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Species differences in nitrate reductase activity are unaffected by nitrogen enrichment in northeastern US forests

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ABSTRACT

Forests in the northeastern United States are typically nitrogen (N) poor, but anthropogenic N deposition may begin to overcome this limitation in the coming decades. Concomitant with this change, soil nitrate may increase in systems previously dominated by ammonium, and thus the ability to reduce nitrate may become an increasingly important plant trait. Here we present results from a survey of nitrate reductase activity (NRA) in foliage and roots of four canopy dominant tree genera (*Betula* spp., *Fagus grandifolia, Quercus* spp., *Acer* spp.) in two northeastern temperate forests (Harvard Forest, MA, and the Catskill Mountains, NY). We found that NRA varied by ~9× across genera, and was consistently greatest in birch (*Betula*) and lowest in maple (*Acer*) species. Root NRA was measured at one site, and was ~10× lower than in foliage. In both Harvard Forest and the Catskill mountains, the amount of NRA in a particular species, and the difference in NRA between species, was unaffected by long-term N fertilization. Despite the order of magnitude differences in NRA between species, NRA did not correlate with foliar %N, C:N ratio, N:P ratio or response of these variables to fertilization. We postulate that NRA may be related to ecological strategy, and that high NRA may be more common in early successional species that thrive in relatively N rich conditions. These species-level differences remain, even as forests mature and N availability diminishes. High NRA may be an important trait for some species, particularly early in ontogeny. But these results suggest that species-level differences in NRA may not be a large driver of species response to continuing N deposition in northeastern forests.

1. Introduction

Low nitrogen (N) availability is common in second growth forests of the northeastern United States (Aber et al., 1989, 1998), largely because the region is dominated by young, post-glacial soils that were intensively farmed during the eighteenth and nineteenth centuries without much fertilizer addition. Yet anthropogenic N deposition has increased five to ten folds in recent decades (Galloway et al., 1984), and currently ranges from ~4 kg N $ha^{-1} year^{-1}$ in western Maine to 11 kg N $ha^{-1} year^{-1}$ in southern New York (Lovett and Rueth, 1999). Preindustrial rates were likely ~1 kg N $ha^{-1} year^{-1}$ (Holland et al., 1999). In light of this increased deposition, Aber et al. (1989) suggested that over time, N accumulation in northeastern forests might lead to increases in primary production and N mineralization, then to an onset of nitrification and N leaching, and finally forests decline as a result of prolonged nitrate leaching and soil acidification. These concerns have not abated (Aber et al., 2003), as anthropogenic N deposition remains elevated (Driscoll et al., 2003). However, tests of this N saturation hypothesis reveal substantial regional variation in response to increased N deposition (Aber et al., 1998; Pardo et al., 2006; Wallenstein et al., 2006). This variability likely results from differences in land use history (Compton et al., 1998; Goodale and Aber, 2001), climate (Rogora and Mosello, 2007; Hole and Engardt, 2008; Rogora et al., 2008), forest community composition (Aber et al., 1998; Magill et al., 2000; Templer et al., 2005), and soil type, all of which appear to affect the degree of N saturation from West Virginia to Maine (Aber et al., 2003). In part because of this variability, our understanding of the effects of continued high inputs of N into N-poor northeastern forests remains limited.

Studies that have explored the community effects of N deposition on forests have primarily focused on the sensitivity of a few species (such as *Acer saccharum* Marsh. and *Picea rubens* Sarg.) to soil acidification (Hutchinson et al., 1998; Kogelmann and Sharpe, 2006; Boggs et al., 2007) and on the effects of N enrichment on understory species (Gilliam, 2006). Yet changing the availability and potential dominant form of N may have additional consequences for northeastern forest communities. For example, increased N deposition may result in a higher abundance of nitrate (NO_3–N) as opposed to ammonium (NH_4–N), which has historically been the dominant N form (Aber et al., 1998). Nitrate must be

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reduced in order to be useful to plants (Ponce and Salas, 1999), and it has been postulated that communities with higher nitrate reductase activity (NRA) may act as nitrate sinks, and reduce the rate of nitrate leaching and soil acidification (Rothstein et al., 1996).

Surprisingly, little is known about NRA in mature northeastern canopy trees. Assessments of NRA in forest ecosystems are rare (Adams and Attiwill, 1982), even though trees have comparable NRA to other plant functional groups (Smirnoff et al., 1984). Recent studies in the tropics suggest that early successional tree species have higher NRA than those that are later in succession (Aidar et al., 2003) – but to our knowledge such analyses have yet to be done in northern temperate forests, where anthropogenic N deposition has increased dramatically over the past hundred years. Comparisons of common northeastern tree seedlings suggest that there is substantial variation in NRA among tree species, with conifers expressing an order of magnitude less NRA than *Acer rubrum* (Downs et al., 1993). Other studies on NRA in hardwood species have focused on only one or two species (Stadler et al., 1993; Truax et al., 1994; Rothstein et al., 1996; Eddy et al., 2008) and have mostly worked with potted seedlings, rather than measuring NRA under field conditions. In light of NRA's potential importance in an increasingly N-rich world, a more comprehensive field study of common northeastern temperate forest species seems warranted.

