

Foliar nitrogen characteristics of four tree species planted in New York City forest restoration sites

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Abstract Urban forests provide important environmental benefits, leading many municipal governments to initiate citywide tree plantings. However, nutrient cycling in urban ecosystems is difficult to predict, and nitrogen (N) use in urban trees may be quite different from use in rural forests. To gain insight into these biogeochemical and physiological processes, we compared foliar N characteristics of several common northeastern deciduous tree species across four newly planted New York City afforestation sites as well as at the Black Rock Forest (BRF), a rural oak-dominated forest in the Hudson Highlands, New York. Foliage sampled at BRF was consistently depleted in ^{15}N compared to urban foliage, and *Amelanchier canadensis*, *Nyssa sylvatica*, *Prunus serotina*, and *Quercus rubra* showed significant variation in foliar nitrogen isotope signatures ($\delta^{15}\text{N}$) among the four urban sites. *A. canadensis* and *P. serotina* showed significantly greater ability to assimilate nitrate at BRF compared to urban sites, as measured through nitrate reductase activity (NRA). There were no significant differences in NRA among tree species growing at the four urban sites. Only *P. serotina* and *N. sylvatica* showed significant variation in foliar N concentrations (%N) both among urban sites and compared to BRF. The isotopic and %N data suggest greater N availability but less available nitrate at the newly planted urban sites compared to BRF, possibly due to different anthropogenic inputs or higher rates of nitrification and nitrate leaching at the recently planted urban sites compared to likely lower rates of N cycling in the intact rural forest. In addition, the tree species varied in their response to N availability at the urban sites, with potential implications for growth and survival. Understanding N cycling in urban systems and the

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associated physiological changes in vegetation is critical to a comprehensive evaluation of urban forest restoration, and may have implications for carbon sequestration and water quality issues associated with nitrate export, two important areas of management concern.

Keywords *Amelanchier canadensis* · Forest restoration · Nitrate reductase · *Nyssa sylvatica* · *Prunus serotina* · *Quercus rubra* · Stable isotopes

Introduction

Urbanization is an important force of environmental change impacting ecosystem functioning on continental and global scales (Miller and Small 2003). Habitat destruction, invasive species, air and water pollution, and the urban heat island effect are all associated with increased urbanization (Baxter et al. 2002; Nowak 2000; Oke 1989). As a result, urban ecosystems may experience decreased air and soil quality relative to rural counterparts (Pouyat and McDonnell 1991; Nowak et al. 2006). One outcome of these human impacts is altered nitrogen cycling and availability, which can have profound effects on ecosystem structure, function, and species composition (Rusek 1993; Schlesinger 2009). Forests embedded within an urban matrix are directly affected by environmental impacts associated with urban land use, and thus provide a useful context for investigating the effects of these anthropogenic factors on forest ecosystems (Groffman et al. 2006).

Nitrogen (N) is an essential nutrient required by plants for protein synthesis. Northeast temperate forests are historically N-limited systems (Aber et al. 1983; Melillo et al. 1983). The soils in these forests generally have low rates of net nitrification, as plants and a variety of microbes out-compete nitrifiers for ammonium (Melillo 1981). However, N deposition from anthropogenic emissions has increased N availability in the northeastern U.S. (Aber et al. 1998) with rates 3–5 times greater in urban than rural areas (Templer and McCann 2010; Rao et al. 2013). This deposition includes nitrate (NO_3^-), which originates mainly from fossil fuel combustion, and ammonium (NH_4^+), which originates from the production and use of agricultural fertilizers (Aber et al. 1998). Lovett et al. (2000) found greater NO_3^- and NH_4^+ deposition in New York City forests than in nearby rural forests, owing largely to particulate deposition. Nearly 70 % of particulate N deposition was found to be in NO_3^- rather than NH_4^+ form.

Previous studies of forest N dynamics on urban to rural gradients have shown that urban land use change has complex effects on soil N cycling that are difficult to predict (Pouyat et al. 2009). Published findings on urban N cycling are inconsistent. Studies in the New York City metropolitan area found significant increases in N mineralization and nitrification in urban forest stands relative to rural stands (Pouyat et al. 1997; Zhu and Carreiro 1999 and 2004). If N availability exceeds plant and microbial uptake for a prolonged period of time, urban forests risk becoming N sources instead of sinks, a condition known as N saturation (Aber et al. 1998; Carreiro et al. 2009). Baxter et al. (2002) found higher rates of nitrification and a lower availability of ammonium in urban forest stands in New York City, possibly due to exotic earthworm activity and lower litter quality. However, White and McDonnell (1988) found lower N mineralization rates in urban soils and Goldman et al. (1995) found no difference in N mineralization when controlling for the earthworm effect. It appears possible that urban site conditions in New York City (warmer temperatures and exotic earthworm activity) may counteract low leaf litter quality in these areas, resulting in urban leaf litter decay rates and N cycling at similar rates to nearby rural forests (Steinberg et al. 1997; Pouyat and Carreiro 2003). However, Groffman et al. (2006) suggest that natural soil factors and changes in species composition in both plant and soil communities are ultimately stronger determinants of soil N

dynamics than urban atmospheric conditions. As a result, the status of the urban N cycle is dynamic, complex and difficult to predict in light of human activities and land use change.

Despite the attention paid to urban soil N dynamics, the physiological response of plants to these changes in nutrient cycling remains relatively unstudied (Cadenasso et al. 2007). Many northeastern temperate tree species are not naturally exposed to large amounts of nitrate, as they tend to grow in nutrient-poor soils with low rates of nitrification (Melillo 1981). However, some species may take advantage of increased nitrate availability by increasing nitrate reductase activity (NRA) (Truax et al. 1994). Furthermore, tree species vary in rates of NH_4^+ vs. NO_3^- uptake, and therefore may differ in their growth response to varying N availability (Adams and Attiwill 1982). These biological changes may ultimately affect the species composition of urban forests, with implications for ecosystem functions such as carbon sequestration and water quality regulation.

