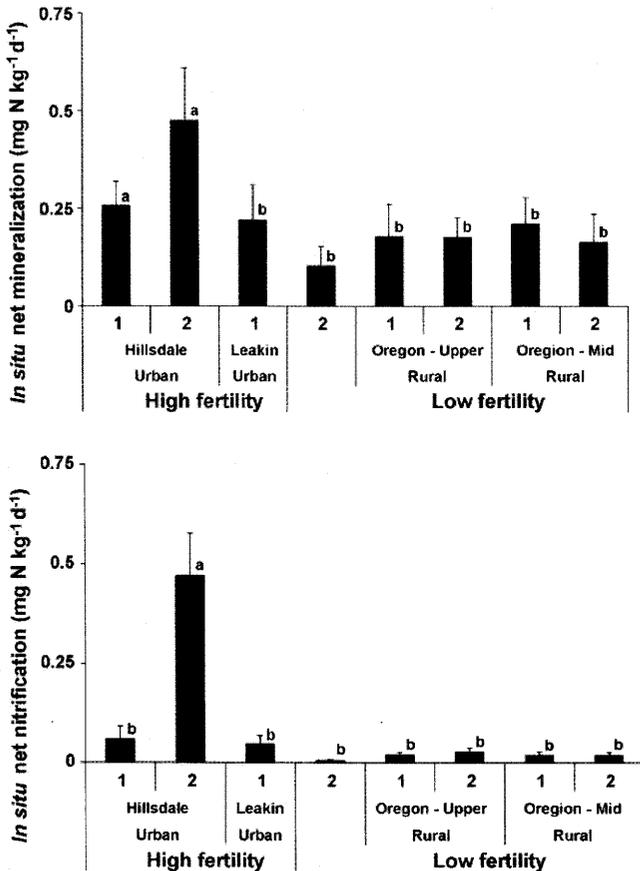


Fig. 1. Mean *in situ* net N mineralization (top) and nitrification (bottom) rates in urban and rural forest sites measured at 15 dates from fall 1998 to summer 2000. Values are mean (standard error). Hillsdale plots 1 and 2 and Leakin plot 1 are located on high fertility soil types while the other plots are located on low fertility soil types. Bars with different superscripts are significantly different at $p < 0.05$ in a one-way analysis of variance with “plot” as the main effect. A two-way analysis of variance with “land use” and “soil fertility” as main effects found no significant land use effect, but soil fertility was significant for both variables.

than at 50 cm depth, and concentrations were much lower at 50 cm. Only data from tension lysimeters are reported as the zero tension lysimeters did not collect solutions efficiently at the four rural sites, likely due to differences in soil texture and structure, especially the presence of a highly permeable layer above the 50 cm depth collectors at the rural plots. This layer was indicated by high saturated hydraulic conductivity values measuring during soil pit characterizations. Solution volumes collected by the tension lysimeters were very similar at the different sites. Annual leaching losses of NO_3^- were low relative to mineralization and nitrification ($< 0.1 \text{ g N m}^{-2} \text{ year}^{-1}$, Table 5).

3.4. Soil:atmosphere trace gas fluxes

Soil:atmosphere fluxes of CO_2 showed marked seasonal patterns, with higher rates during the warmer seasons than the colder seasons, but fluxes of N_2O and CH_4 did not (Fig. 4). We also observed a strong influence of soil moisture on CO_2 flux,

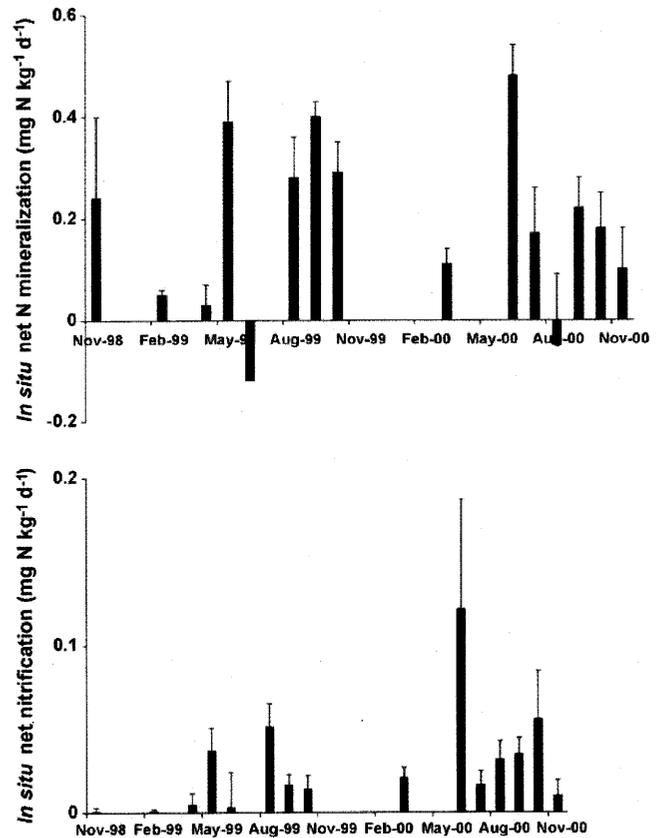


Fig. 2. Mean *in situ* net mineralization (top) and nitrification (bottom) in seven urban and rural forest stands from November 1998 to November 2000. Values are mean (standard error). A one-way analysis of variance with “year” as the main effect found that nitrification was significantly ($p < 0.10$) higher in 2000 than in 1999.