In this context, we measured foliar and root NRA of several northeastern canopy-dominant tree species, and asked how foliar NRA varies after fertilization with N. In order to understand both natural variability in NRA and its response to N enrichment, we focused on mature, canopy hardwoods at Harvard Forest, MA, and in the Catskill Mountains, NY, which are both sites of long-term N fertilization experiments (Aber and Magill, 2004; Lovett and Mitchell, 2004). We hypothesized that NRA would vary among species, and would be upregulated in response to increases in soil N availability induced by long-term fertilization. We also asked whether NRA correlated with time since fertilization, since NRA is sensitive to environmental changes (Gutschick, 1981). Finally, we investigated if variation in NRA resulted in significant differences in nutrient acquisition of the trees, as measured by foliar N, δ^{15}N, C:N and N:P ratios or the response of these parameters to fertilization.

2. Methods

We utilized two ongoing, long-term N fertilization experiments in northeastern forests, one in Harvard Forest, MA, and one in the Catskill Mountains, NY (Fig. 1a–c). At Harvard Forest we worked both within a long-term fertilization experiment (Aber and Magill, 2004), and in other unfertilized sites, and sampled over the summers of 2009 and 2010. In the Catskill Mountains, NY, we sampled in the summer of 2010 and compared foliage in control and N-fertilized plots previously described by Christenson et al. (2009). These sites share a similar history of deglaciation at the start of the Holocene, and development of similar forests on glacial till-derived soils (Table 1). Our overall goal was to use these sites to ask whether NRA responded to N enrichment, and, in turn, whether higher NRA led to a larger response to N fertilization. Our sampling locations, dates of sampling, and analyses run are presented in Tables 2 and 3.

2.1. Site descriptions

Harvard Forest (42.5°N 72.0°W) is in north-central Massachusetts, USA. The region was mostly deforested and continuously farmed in the 1700s and 1800s before abandonment towards the end of the nineteenth century (Foster et al., 2003). The soils are sandy loams derived from glacial till, alluvial or colluvial deposits,

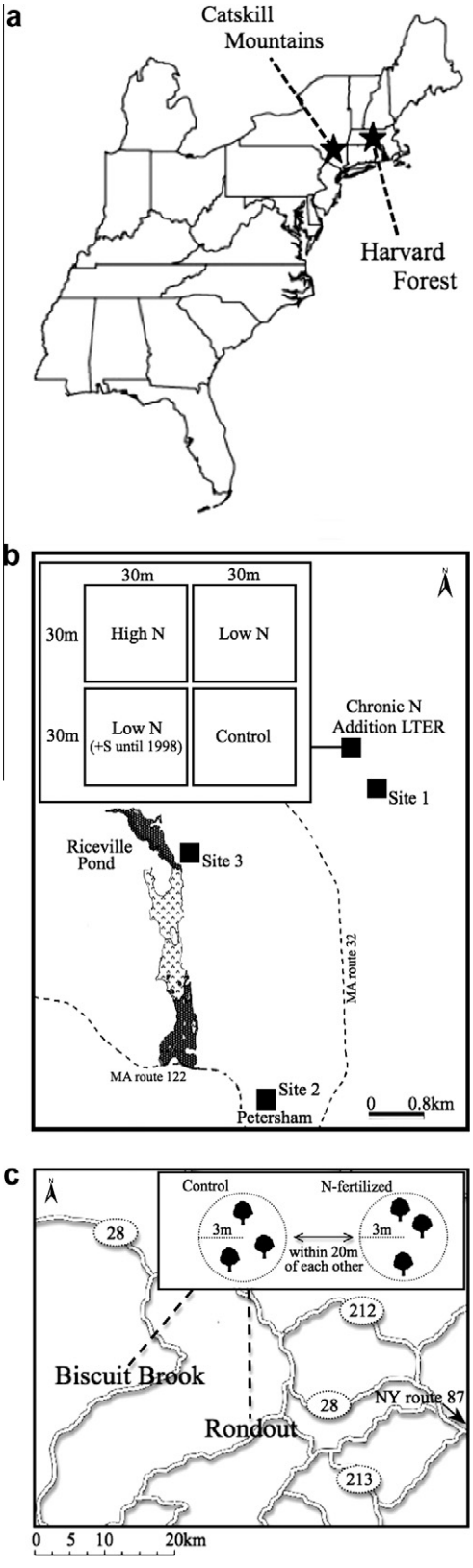

Fig. 1. (a) Site locations for Harvard Forest, MA and the Catskill Mountains, NY. (b) Layout of plots at Harvard Forest and (c) in the Catskill Mountains N fertilization sites.