Natural abundance nitrogen isotopic composition of foliage ($\delta^{15}\text{N}$) can be used as integrated measures of terrestrial N cycling, with the potential to reveal spatial and temporal patterns of N cycling as well as how disturbances alter the N cycle (Robinson 2001; Craine et al. 2009; Pardo and Nadelhoffer 2010). Enhanced N deposition may result in a greater availability of both ammonium and nitrate in urban forest soils and can eventually lead to an N pool enriched in ^{15}N if excess (lighter) N is lost from the system. Many soil microbial processes discriminate against the heavier ^{15}N isotope, including decomposition, mineralization, nitrification, and denitrification (Nadelhoffer and Fry 1994). As a result, the products of these processes (NO_3^- and NO gas) are depleted in ^{15}N and are more easily removed from the system via leaching or efflux, and leave behind a ^{15}N -enriched soil N pool, which then is reflected in the leaves after uptake (Nadelhoffer and Fry 1994).

Despite the complex interactions between soil, microbes, fungi and plants that interact to determine the spatial patterns of ^{15}N abundance in a forest, it is still possible to draw meaningful interpretations from observed patterns (Garten 1993). Many studies have demonstrated the relationship between altered N cycling and small changes in vegetation ^{15}N values. Enrichment of foliar ^{15}N has been observed as a result of increased nitrification and loss of nitrate in response to many forest disturbances including clear-cutting (Pardo et al. 2002), widespread tree mortality (Falxa-Raymond et al. 2012), forest decline (Gebauer and Schulze 1991), N deposition (Emmett et al. 1998; Pardo et al. 2006) and N additions (Högberg 1990; Högberg and Johannisson 1993). In addition, foliar $\delta^{15}\text{N}$ values have been found to be positively correlated with N availability in surface soil (Garten and Van Miergroet 1994; Craine et al. 2009). The correlation between foliar ^{15}N abundance and both soil N loss and net nitrification potential suggests that measurements of foliar ^{15}N abundance may help to identify the position of forests along a gradient from N deficiency to N saturation (Högberg 1990; Garten 1993).

We are only aware of one previous study of urban foliar $\delta^{15}\text{N}$, in which Vallano and Sparks (2012) examined the importance of the direct foliar uptake of gaseous reactive N on foliar $\delta^{15}\text{N}$ in adult stands of red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), black birch (*Betula lenta*), and red oak (*Quercus rubra*) along a regional N deposition gradient in New York State. Although direct foliar uptake of atmospheric reactive N can impact foliar $\delta^{15}\text{N}$ signature, Vallano and Sparks (2012) found soil $\delta^{15}\text{N}$ to be the primary factor influencing foliar $\delta^{15}\text{N}$ in several tree species, including *Q. rubra*. In this study, we set out to establish a basic understanding of foliar N characteristics of four tree species planted extensively in New York City afforestation efforts. Part of New York City's long term sustainability plan, the MillionTreesNYC initiative is a public-private partnership between the NYC Department of Parks & Recreation and the non-profit New York Restoration Project, with the goal of planting one million trees between 2007 and 2017. By the end of the initiative, 488,000 of those trees

will be planted on NYC parkland and other public open spaces with the goal of creating multi-story, ecologically functioning forests. A citywide research program is leveraging the large-scale tree planting activities of the campaign, looking at the effects of MillionTreesNYC forest restoration efforts on urban ecosystem structure and functioning (McPhearson et al. 2010). Forest restoration at these sites includes invasive plant removal, dense tree sapling and shrub plantings, and mulching (McPhearson et al. 2010).

This study compares the concentration and isotopic signature of foliar C and N ($\%C$, $\delta^{13}C$, $\%N$ and $\delta^{15}N$) and foliar nitrate reductase activity (NRA) of saplings of four native tree species across four urban forest sites and one rural forest. We hypothesized that saplings in urban forests would have significantly different N use patterns than saplings of the same species in a rural forest, due to the changes in N availability in the urban environment. We also hypothesized that foliar N characteristics would vary among urban sites, each of which has a different history of anthropogenic modification and use, including soil disturbance and previous vegetation cover. Finally, we quantify heterogeneity in N use patterns among tree species

Experimental methods

Study sites

This study included four urban afforestation sites that are part of a citywide research program looking at the effects of MillionTreesNYC forest restoration efforts on urban ecosystem structure and functioning (McPhearson et al. 2010). These urban sites were sections of four New York City parks afforested in Fall 2009: Marine Park in Brooklyn, and Alley Pond Park and Roy Wilkins Park in Queens, and Clove Lakes in Staten Island (Fig. 1).

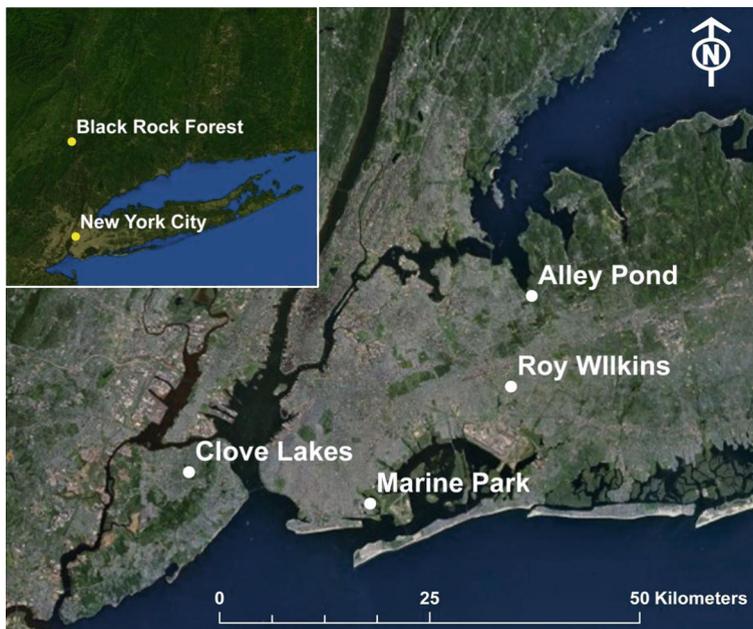


Fig. 1 Map showing urban afforestation sites within New York City. Inset shows the location of Black Rock Forest in the Hudson Highlands of New York State