with low fluxes during the dry summer of 2000 and very low fluxes during very dry conditions in summer 2002. Production of CO_2 was higher ($p < 0.05$), and consumption of CH_4 was lower ($p < 0.05$) in the urban than the rural plots (Fig. 5). Consistent with other N cycle process data, Hillsdale plot 2 had high N_2O flux relative to the other sites. Annual fluxes of N_2O ranged from 0.03 to $0.14 \text{ g N m}^{-2} \text{ year}^{-1}$.

Table 5

Annual ($\text{g N m}^{-2} \text{ year}^{-1}$) net N mineralization, nitrification, nitrate leaching and nitrous oxide flux, 1999–2002

	1999	2000	2001	2002
Net N mineralization ^a	6.1 (0.6)	7.1 (0.9)	ND	ND
Net nitrification ^a	0.6 (0.1)	1.6 (0.5)	ND	ND
Nitrate leaching ^b	ND	0.06 (0.01)	0.05 (0.01)	0.03 (0.01)
Nitrous oxide flux	0.14 (0.02)	0.07 (0.02)	0.10 (0.02)	0.03 (0.02)

Values are the mean (standard error) of seven forest plots for mineralization, nitrification and leaching, and eight plots for nitrous oxide flux. ND = not determined.

^a Hillsdale plot 2 was not included in these calculations because mineralization and nitrification were only measured in 2000 on this plot.

^b Hillsdale plot 2 was not included in these calculations because values were so much higher for this plot than all other plots (see Fig. 4).