typical of that found in northeastern forests. Current atmospheric N deposition is 6.6–8.0 kg N ha^{-1} year^{-1} (Ollinger et al., 1993; Munger et al., 1996), well above the estimated preindustrial flux

Table 1
Site characteristics of Harvard Forest and the Catskill Mountain sites. Data compiled from Stoddard and Murdoch (1991), Ollinger et al. (1993), Munger et al. (1996), Lovett and Rueth (1999), Kudish (2000), Magill et al. (2004), Lovett et al. (2004), and Templer et al. (2005).

Location	Study site	Plot characteristics	Geology	Mean annual precipitation	Mean temperature (°C)	Forest type	N deposition (kg N $ha^{-1}year^{-1}$)
Harvard Forest, MA (42.5°N 72.0°W)	Sites 1–3 (Fig. 1b) Chronic N Addition LTER	3 Unfertilized sites Control 50 kg N ha^{-1} $year^{-1}$ 50 kg N ha^{-1} $year^{-1}$ (+S until 1998) 150 kg N ha^{-1} $year^{-1}$	Glacial till; bedrock of granite, gneiss, schist	112 cm	19 (July) −12 (January)	Mixed hardwoods secondary growth forest	6.6–8.0
Catskill Mountains, NY (42.1°N 74.3°W)	Biscuit Brook Rondout	Control and 50 kg N ha^{-1} $year^{-1}$ paired-plots	Glacial till; bedrock of conglomerate, sandstone	153 cm	17 (July) −9 (January)	Monospecific stands in secondary forests	11

Table 2
Species sampled at Harvard Forest and the Catskill Mountains.

Species	Harvard Forest	Catskill Mountains
Acer		
A. rubrum	X	
A. saccharum		X
Betula		
B. lenta	X	
B. papyrifera	X	
B. alleghaniensis		X
Fagus grandifolia	X	X
Quercus spp.	X	
Tsuga canadensis		X

(1 kg $ha^{-1}year^{-1}$; Holland et al., 1999). Nevertheless, Harvard Forest hosts very N-poor soils (Aber et al., 1998) with virtually no nitrate or detectable nitrification (Tang, M.H., unpubl. data). Our first goal at Harvard Forest was to test for NRA differences among species under ambient soil N availability. In the summer of 2009, we collected foliar samples from hardwoods in three unfertilized sites (Fig. 1b, Harvard Forest Sites 1–3) and tested for species differences in NRA. In order to test the effects of N enrichment on NRA and the N economy of plants, we returned to Harvard Forest in the summer of 2010 and collected foliar and soil samples from Harvard Forest's Chronic N Addition Long-Term Ecological Research (LTER) site (Fig. 1b). This fertilization experiment consists of four unreplicated 30 m × 30 m plots: (1) Control, (2) Low N treatment (50 kg N $ha^{-1}year^{-1}$ as NH_4NO_3), (3) Low N + S treatment (50 kg N $ha^{-1}year^{-1}$ as NH_4NO_3; 50 kg S $ha^{-1}year^{-1}$ as Na_2SO_4 until 1998, when S additions were discontinued); and (4) High N treatment (150 kg N $ha^{-1}year^{-1}$ as NH_4NO_3), respectively. These plots have been fertilized in six equal applications over the growing season (May–September) since 1988. Finally, to test for differences between foliar and root NRA, in 2010 we returned to one of the unfertilized plots we studied in 2009 (Site 1) and collected overstory foliage and fine roots from each sampled tree.

To further explore N-enrichment effects on NRA, in the summer of 2010, we also collected foliage from the long-term N fertilization experiment in the Catskill Mountains, NY. Similar to Harvard Forest, this site is characterized by post-glacial colonization of till-derived

Table 3
Measurements made at each study site.