Marine Park (elevation 3 m) is part of the historical extent of the Jamaica Bay estuary, which was used as a dumping ground in the early twentieth century and became filled in over time. The study plot lies on the margins of a large black locust stand (*Robinia pseudoacacia*) and the soil is the most acidic of the urban sites, with pH averaging 4.9. The soils are of the Bigapple-Fortress complex, moderately- to well-drained gneissic outwash plains partially covered with anthropogenic fill in the form of sandy dredge deposits and concrete rubble deposited in the mid-twentieth century as the result of nearby school construction activities (McPhearson et al. 2010; Mike Feller, NYC Department of Parks & Recreation, pers. comm.).

Soils at Alley Pond Park (elevation 3 m) are also likely to be heavily disturbed and of the Inwood-Laguardia-Ebbets complex, which consists of a well-drained mixture of loamy fill and construction debris (McPhearson et al. 2010). Alley Pond soil averages a pH of 6.9 and is the most compacted of all the urban sites. The plot was originally in the middle of a creek, which was a navigable channel until the 19th century and later filled in. The site served as a garbage basin during the 20th century until the 1970s when landfilling became regulated in New York City. The site was never formally capped but may have been covered with urban fill when an adjacent golf driving range was constructed in 1945 (Mike Feller, NYC Department of Parks & Recreation, pers. comm.). The study plot is located immediately adjacent to a major road and a parking lot for the driving range as well as open woodland that separates the site from marshland.

Roy Wilkins Park (elevation 8 m) was originally part of a rural pastoral landscape and lies in a low wooded area near an old streambed. Soils appear to consist of the Flatbush-Riverhead complex with parent material of both glacial outwash and anthropogenic fill over glacial outwash (McPhearson et al. 2010). However, this site was likely less altered than Alley Pond Park or Marine Park, having been disturbed but not filled with outside material (Mike Feller, NYC Department of Parks & Recreation, pers. comm.). The saplings in this location were also planted in a deep layer of previously dumped mulch and soil pH averages 6.9.

Among the urban sites, Clove Lakes (elevation 56 m) is the only park that lies above the coastal plain, well above sea level. This upland site sits on serpentine ridge parent material bedrock in the interior of a large park and has never been used as a dumping ground or been covered with urban fill. As a result, the site has likely experienced the least alteration of the urban parks in this study and has the least disturbed soils, which are of the Wethersfield-Ludlow-Wilbraham complex, relatively undisturbed glacial till (NYC Reconnaissance Soil Survey 2006; MCPhearson et al. 2010). Patches of mature forest near the plots appear relatively undisturbed except for invasive vines and shrubs and soil pH averages 5.3.

For comparison, foliar N characteristics were also measured at the rural Black Rock Forest (BRF), a 1,550 ha preserve located in the Hudson Highlands Region of southeastern New York State (Fig. 1). BRF is a mixed hardwood forest with a canopy comprised of about 67 % oak and 33 % non-oaks (Schuster et al. 2008). Red oak and chestnut oak (*Quercus prinus*) dominate the canopy, while the understory is dominated by red maple (*Acer rubrum*). The soils are mostly medium textured loams, with granite gneiss bedrock or glacial till parent material at 0.25–1 m depth (Olsson 1981). Soil series in the study area include Swartswood and Mardin very stony soils (USDA 2013). Site condition ranges from poor to good with soils generally acidic and low in nutrients with an average soil pH of 4.0 (Lorimer 1981; Schuster et al. 2008). Soils at BRF are more acidic than at any of the four urban forest sites.

The urban and rural sites both experience strongly seasonal air temperatures, ranging from a mean of 5.6 °C in January to 24.7 °C in July in New York City, and a mean of –2.8 °C in January to 23.6 °C in July at BRF. Average annual precipitation is 1262 mm in New York City and 1285 mm at BRF (NOAA 2002).

Soil pH in the urban sites was analyzed from composite soil samples collected at each of the four study sites in NYC and were subsequently analyzed at the Cornell Nutrient Analysis Lab. Samples were composited from five undisturbed soil cores at each of the four study sites (see McPhearson et al. 2010 for additional detail on sampling locations and methods). At BRF, soil pH was determined from top and subsoil composite samples from eight subsamples in each of eight long term plots established in the forest (see Schuster et al. 2008 for additional detail on sampling locations and methods).

Sapling selection and foliage sampling

At each site, five saplings were selected of each study species: serviceberry (*Amelanchier canadensis*), blackgum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and red oak (*Quercus rubra*). These species were chosen for the study because they are commonly used in large scale afforestation and reforestation efforts throughout New York City and are also commonly found in northeastern deciduous forests such as BRF. With the exception of *Q. rubra*, foliar N characteristics of these species have not been studied in an urban context.

The saplings at the four urban sites were grown in 1-gal (3.8 L) containers and planted in fall 2009 in a randomized grid design in 900 m² open-canopy plots within these parks. At the time of sampling the saplings were approximately 125 cm tall. The plots include equal proportions of the four species in this study as well as hackberry (*Celtis occidentalis*) and scarlet oak (*Quercus coccinea*). Saplings were planted 4 ft apart on center according to NYC Parks Department best practices, and site selection was based on availability of forest restoration sites of appropriate size and canopy openness (in order to limit variation caused by shading from mature trees). All of these urban forest sites were prepared for planting using the same techniques, and all plant material was sourced from nearby nurseries following NYC Parks Department contracting procedures, was planted at the same time, and was subject to the same management regime. Additional information about this planting design can be found in McPhearson et al. (2010).