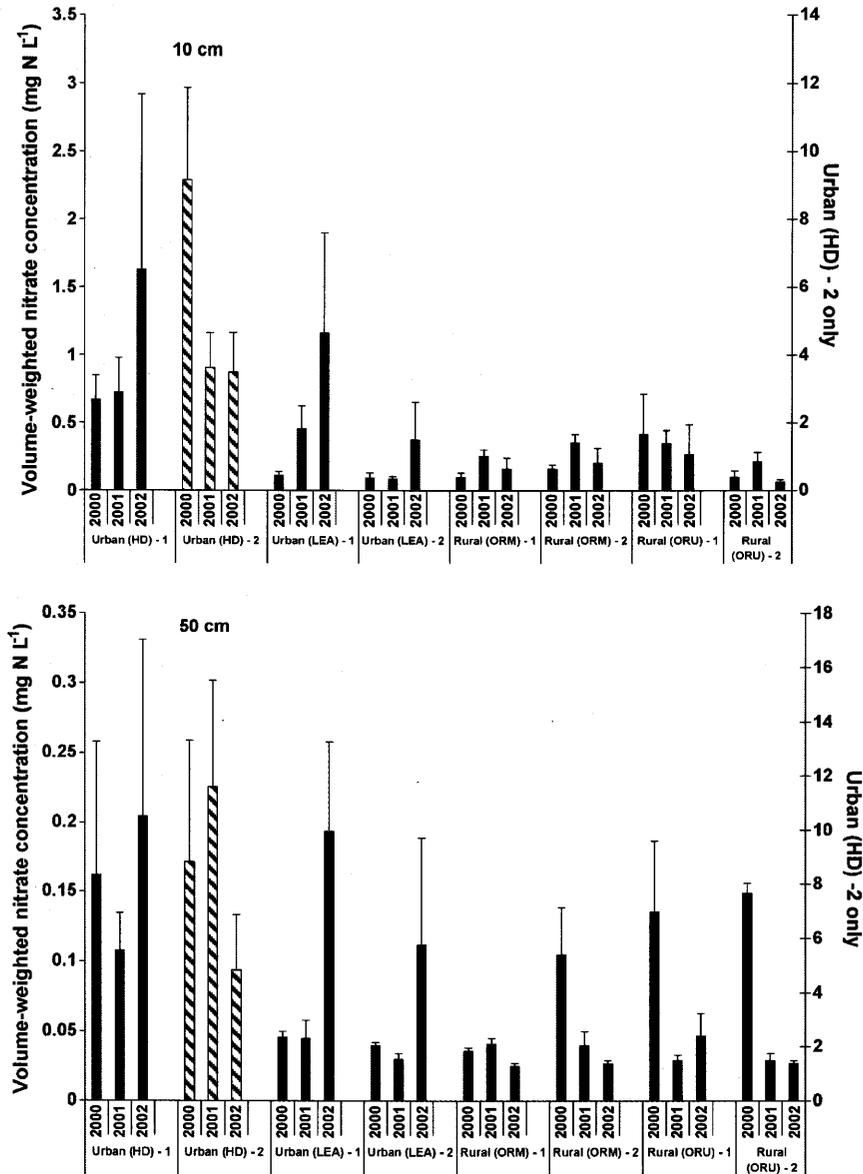


Fig. 3. Volume-weighted nitrate concentrations in tension lysimeters at 10 cm (top) and 50 cm (bottom) depth in eight urban and rural forest stands from fall 1999 to fall 2002). Note the separate y-axis that applies only to the Urban (HD) 2 site. Values are the mean of four replicate lysimeters at each depth that produced samples from 1 to 10 times each year. Hillsdale (HD) plots 1 and 2 and Leakin (LEA) plot 1 are located on high fertility soil types while the other plots are located on low fertility soil types. A two-way analysis of variance with “land use” and “soil fertility” as main effects found no significant land use effect, but soil fertility was significant at 10 cm depth.

4. Discussion

The importance of geology and soil parent material as a controller of forest vegetation and N cycling processes has been studied in many locations (Pastor et al., 1982, 1984; Schimel et al., 1985; Groffman and Tiedje, 1989; Zak et al., 1989; Scott and Binkley, 1997; Amundson and Jenny, 1997; Finzi et al., 1998). Our objective here was to determine if these controls are still important in human-dominated landscapes where remnant forests are surrounded by urban and suburban land use. This objective is hard to achieve, as land development patterns do not vary systematically with patterns of geology and soil parent

material. Our approach was to quantify natural soil patterns with soil profile descriptions and sampling, and then to analyze how plant community composition and soil C and N cycling processes vary in response to those patterns in both urban and rural land use contexts.

Our results show that fundamental, “natural controls” are still important in forests affected by the complex environmental changes induced by urban land use change. Forest productivity and N cycling varied more with soil type than with proximity to urban land use. On the other hand, forest community composition and soil:atmosphere fluxes of CO₂ and CH₄ appeared to be more strongly influenced by exposure to altered

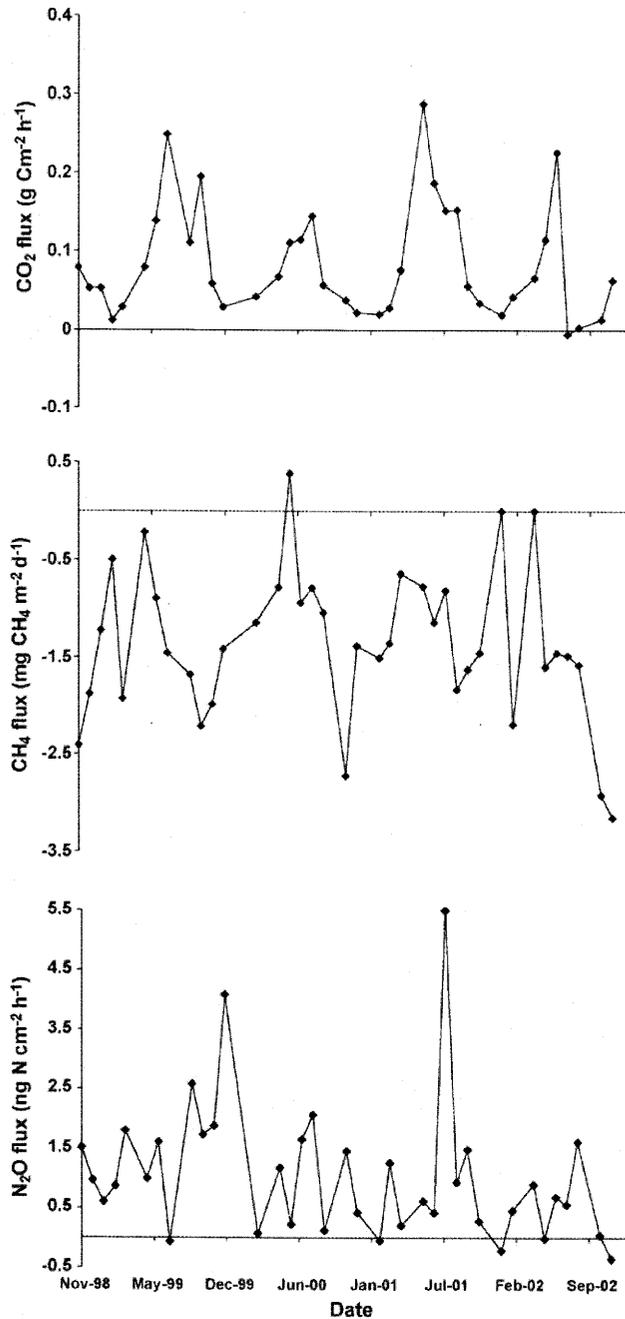


Fig. 4. Soil:atmosphere fluxes of CO_2 , CH_4 and N_2O from fall 1998 to fall 2002. Values are the means of four *in situ* flux chambers in eight forest plots.

disturbance regimes and atmospheric chemistry associated with urbanization. These measures varied strongly between urban and rural sites, independent of soil type. Our results also show that the magnitude of natural processes is important in the context of urban landscapes, i.e. production of (and annual variation in) inorganic N in forest patches was large relative to atmospheric deposition, fertilizer use and food/sewage fluxes that have been measured in BES urban and suburban watersheds.