At the urban sites, saplings were selected at random from research plots, while the saplings at BRF were chosen haphazardly based on their size. There are few saplings in the BRF understory due to heavy deer browsing, so the trees sampled were the smallest available trees of each species (approximately 125 cm tall). *P. serotina* and *A. canadensis* saplings were found in small canopy gaps and near trail edges. *Q. rubra* saplings were found in deer exclosures under closed canopy. We were unable to find *N. sylvatica* saplings and used mature trees (mean DBH 9 cm) found under closed canopy. All leaf samples were collected on bright sunny days between 11 AM and 1 PM from August 30 to September 2, 2010 to limit variation in climate or light availability.

N. sylvatica and *Q. rubra* are shade tolerant species, while *P. serotina* and *A. canadensis* require more light to persist and thrive. All species are at least moderately drought tolerant. *P. serotina* is considered to adapt well to varied site conditions and has a shallow and spreading root system, while *N. sylvatica* has a long taproot.

Nitrate reductase assay

To measure nitrate reductase activity (NRA), leaves were collected on consecutive sunny days between 11 AM and 1 PM in order to ensure the presence of the light-activated nitrate reductase enzyme. Two to four fully expanded leaves were selected and cut from the top of each sapling and then hole-punched into 6 mm discs. A composite of leaf discs from an individual sapling was weighed to produce approximately 0.2 mg of fresh leaf tissue per sample. The samples were then analyzed for nitrate reductase activity based on the method of

Stewart et al. (1986). Five ml of assay solution (100 mM sodium phosphate buffer, pH 7.5; 200 mM KNO_3 ; 3 % (v/v) n-propanol) were added to the leaf tissue, and the samples were then incubated for 1 h in darkness and were shaken every 15 min. Samples were vacuum infiltrated three times to ensure that the solution penetrated into the leaf tissue.

Nitrite is the product of nitrate reductase activity; to quantify the nitrate reductase enzyme activity, the amount of nitrite in the solutions was calculated using a colorimetric analysis. 1 ml of the incubation solution was mixed with 1 ml sulphanilic acid and 1 ml α -naphthyl ethylenediamine dihydrochloride (NED) and the new mixture was vortexed. Tubes were incubated for an additional 20 min at room temperature and absorbance was then measured on a spectrophotometer (Unico 1100 Series, United Products and Instruments Inc., Dayton, NJ, USA) at 540 nm and zeroed against a blank (water+sulphanilic acid+NED). A standard curve was generated using known concentrations of nitrite. The amount of NRA was calculated based on the amount of nitrite in the solution and scaled to the mass of the sample analyzed using the following equation:

$$\text{NRA} = \frac{\text{nmol NO}_2^-}{\text{ml}} \times \frac{5 \text{ ml solution}}{\text{leaf fresh weight (mg)}}$$

$\delta^{13}\text{C}$, %C, $\delta^{15}\text{N}$ and %N

Four leaves from each sapling were collected as described above, oven-dried at 60 °C, and subsequently ground to a fine powder, creating a composite sample for each sapling (Cianflone model 2601, Cianflone Scientific Instruments Corporation, Pittsburgh, PA, USA). Samples were loaded into tin capsules and sent to Washington State University for leaf tissue nutrient and stable isotope analysis to obtain values for %C, $\delta^{13}\text{C}$, %N and $\delta^{15}\text{N}$. Isotopic analysis was performed using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) followed by a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen). Samples were referenced against concurrently run corn and acetanilide standards. The precision (SD) of internal standards was $\pm 0.08\%$ (acetanilide) and $\pm 0.03\%$ (corn) for the $\delta^{13}\text{C}$ analysis, and $\pm 0.30\%$ (acetanilide) and $\pm 0.08\%$ (corn) for the $\delta^{15}\text{N}$ analysis. NIST peach leaves were used for quality control (NIST 1547) with a precision (SD) of $\pm 0.01\%$ for $\delta^{13}\text{C}$ and $\pm 0.05\%$ for $\delta^{15}\text{N}$. N isotope data are reported as $\delta^{15}\text{N}$ values, which express foliar $^{15}\text{N}:^{14}\text{N}$ ratios relative to the ratio of $^{15}\text{N}:^{14}\text{N}$ in atmospheric N_2 . $\delta^{15}\text{N} (\%) = (\text{R}_{\text{sample}}/\text{R}_{\text{atm}} - 1) \times 1000$, where $\text{R}_{\text{atm}} = 0.0036765$ and the $\delta^{15}\text{N}$ of atmospheric N_2 by definition is 0.0%. Similarly, $\delta^{13}\text{C}$ values represent the ratio of $^{13}\text{C}:^{12}\text{C}$ in leaf tissue relative to the ratio of $^{13}\text{C}:^{12}\text{C}$ in atmospheric CO_2 .

Statistical analysis

All data were analyzed by species with generalized linear mixed models (GLMM), using tree within site as a random effect and site as a fixed effect. To account for the spatial dependence of trees within a site the unstructured covariance structure was used in the G matrix. Tukey's HSD tests were used to determine differences in foliar N and C characteristics between sites for each species. We used a contrast to test for differences between the one rural and four urban sites. Because site is a fixed effect, inferences can be made to these sites only. However, general site comparisons are made where appropriate. For the majority of response variables (%N, $\delta^{15}\text{N}$, NRA, $\delta^{13}\text{C}$, and C:N), the normal distribution was deemed an appropriate fit and was used throughout the analyses. Tests for homogeneity of variances and normality of residuals were met with the exception of *P. serotina* NRA, which was zero at the urban sites. Significance

levels for all tests were $p < 0.05$. Statistical analyses were conducted in the statistical software program SAS version 9.3 using PROC GLIMMIX (SAS Institute, Inc. 2011).

Results

%N and %C

Individuals of most species showed the highest foliar N concentrations in Roy Wilkins Park, with *P. serotina* and *N. sylvatica* showing significant differences between sites ($p < 0.01$ and $p < 0.0001$ respectively, Fig. 2). These two tree species had the lowest foliar N concentration at Black Rock Forest, the rural site. *P. serotina* foliar N concentration was 53.9 % greater at Roy Wilkins Park than at Alley Pond Park and 79.6 % higher than at Black Rock Forest. *N. sylvatica* foliar N concentration was 27.4 % higher at Roy Wilkins Park than at Alley Pond Park and 55.2 % higher than at Black Rock Forest. Similarly, only *P. serotina* and *N. sylvatica* showed significantly lower foliar C:N at urban sites than at BRF ($p < 0.05$ and $p < 0.0001$ respectively, Table 1).

While there were no significant differences in foliar %N or C:N ratio across species at BRF, *A. canadensis* had significantly lower foliar %N and higher foliar C:N than the other species across all urban sites ($p < 0.0001$ and $p < 0.001$ respectively, Table 1).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

All tree species showed significant differences in foliar ^{15}N enrichment among sites, with Marine Park always having the highest values and Black Rock Forest the lowest values, while Clove Lakes consistently had the lowest values of any urban site (Fig. 3). While there were no significant differences in $\delta^{15}\text{N}$ among species across urban sites, there were species differences

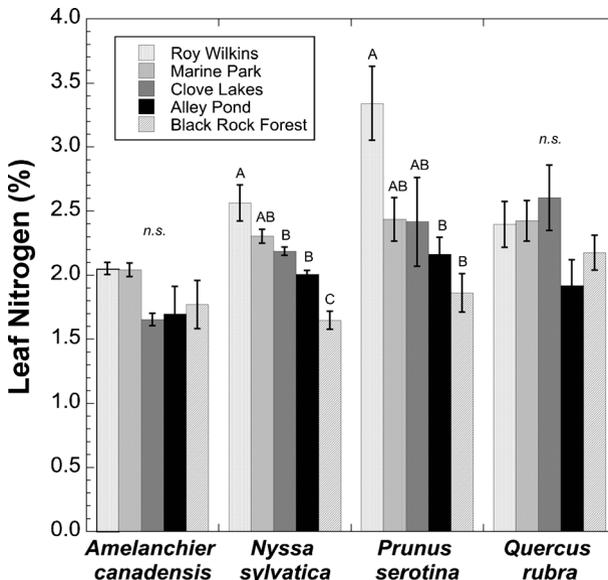


Fig. 2 Foliar %N from trees of each species at each site. Mean values (\pm SE) for $n=5$ trees of each species per site. Bars with different letters within species are significantly different (GLMM with the Tukey HSD test ($\alpha < 0.05$)). *n.s.* not significant

Table 1 Foliar N characteristics by species

Species	%N	$\delta^{15}\text{N}$ (‰)	NRA	$\delta^{13}\text{C}$ (‰)	C:N
Urban					
<i>Amelanchier canadensis</i>	1.86(±0.07)b	0.76(±0.23)***	65.34(±6.98)b*	-27.73(±0.33)b***	26.78(±1.28)b
<i>Nyssa sylvatica</i>	2.27(±0.06)a***	0.60(±0.17)***	95.14(±9.85)a	-26.55(±0.18)a***	21.36(±0.54)a***
<i>Prunus serotina</i>	2.59(±0.15)a*	0.18(±0.29)***	0.00(±0.00)c***	-26.44(±0.27)a***	20.02(±1.17)a*
<i>Quercus rubra</i>	2.33(±0.11)a	0.39(±0.29)***	56.45(±9.77)b	-26.60(±0.23)a***	21.20(±1.20)a
Black Rock Forest					
<i>Amelanchier canadensis</i>	1.77(±0.19)	-3.89(±0.25)b***	122.70(±29.66)a*	-30.76(±0.59)ab***	29.10(±2.79)
<i>Nyssa sylvatica</i>	1.65(±0.07)***	-2.38(±0.31)a***	101.53(±3.50)a	-32.06(±0.23)b***	27.76(±1.05)***
<i>Prunus serotina</i>	1.86(±0.15)*	-2.92(±0.57)ab***	3.12(±1.20)b***	-29.30(±0.55)a***	25.64(±1.51)*
<i>Quercus rubra</i>	2.18(±0.14)	-1.59(±0.12)a***	91.65(±4.98)a	-29.78(±0.37)a***	23.03(±1.36)

n=20 for each species at urban sites and *n*=5 for each species at Black Rock Forest. NRA is measured in nmol NO₂ produced h⁻¹ g⁻¹ fresh leaf weight. Within a column, values with distinct letters are significantly different (GLMM with Tukey HSD test ($\alpha<0.05$)). Significant differences between urban and Black Rock Forest values are indicated as follows: *=*p*<0.05, ***=*p*<0.0001

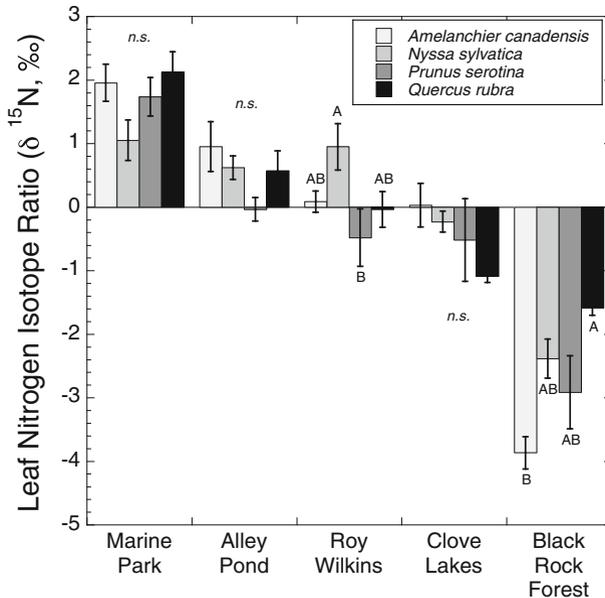


Fig. 3 Foliar $\delta^{15}\text{N}$ signatures (‰) from trees of each species at each site. Mean values (\pm SE) for $n=5$ trees of each species per site. Bars with different letters within sites are significantly different (GLMM with the Tukey HSD test ($\alpha < 0.05$)). n.s. not significant

at BRF, with *A. canadensis* significantly depleted in ^{15}N compared to *N. sylvatica* and *Q. rubra* ($p < 0.01$, Table 1).