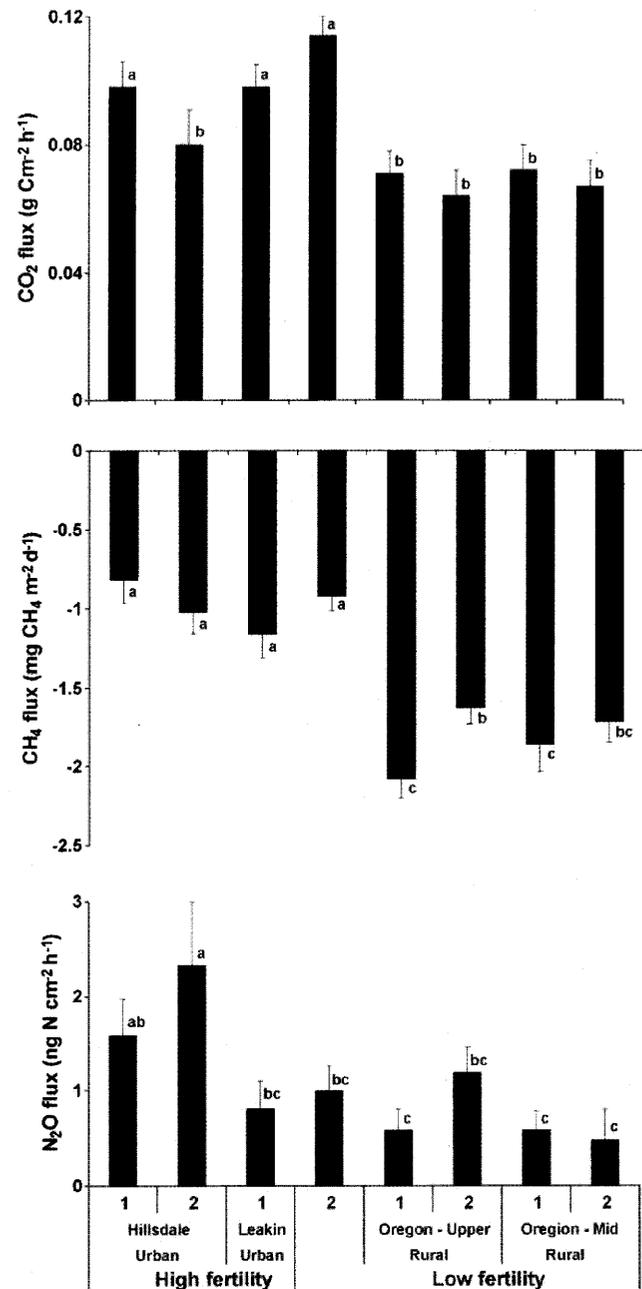


Fig. 5. Mean soil:atmosphere CO_2 (top), CH_4 (middle) and N_2O (bottom) flux in urban and rural forest sites measured at 38 dates from fall 1998 to fall 2002. Values are mean (standard error). Hillsdale plots 1 and 2 and Leakin plot 1 are located on high fertility soil types while the other plots are located on low fertility soil types. Bars with different superscripts are significantly different at $p < 0.05$ in a one-way analysis of variance with "plot" as the main effect. A two-way analysis of variance with "land use" and "soil fertility" as main effects found that land use was significant for CH_4 and CO_2 and soil fertility was not significant for any variable.

4.1. Soils

In the Baltimore metropolitan area, urban land use change has taken place on top of significant natural variation in geology and soil parent material that creates natural variation in soil

fertility. Low fertility soils in the region, e.g. the Manor, Glenelg and Occoquan soils on our plots, formed in acid crystalline rocks such as gneiss and micaceous schist and thus were strongly acid. The relatively high fertility soils in the region, e.g. the Legore and Jackland soils in our plots, formed in mixed mafic rocks and material weathered from amphibolite, diabase, or other basic igneous rocks.

Unfortunately, soil properties vary in a confounded way with land use patterns in the Baltimore region. Older, denser urban areas tend to be underlain by high fertility soils, while low fertility soils dominate at the rural fringe. This pattern confounds our ability to evaluate the relative importance of natural soil versus land use matrix effects on forest processes. In Leakin Park, we have a direct comparison of high versus low fertility soil types in an urban context, i.e. Leakin plot 1 is on the high fertility soil that dominates the urban core and Leakin 2 is on an inclusion of low fertility material in Leakin Park. But this comparison is unreplicated, and is not matched by a soil fertility comparison in a rural context.