A. canadensis did not have significantly different foliar $\delta^{13}\text{C}$ values than other tree species at BRF, but was significantly depleted in ^{13}C compared to all other species across urban sites ($p < 0.01$, Table 1). All species had the lowest foliar values of $\delta^{13}\text{C}$ at BRF, often followed by Clove Lakes (Fig. 4).

Nitrate reductase activity

A. canadensis showed significant differences in foliar nitrate reductase activity (NRA) among sites, with foliage at Black Rock Forest showing 209.7 % greater NRA than foliage at Alley Pond Park ($p = 0.05$, Fig. 5). *P. serotina* foliage was found to have no NRA in any of the urban sites, but produced $3.11 \text{ nmol NO}_2^- \text{ h}^{-1} \text{ g}^{-1}$ fresh leaf weight at BRF.

Discussion

In this study, we found significant differences in sapling foliar N characteristics between a rural forest and newly afforested urban sites, among urban sites, and across species. These differences reveal variation in N cycling and availability across sites that could impact urban ecosystem structure and function. All tree species showed similar trends of increased %N and $\delta^{15}\text{N}$, and decreased C:N, $\delta^{13}\text{C}$, and NRA in the urban forests compared to the rural forest. Furthermore, there was often variation between urban sites, likely reflecting varied site history and soil conditions. Differences in foliar C and N characteristics among species suggest that they may vary in their ability to access nutrients across sites.

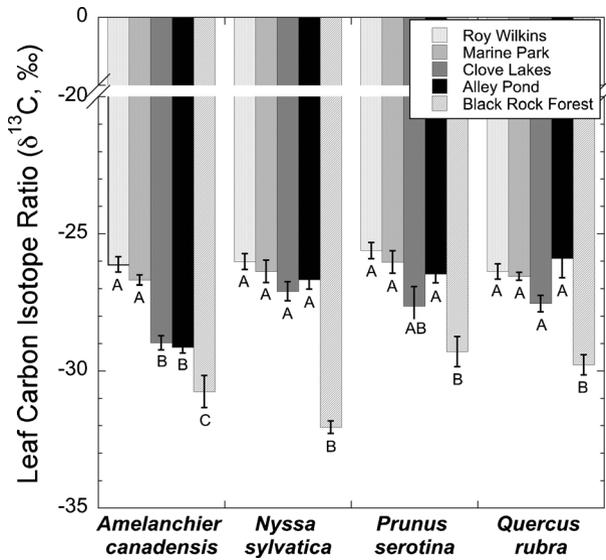


Fig. 4 Foliar $\delta^{13}\text{C}$ (‰) from trees of each species at each site. Mean values ($\pm\text{SE}$) for $n=5$ trees of each species per site. Bars with different letters within species are significantly different (GLMM with the Tukey HSD test ($\alpha<0.05$))

Site differences

Urban soils can be highly heterogeneous, making it difficult to describe a typical urban soil, or even a typical New York City soil (Pouyat et al. 2007 and 2009). The urban plots in this study

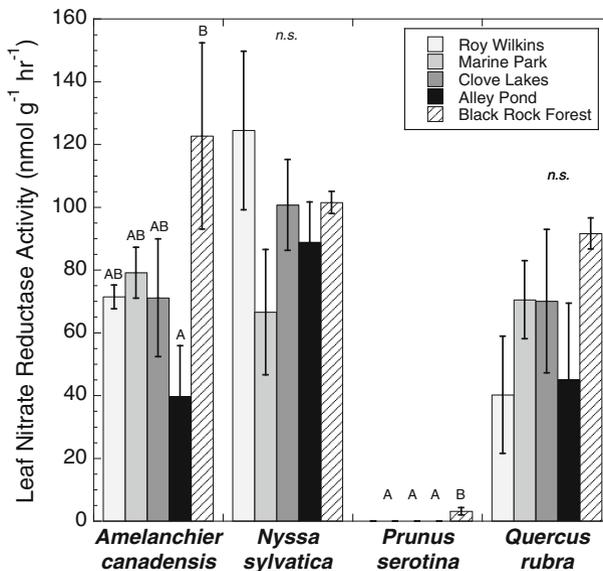


Fig. 5 Foliar nitrate reductase activity (nanomoles of NO_2 produced per hour per gram fresh leaf weight) from trees of each species at each urban site. Mean values ($\pm\text{SE}$) for $n=5$ trees of each species per site. Bars with different letters within species are significantly different (GLMM with the Tukey HSD test ($\alpha<0.05$)). *n.s.* not significant

have different site histories and adjacent land use types that affect the soil quality and herbaceous vegetation. These site histories are reflected in the foliar N characteristics reported here. In the two species that showed significant differences among sites (*N. sylvatica* and *P. serotina*), foliage at Roy Wilkins had the greatest N concentrations (and lowest C:N ratios). The thick layer of leaf litter added at Roy Wilkins is likely providing an N-rich substrate for the planted saplings, which may explain the higher foliar %N at this site. The lowest values of foliar N concentrations in *N. sylvatica* and *P. serotina* were found at BRF, which is an N-limited system and experiences less N deposition than New York City (Lovett et al. 2000). Sun leaf N is considered a reasonably reliable proxy for soil N availability (Ordoñez et al. 2009; Dybzinski et al. 2013). Although we are comparing fully expanded foliage on saplings of similar size and age, we acknowledge that the saplings at BRF experienced a lower light environment and possibly greater competition for N than the trees at the urban sites that were growing in recently planted clearings. These confounding factors affect our interpretation of the differences in foliar N concentration between BRF and the urban sites.