Although our experimental design is imperfect, our results show coherent linkages between soil properties and N cycle processes. In a combined analysis of all low versus high fertility horizons (Table 2), we observed significant differences in soil C:N ratio, percent sand, soil pH and percent base saturation between the low fertility and high fertility soil types. And these differences appear to cut across the urban–rural gradient. For example, Leakin plot 2 was similar in soil chemistry and nitrogen cycling to the rural Oregon Ridge plots, while Leakin plot 1 was similar in most properties to the other high soil fertility urban plots. Moreover, these changes in basic soil properties are consistent with the significant differences that we observed in N mineralization, nitrification and soil and soil solution NO_3^- levels between plots, and with previous studies that have examined links between soil properties and N cycling (Pastor et al., 1984; Lovett et al., 2002; Ross et al., 2004). These results suggest, albeit imperfectly, that natural soil controls are still expressed, and are still important regulators of N dynamics in urban forests.

4.2. Vegetation

Variation in geology and soils has been found to be a strong controller of variation in forest community composition and dynamics at ecosystem, landscape and regional scales (Pastor et al., 1982; Zak et al., 1989; van Breemen et al., 1997; Finzi et al., 1998). In these studies, variation in soil water and nutrient holding capacity leads to variation in forest composition, productivity and C and N dynamics. At finer scales, site history and disturbance regime also become important in determining forest community structure (Pickett et al., 1989). At the scale of our comparison, natural controls on forest composition are modified by human factors, especially in the forests situated in an urban context, with the effects on C and N dynamics dependent on the nature and extent of the modification.

The most marked human effects on forest composition were observed in the plots in Hillsdale Park. This park is a relatively small patch of forest between a residential neighborhood and a

golf course, while the other urban park (Leakin) and the rural park (Oregon Ridge) are much larger tracts of relatively intact forest. As a result, the Hillsdale forest is more exposed to external sources of disturbance and loss of canopy trees. Less than 50% of the Hillsdale 2 plot had a tree canopy. This loss of canopy may allow greater vegetation density in lower canopy layers. Increased density was not seen in the sapling and seedling layers, which may not have had sufficient time since canopy loss to establish. However, the shrub, vine, and ground layers were very dense, maintaining covers much higher than any other urban or rural plot. Alternatively, the loss of canopy trees, especially in a small isolated forest, may result in the loss of source trees for seeds and consequently less establishment of seedlings and saplings. In addition, the shrub layer in Hillsdale 2 was more than twice the height of shrub layers in any other plot. The loss of canopy may be recent in Hillsdale 2 as standing dead stems were the largest component of the basal area in the plot and there was no mortality recorded among the few regenerating saplings. Hillsdale 1, on the other hand, had greater than 80% canopy cover. The sapling and seedling layers in this plot were very dense and the shrub, vine and ground layers were much less dense than in Hillsdale 2. In fact, the shrub layer in Hillsdale 1 was surprisingly sparse, most likely due to the very thick sapling layer. The relatively high number of trees per hectare and low total basal area in the Hillsdale plots indicate that this forest may be younger than the forests in Leakin and Oregon Ridge Parks.

Leakin Park, the other urban forest, was similar in tree canopy structure to the rural Oregon Ridge Park plots and similar to Hillsdale Park in the structure of the understory layers. This may indicate a difference in response times to altered environments by the different canopy layers. Many of the canopy trees in Leakin Park were present as the city grew around the Park's perimeters. This canopy layer may be slower to respond to altered environmental conditions ushered in by the change in adjacent land cover. The canopy layer heights, tree density and basal areas in Leakin Park were similar to those in the Oregon Ridge plots. The lower canopy layers, however, may respond faster to altered conditions and the structure of these layers varied between the Parks (Cadenasso et al., in press). The sapling layer in Leakin Park was denser and the saplings smaller than in Oregon Ridge. In addition shrub cover was lower and vine and herbaceous cover was higher in Leakin Park.

The four plots in Oregon Ridge Park were very similar in structure and were characterized by closed canopies, large tall trees and a well-developed sapling layer. The understory maintained an even cover of shrubs. The consistency in vegetation structure indicates a similar age and conditions among the four plots in this forest.

To compare the structure of the urban and rural plots, Hillsdale 2 and Leakin 2 were removed because of the loss of tree canopy and a different soil type, respectively. Comparing Hillsdale 1 and Leakin 1 to the Oregon Ridge plots reveals that the urban plots had a less continuous tree canopy as the taller older trees are beginning to senesce or were otherwise damaged. The greater density of saplings in the urban plots

relative to the rural forest may reflect the more open canopy in these plots. The urban and rural forests tend to vary in the density of alternate canopy layers which may be a response to competition among canopy layers. For example, in the urban plots, the tree canopy had more gaps, the sapling layer was denser, the shrub layer was sparser, and seedlings were denser and herbaceous cover greater. Alternatively, in the rural plots, the canopy was closed, the sapling layer was sparser, the shrub layer was denser and seedling density and herbaceous cover were lower. Canopy openness may drive resource availability in the system and consequent vegetation layer structure. Lower seedling and sapling density in the rural forest may, however, indicate greater herbivore pressure.

Vegetation composition also varied among the plots along the urban–rural gradient. Composition is a product of both dispersal and plant performance. Both of these mechanisms may be altered by the urban environment. The tree and sapling layers contained similar species along the gradient but the shrub, vine, and herbaceous layers differed greatly. This may result from the tree species responding more slowly to altered conditions and adjacent land uses relative to the lower canopy layers. The dominant shrub species were the same among plots within the same location (urban versus rural) but species did not overlap among plots across gradient locations. Though the urban plots were similar to the rural plots in that one species of shrub dominated, albeit a different species from the rural plots, there were also many more species of shrubs in the urban plots. Vines played a much larger role in the urban plots than the rural plots which may be due to the greater gapiness of the urban forest allowing light to reach the forest floor and facilitate vine growth. The vine community in the urban plots was much more species rich and six species occurred only in the urban plots. Herbaceous species richness was also higher in the urban plots than the rural plots. This may be due to a greater seed source in the urban matrix and higher soil fertility.

One of the surprising results from this sampling is that exotic species played a minor role in these communities. The few exotic species that we observed occurred primarily in the urban plots but not in large numbers or percent cover. One exception was the vine layer in Hillsdale 2. This may be a product of canopy loss through senescence or damage by insects and storms, releasing resources for the lower canopy layers or as the forests are exposed to more seed influx from the surrounding landscape. Exotic species presence in the forest may also be higher along edges and pathways (Bertin et al., 2005), two features purposely avoided in the site selection.

Vegetation structure varied among the forest plots but the cause of that variation is unclear. Stand age and the amount of disturbance to the forest canopy distinguish the plots structurally. Whether the amount of canopy disturbance and urban landscape context are correlated is a question open for further research. Some differences such as higher sapling density in the urban plots may be a factor of both landscape context and soil type. The urban landscape context may result in canopy openness and this greater openness and more fertile soil may both lead to denser understory vegetation. However, the variation among plots in species composition was most likely

due to the landscape context. The canopy trees in all plots were the same suite of species—*L. tulipifera* and *Quercus* spp. In contrast, the plots maintained different species in the sapling, shrub, vine, and herbaceous layers. These differences were consistent across the urban to rural contrast, but not across soil types. The urban landscape and related alterations of biophysical conditions have been dynamic on the temporal scale of the understory populations; less so on the temporal scale of the tree canopy. It is likely that as the tree canopy is disturbed, the urban forest structure and composition will continue to diverge from the rural forest. The relatively small size of the Hillsdale forest patch may contribute to the canopy of this forest experiencing more disturbance than Leakin Park and the Hillsdale forest may, consequently, be diverging faster.

4.3. Carbon dynamics

Given that all of our stands are roughly the same age (80–100 years), leaf area index (LAI) provides a rough index of productivity, or site quality for our sites. As such, it is not surprising that LAI was higher on the high fertility sites than the low fertility sites. LAI values for our plots are high relative to (but within the range of) other temperate forests, consistent with their mature status (Asner et al., 2003). It is interesting to note that Leakin 2, the low fertility site in an urban land use context, had higher LAI than the rural sites, suggesting a possible stimulation of productivity in the urban core. Such a result would be consistent with other studies that have found high productivity in cities due to higher atmospheric CO₂ and/or lower ozone levels relative to suburban or rural areas (Gregg et al., 2003; Ziska et al., 2004). Higher levels of atmospheric CO₂ would be particularly important at relieving water stress, which is more likely on the coarse-textured low fertility soils (Norby and Luo, 2004).

In addition to stimulating productivity, an urban atmosphere effect on carbon dynamics is also apparent in the soil:atmosphere fluxes of CO₂ and CH₄. Soil:atmosphere CO₂ flux is a measure of total soil respiration (roots plus microorganisms) and was consistently higher in the urban stands than the rural stands. Total soil respiration is influenced by several factors including litter quality, which influences decomposition rate, soil moisture, which controls microbial and root activity, soil texture, which influences microbial access to substrates and soil moisture, and the flow of labile C from aboveground production (Fahey et al., 2005). The flow of labile C is highly responsive to increased atmospheric CO₂ levels (Zak et al., 2003), therefore, the consistent increase that we observed in the urban stands, over a range of litter quality and soil conditions, suggests an atmospheric effect.

Our estimates of respiration (approximately 700 g C m⁻² year⁻¹) are high relative to rates measured in the northern hardwood forests at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire using the same methods used here (Groffman et al., 2006) which is logical given the higher temperatures and longer growing season in Baltimore. Our estimates are similar to other measurements at the HBEF and at other forest sites in the northeastern U.S. made using fast

response detectors (infrared gas analyzers) and short-term incubations. Fahey et al. (2005) report total soil respiration ranging from 540 to 800 g C m⁻² year⁻¹ in eight stands at the HBEF sampled from 1998 to 2000, while Savage and Davidson (2001) reported soil respiration rates of greater than 500 g C m⁻² year⁻¹ from upland sites at the Harvard Forest in Massachusetts, and greater than 800 g C m⁻² year⁻¹ from upland sites at the Howland Forest in Maine. In addition to using fast response detectors, these other studies were based on more high resolution sampling than we did, which captures episodes of high flux that are missed with our less frequent sampling (Parkin and Kaspar, 2004).