Overall, foliar NRA was found to be lower in the urban forests, despite the higher availability of light at those sites. Saplings at BRF were often found under lower light conditions due to the intact forest canopy, while the urban saplings were grown in recently planted areas with open canopies. Significant differences in NRA between sites were only found in *A. canadensis* and *P. serotina*, which displayed the greatest amount of enzyme activity at BRF, a pattern that was also observed (but not statistically significant) in *Q. rubra*. An energy intensive process like NRA may decrease when a plant experiences environmental stress and depleted energy stores; a possible explanation for the low NRA values in New York City is that the disturbance associated with being recently planted caused the urban saplings to experience more environmental stress than the more established saplings at BRF. Furthermore, the urban forests may have experienced drought stress when sampled at the end of a hot, dry summer in 2010. Foliar $\delta^{13}\text{C}$ correlates with water-use efficiency in C_3 plants (Farquhar and Richards 1984; Farquhar et al. 1989) and was significantly more negative at BRF than at urban sites across all tree species (Table 1). This supports a greater degree of drought stress in the urban saplings, as they were planted in exposed areas with no canopy cover.

As in all studies of leaf NRA, we use caution in drawing conclusions about whole plant NO_3^- assimilation capacity. The enzyme activity fluctuates diurnally (Lillo 1983; Aslam et al. 2001) and seasonally (Koyama et al. 2008), and among species nitrate reductase levels vary between leaves, stems and roots (Black et al. 2002). Many plants divide the processing of nitrate between the roots and shoots, and full evaluation of nitrate reductase activity relies upon the sampling of both, something we urge future research to consider. *Q. rubra* has been shown to reduce nitrate in its roots and leaves (Truax et al. 1994), but we are unaware of any published studies of other tree species in this study.

The higher N concentrations found in the urban foliage compared to BRF suggests that there may be more N available in these urban soils, possibly due to increased deposition (Lovett et al. 2000; Templer and McCann 2010; Rao et al. 2013) or the differences in soil physical, chemical, and biological characteristics between the established forest at BRF and the newly afforested sites in New York City. New York City soils have also been found to have elevated nitrification rates compared to nearby rural forests, likely due to exotic earthworm activity (Steinberg et al. 1997). Furthermore, soil pH is also positively correlated with nitrification rates and was higher at our urban sites than at BRF, although to varying degrees. However, the lower NRA and higher $\delta^{15}\text{N}$ in the urban saplings indicate that the urban sites may not have higher soil nitrate availability than rural forests, which are generally N limited with low rates of nitrification and low levels of available nitrate in forest soils. Nitrate may be

leaching out of urban forest soils at a faster rate, leading to the enriched N isotope signatures found in our urban saplings.

Saplings at the rural site consistently had the lowest values of foliar $\delta^{15}\text{N}$ and those at the relatively undisturbed urban Clove Lakes site had the next lowest values, while saplings growing on the construction fill soils of Marine Park consistently showed the greatest degree of foliar ^{15}N enrichment. Construction fill imports materials into a site, leaving a legacy effect of altered soil physical and chemical conditions. Trammell et al. (2011) found forest soils that had experienced disturbance from highway construction had reduced woody plant biodiversity, increased exotic species presence, and diminished tree recruitment. These factors (including exotic earthworms) may help contribute to higher rates of nitrification and/or lower rates of N retention at Marine Park, leading to foliage enriched in ^{15}N (Steinberg et al. 1997; Groffman et al. 2006).

The urban forests in this study have been recently planted in areas lacking forest vegetation and are likely to have less soil organic matter compared to the rural BRF site. Furthermore, urban parks can receive heavy stormwater flows and experience a great deal of erosion because they are often surrounded by impermeable surfaces and have relatively little vegetation to hold soil or water in place. These conditions may result in nitrate leaching out of urban soils, which is most likely to occur in coarse textured, sandy soils and after rain events or when soils are irrigated. As the urban forest matures, more ^{14}N relative to ^{15}N may be retained in the system through recycling of organic matter. For example, Clove Lakes soil is less sandy than the other urban sites and had the lowest urban foliar $\delta^{15}\text{N}$, meaning that there may be greater water retention at the site and less nitrate leaching (P. Timon McPhearson, unpublished data). Additionally, stormwater runoff can be a source of ^{15}N -enriched NH_4^+ ; isotope enrichment may be caused by the volatilization of ammonia or nitrification as rainwater flows over heated impervious surfaces (Dillon and Chanton 2005). However, Vallano and Sparks (2012) found the opposite trend of depleted foliar %N and $\delta^{15}\text{N}$ values in New York City sites compared to rural sites in eastern New York State, and attributed the isotopic differences to varying sources of N deposition.

If the higher values of $\delta^{15}\text{N}$ found in our urban foliage indicate that N is cycling at a faster rate in urban soils and that some nitrate is being lost from the system, there may be a limited amount of nitrate available to plant roots and NRA. The unexpectedly lower NRA values at the urban sites may reflect an available soil N pool composed primarily of NH_4^+ . With ample NH_4^+ available in the urban soils, there would be a reduced need for the saplings to expend extra energy on NO_3^- assimilation.

Because N transferred to plants by mycorrhizal fungi is depleted in ^{15}N , foliar $\delta^{15}\text{N}$ may also increase if the proportion of N acquired by plants that is supplied by fungi decreases (Hobbie et al. 2000; Hobbie and Colpaert 2003; Hobbie and Hobbie 2008). Foliar $\delta^{15}\text{N}$ may be higher at the urban sites than at BRF because the newly planted saplings are in a more disturbed environment and lack established and diverse mycorrhizal associations (Baxter et al. 1999; Karpati et al. 2011).