There were significant differences in CH₄ uptake between the urban and rural stands. This uptake is strongly influenced by soil texture and moisture, with coarse-textured, dry soils, having higher rates of uptake due to enhanced diffusion of atmospheric CH₄ into the soil (Castro et al., 1995; Smith et al., 2000). Uptake is also influenced by N status, with N additions having an inhibitory effect in many, but not all, studies (Stuedler et al., 1989; Goldman et al., 1995; Reay and Nedwell, 2004). Thus, the low rates of uptake in our urban sites are likely due to both natural soil factors as well as the high rates of N deposition that are common in urban areas (Lovett et al., 2000). The low rates of uptake at Leakin 2, the urban site with coarse soil texture, suggest that the N deposition effect is more important than the soil texture effect. Goldman et al. (1995) also found reduced CH₄ uptake in urban forests.

The CH₄ uptake rates observed in our rural sites (approximately 665 g CH₄ m⁻² year⁻¹) were similar to those measured at forested sites in the northeastern U.S. but the rates at our urban sites (approximately 350 g CH₄ m⁻² year⁻¹) are lower than most previous studies in this region (Castro et al., 1995). Forests in the northeastern U.S. tend to have high CH₄ uptake relative to forests in other parts of the world (Smith et al., 2000).

4.4. Nitrogen dynamics

While several parameters related to C dynamics were clearly influenced by the urban land use context, N dynamics appeared to be more strongly influenced by natural soil factors. Rates of N mineralization and nitrification and soil and soil solution NO₃⁻ levels were all higher in the high fertility sites than the low fertility sites. The consistent grouping of Leakin plot 2, the urban site on the low fertility soil, with the rural sites, which are all on the low fertility soil, amplifies the idea that natural soil factors dominate over land use context in controlling soil N dynamics among our sites.

As expected, mineralization and nitrification were large internal fluxes in the nitrogen cycle. The Hillsdale 2 site, which showed evidence of extensive disturbance to the plant community and extensive invasion by exotic species, had the highest mineralization rates, and particularly high rates of nitrification.

The rates of mineralization and nitrification that we observed in our urban forests were somewhat higher than those measured in mixed oak forests at the Coweeta Hydrologic

Laboratory in North Carolina (Knoepp and Swank, 1998) and lower than those measured in oak–maple forests at the Fernow Experimental Forest in West Virginia (Peterjohn et al., 1999), using similar methods. Summer *in situ* N mineralization rates at Coweeta averaged 0.06 mg N kg⁻¹ day⁻¹, while summer rates at our sites were generally greater than 0.2 mg N kg⁻¹ day⁻¹. Our nitrification rates were also higher than those observed at Coweeta where summer rates averaged 0.007 mg N kg⁻¹ day⁻¹ compared to rates of approximately 0.05 at our sites. At Fernow, annual N mineralization ranged from approximately 8 to 16 and nitrification ranged from 0.7 to 12 g N m⁻² year⁻¹ compared to mineralization rates of 6.6 and nitrification rates of 1.1 g N m⁻² year⁻¹ at our sites.

Nitrate leaching losses were quite low (<0.1 g N m⁻² year⁻¹, Table 5) from most of our sites (except for Hillsdale 2, which had leaching losses greater than 2.5 g N m⁻² year⁻¹, data not shown), supporting the idea that forests have high retention of N, even when atmospheric inputs (approximately 0.9 g N m⁻² year⁻¹) and internal cycling through mineralization and nitrification are high. Similar to mineralization and nitrification, the soil solution NO₃⁻ levels that we observed (approximately 0.05 mg N L⁻¹) were higher than those observed at Coweeta (0.008 mg N L⁻¹, Montagnini et al., 1991) and lower than those observed at Fernow (0.07–2.3 mg N L⁻¹, Peterjohn et al., 1999).

Our leaching losses may be somewhat of an underestimate because we used concentration data derived from tension lysimeters, which sample water that is also accessible to plants (Lajtha et al., 1999). Zero tension lysimeters, which sample more freely draining water may provide better estimates of NO₃⁻ losses, but these did not work at our rural forest sites. We were able to directly compare volume-weighted NO₃⁻ concentrations in tension and zero tension lysimeters at the Leakin and Hillsdale sites, where both types of lysimeters routinely produced large sample volumes. This comparison showed that tension lysimeters produced lower NO₃⁻ concentrations than zero tension lysimeters (as expected) at Leakin Park (0.48 mg N L⁻¹ in zero tension, 0.09 mg N L⁻¹ in tension) while we observed the opposite pattern at Hillsdale Park (2.2 mg N L⁻¹ in zero tension and 4.3 mg N L⁻¹ in tension). It is therefore, impossible for us to determine if we have systematically underestimated leaching losses.

The high leaching losses at the Hillsdale 2 site are consistent with the high rates of mineralization, nitrification and soil NO₃⁻ levels at this site, and confirm the idea that this is a highly disturbed site. In contrast to all of the other sites, NO₃⁻ concentrations in soil solution were much higher at 50 cm than at 10 cm, suggesting that there may be a history of soil disturbance at this site, in addition to the evident disturbance of the plant community.

Mean summer nitrous oxide fluxes at our sites (1.5 ng N cm⁻² h⁻¹) were similar to those measured at Fernow (0.5–0.7 ng N cm⁻² h⁻¹, Peterjohn et al., 1998). Our estimates of annual N₂O flux (0.08 g N m⁻² year⁻¹) are at the high end of rates reported for deciduous forests (Groffman et al., 2000; Bowden et al., 2000). Rates were highest at the disturbed Hillsdale 2 site, but were also relatively high at the Hillsdale 1

site. These sites had the finest textured soils among our sites, which often leads to higher N_2O fluxes.

Our results confirm the idea, developed in previous studies, that urban land use change has complex effects on forest N dynamics that are difficult to predict. Studies along an urban to rural gradient in the New York City metropolitan area found significant increases in N mineralization, and especially nitrification, in urban and suburban oak stands relative to rural stands with closely matched soil and land use history conditions (Pouyat et al., 1995; Steinberg et al., 1997; Zhu and Carreiro, 1999, 2004). However, this effect was largely driven by the presence of large numbers of earthworms that stimulated decomposition and N cycling despite lower litter quality in the urban sites (Carreiro et al., 1999; Pouyat and Carreiro, 2003). Goldman et al. (1995) found no difference in N mineralization between urban and rural stands along the New York City urban to rural gradient when comparisons were made by soil horizon, which controls for the earthworm effect. Baxter et al. (1999, 2002) also found no difference in mineralization between urban and rural stands on the New York City gradient, but found that N and P availability to plants and ectomycorrhizal colonization were lower in the urban stands due to earthworm activity and lower litter quality. Carreiro et al. (in press) found that N mineralization was higher in urban stands than rural stands along an urban to rural gradient centered on Louisville, KY, but that nitrification was negligible in all stands. Pavao-Zuckerman and Coleman (2005) found that N mineralization was higher in urban soils along an urban to rural gradient centered on Asheville, NC, likely due to higher temperatures in the urban sites, i.e. the “urban heat island” effect. The variable results along urban to rural gradients support the idea that natural soil factors (discussed above) and species change (discussed below) are stronger controllers of soil N dynamics than exposure to urban atmospheric change (elevated temperature, ozone, nitrogen).

One pattern that emerges from our results and from previous studies is that species change, whether in the plant community such as we observed at Hillsdale plot 2 or in the soil community, as was observed in the New York City sites, is a powerful driver of N cycling along urban to rural gradients (Ehrenfeld et al., 2001; Ashton et al., 2005). Hillsdale plot 2, which showed evidence of significant vegetation disturbance, with a high percent of exotic and pioneer species, had markedly higher rates of mineralization, nitrification, soil and soil solution NO_3^- levels and N_2O flux than any of the other plots. Results from our other plots confirm the idea that in the absence of species change, the complex atmospheric changes caused by urban land use conversion do not overwhelm natural soil controls on N cycling.

5. Conclusions

Our results suggest that natural N cycling processes are important relative to watershed-scale atmospheric deposition, fertilizer use and food/sewage fluxes that have been measured in other studies in these study landscapes. Within the Gwynns Falls watershed as a whole, which is 20% forested, natural

production of inorganic N by mineralization in forests ($6.6 \text{ g N m}^{-2} \text{ year}^{-1}$) is greater than atmospheric N deposition ($1.1 \text{ g N m}^{-2} \text{ year}^{-1}$, Groffman et al., 2004b), even if we assume that no mineralization occurs in the non-forested portions of the watershed, which is clearly not the case. If we consider the 80 ha headwater catchment of the Gwynns Falls (Glyndon, Groffman et al., 2004b), which has approximately 20% impervious surface, and we assume that all the pervious surface has our average mineralization rate, then natural soil N production (4224 kg) exceeds atmospheric deposition (896 kg) by almost a factor of 5. Natural N production also exceeds fertilizer input to home lawns (1152 kg N, Groffman et al., 2004b; Law et al., 2004) and food imports (2800 kg N, Groffman et al., 2004b) by a large margin, although it is important to note that the intensity of fertilizer input (input per unit area) is quite high. It is also difficult to compare internal fluxes such as mineralization, with inputs such as fertilizer and deposition. However, our analysis shows that the N cycle in suburban watershed ecosystems is still dominated by natural processes. The variance in natural processes also appears to be significant, especially for nitrification, which varied by nearly a factor of 3 in the 2 years of our study. These results suggest that natural soil N cycle processes must be considered in the assessment and management of urban watersheds in water quality, air quality and carbon sequestration contexts.

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