Species differences

Species variation in foliar N characteristics may reflect a plant's likelihood of uptake of NO_3^- vs. NH_4^+ . Little is known about N use in *A. canadensis* or *N. sylvatica*, but *Q. rubra* growth has been found to be limited by NH_4^+ availability rather than NO_3^- (Bigelow and Canham 2007). *P. serotina* foliage showed very little NRA at any site, although a previous study found this species to grow best in a greenhouse experiment when provided with a high ratio of $\text{NO}_3^-/\text{NH}_4^+$ (Horsley 1988). In this study, it seems that *P. serotina* may have responded strongly to

greater NH_4^+ availability in the urban sites, as foliar %N in that species was significantly higher in the urban forests compared to BRF. However, a possible explanation for this result is that *P. serotina* reduces nitrate primarily in its roots rather than its leaves, although this has not been tested. *P. serotina* is also shade intolerant and the increased foliar NRA and %N at the urban sites may be due to greater light availability.

Nitrogen deposition has been found to enhance the growth of tree species with arbuscular mycorrhizal fungal associations, as they lack the enzymes of ectomycorrhizal fungi that break down soil organic N (Thomas et al. 2010). In our study, this may help explain the higher foliar N concentrations in urban *P. serotina* and *N. sylvatica* compared to saplings at BRF while *Q. rubra*, an ectomycorrhizal species, showed no significant difference between site types.

Amelanchier canadensis had significantly lower foliar N concentrations (and higher C:N ratios) than the other species at urban sites and also had a large decrease in NRA. This species may have had the most difficulty accessing N in urban conditions. All tree species had significantly higher values of $\delta^{13}\text{C}$ in urban foliage than at BRF. As mentioned previously, this may suggest that the urban saplings were more water stressed, as foliar $\delta^{13}\text{C}$ is known to correlate with water-use efficiency in C_3 plants (Farquhar and Richards 1984; Farquhar et al. 1989). *A. canadensis* was the only tree species that showed significant variation in $\delta^{13}\text{C}$ among urban sites, with significantly higher $\delta^{13}\text{C}$ values at Marine Park and Roy Wilkins than at Alley Pond and Clove Lakes. The variation in water use efficiency may indicate that this tree species is more sensitive to water availability.

Finally, we found statistically significant variation in foliar $\delta^{15}\text{N}$ variation among species at BRF but not at the urban sites. Species specific fungal associations may explain this trend. Ectomycorrhizal plants tend to fractionate against ^{15}N during N uptake and are therefore more depleted in ^{15}N than arbuscular mycorrhizal plants (Högberg 1997; Craine et al. 2009). As mentioned previously, it is possible that the newly established urban saplings may not have had time to establish diverse mycorrhizal associations. However, we found that *Q. rubra*, the only ectomycorrhizal species, was enriched in ^{15}N compared to the other tree species at BRF. Other explanations for the differences in ^{15}N variation could include greater environmental heterogeneity between species sites at BRF. At each urban site, all tree species were growing in close proximity; however, the saplings at BRF were sampled throughout an area of the forest where they were found growing naturally. This difference in spatial arrangement may have contributed to greater variation in N sources or uptake mechanisms among species at BRF depending on their local environments.

Tree species are likely to control N cycling and retention in forest ecosystems (Finzi et al. 1998; Lovett et al. 2004; Templer et al. 2005). However, factors controlling N mineralization are different from those controlling nitrification, and are more complex than simple measures of leaf litter quality and resulting soil organic matter produced (Lovett et al. 2004). These mechanisms result in patchy N cycling depending on the dominant species in each location. With the exception of *Q. rubra*, whose growth is known to be limited by NH_4^+ availability and whose litter inhibits NO_3^- production and loss (Lovett et al. 2002 and 2004; Bigelow and Canham 2007), little is known about N use in any of these tree species, let alone in an urban context. However, they are being chosen for large urban afforestation projects in New York City and their ability to use N in an urban system may affect the ecosystem services they provide.

Conclusion

The data presented in this study provide a critical first look at the differences in foliar N concentration, natural isotope abundances, and NRA between urban afforestation sites in New

York City and a nearby rural forest. Although we cannot identify the exact causal mechanisms, the data suggest differences in nitrogen availability between New York City parks and a nearby rural forest, possibly due to different anthropogenic inputs, higher rates of nitrification and nitrate leaching, or an absence of mycorrhizal associations at the recently planted urban sites compared to the intact rural forest. In addition, our findings illustrate the intersite variation within a city that urban land managers must address when planning forest restoration efforts throughout a diverse landscape such as New York City. Local site history and soil conditions are important to consider when deciding which species to plant. The four tree species in our study varied in their response to changes in N availability both within New York City and between the urban and rural systems, with potential implications for species composition in urban forests. Greater N supply in urban soils could differentially stimulate primary production of species able to take advantage of increased N availability, thereby altering plant community composition despite restoration efforts (Tamm 1991). High rates of N mineralization and nitrification have been strongly correlated with a greater degree of invasion by non-native plant species in southeastern New York forests (Howard et al. 2004), making it important to establish desirable native tree species in urban forests.

Nitrogen use by trees in urban forests may have cascading, ecosystem-level effects on urban watersheds and the establishment of urban forests should help to prevent N saturation and associated responses of tree mortality and N export to surrounding habitats (Aber et al. 1998). Increased urban soil N availability and nitrification caused by greater exotic earthworm activity and atmospheric N deposition may lead to excess nitrate, which is easily dissolved in water and subsequently leaches into nearby water sources. If too much nitrate is leached out of the system, waterways become depleted of oxygen, disrupting the ecological functioning of the watershed. Although they do not retain N as effectively as intact rural forests, mature urban forests can still play an important role in N retention, preventing runoff to nearby water bodies (Groffman et al. 2004 and 2009; Raciti et al. 2008). By taking up excess N and helping to mitigate stormwater surges, urban forests such as those in our study can help prevent water pollution as they grow into mature forests.

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