Measurement	Location	Plot type	2009	2010
NRA	Harvard Forest	Unfertilized sites	Sunlit canopy, $n = 3$ sites 5 species × 15 trees per site*	Sunlit canopy and roots, only at Site 1, $n = 1$ 5 species × 3 trees**
			Understory, $n = 3$ sites 4 species × 15 trees per site*	
		Chronic N Addition LTER		22nd July***, 30th July and 31st August**** 3 species × 4 trees per treatment per day (in addition, all *F. grandifolia* and *B. papyrifera* (1–2 individual trees per treatment plot) were sampled)
	Catskills	Rondout		10th August
		B. alleghaniensis		1 paired-plot
		F. grandifolia		2 paired-plots
		T. canadensis		1 paired-plot
		Biscuit Brook		20th August
		A. saccharum		2 paired-plots
		B. alleghaniensis		2 paired-plots
		F. grandifolia		1 paired-plot
Foliar C, N	Harvard Forest	Unfertilized sites	All overstory samples	
		Chronic N Addition LTER		30th July samples
	Catskills			All samples
Foliar P	Harvard Forest	Chronic N Addition LTER		30th July samples
	Catskills			All samples
Foliar $\delta^{15}N$	Harvard Forest	Unfertilized sites	All overstory samples	

* Unequal sample sizes due to sample losses; no. of trees sampled for *B. lenta*, *B. papyrifera*, *F. grandifolia*, *Quercus* spp., *A. rubrum* were 6, 13, 13, 14, 15 in the overstory, and 15, N/A, 13, 15, 14 in the understory.
** With the exception of *B. lenta*, which had four individual trees sampled.
*** Due to sample loss, one *Quercus* spp. sample at the 50 kg N $ha^{-1}year^{-1}$ (+S) treatment, and three *A. rubrum* samples at the 150 kg N $ha^{-1}year^{-1}$ treatment were sampled, respectively.
**** Five *A. rubrum* samples at the 50 kg N $ha^{-1}year^{-1}$ (+S) treatment and the 150 kg N $ha^{-1}year^{-1}$ treatment were sampled, respectively.

soils. Soils are somewhat richer in N than Harvard Forest, with substantial variation in N richness in soils under different tree species (Lovett et al., 2004). More detail about the site and fertilization experimental design is provided by Lovett et al. (2004) and Templer et al. (2005). Briefly, monospecific stands of paired control vs. N-fertilized plots are spread across a 60 km × 60 km region, roughly centered on 42.1°N and 74.3°W. Each pair of control and N-fertilized plots are within 20 m of each other, and each plot is 3 m in radius, including 2–3 canopy dominant trees of the same species (Fig. 1c). The fertilized plots received 50 kg N ha^{-1} $year^{-1}$ as NH_4NO_3, applied in four equal doses per year from 1997 to 2009 (Christenson et al., 2009). This level of fertilization is the same as in the Low N plots at Harvard Forest. Ambient atmospheric nitrogen deposition in the Catskills is approximately 11 kg N ha^{-1} $year^{-1}$ (Lovett and Rueth, 1999), which is relatively high for the northeast and probably an order of magnitude higher than natural rates (Holland et al., 1999).

2.2. Foliar and root sample collection for NRA

In vivo NRA can vary with light intensity, because nitrate reduction may have to compete with carbon fixation for energy under shaded conditions (Gutschick, 1981; Jiang and Hull, 2000). Thus we collected all overstory foliar samples using a shotgun between 10 AM and 2 PM. At Harvard Forest, we collected only on cloudless days; sampling days in the Catskills had scattered clouds. Foliage from each tree was analyzed separately.

2.3. Foliar NRA sampling

At Harvard Forest, we sampled five hardwoods that are common in the region: *Betula lenta* (black birch), *Betula papyrifera* (paper birch), *Fagus grandifolia* (American beech), *Quercus* spp. (hybridized red and black oaks) and *A. rubrum* (red maple). In the summer of 2009, we sampled both sunlit canopy foliage (6th August 2009) and understory (24th July 2009) hardwoods from the three unfertilized sites (Sites 1–3, Fig. 1c). We sampled fifteen canopy-emergent individuals of each species at each site, as well as understory individuals of all species except *B. papyrifera*, which was not found in the understory in our plots.

In the summer of 2010, we sampled canopy foliage from all the plots in the Harvard Forest Chronic N Addition LTER Experiment (Fig. 1b). To test for transient effects of fertilizer addition on NRA, we repeatedly sampled from the same trees at three different times since fertilization. We collected foliage on 22nd July 2010 (during fertilization), 30th July 2010 (eight days post-22nd July 2010 fertilization), and 31st August 2010 (four days post-27th August 2010 fertilization). We sampled foliage from four individual trees per species per treatment for the dominant species: *B. lenta, Quercus* spp., and *A. rubrum*. We also sampled all *B. papyrifera* and *F. grandifolia* (1–2 individual trees) present in each plot.

In the Catskills, we sampled canopy leaves in two separate locations on the 10th and 20th August 2010. Each paired control and N-fertilized plot was sampled on the same day. We sampled three paired control vs. N-fertilized stands of monospecific *Betula alleghaniensis* (yellow birch) and *F. grandifolia*, two pairs of *A. saccharum* stands (sugar maple), and one pair of *Tsuga canadensis* stands (Eastern hemlock). In each monospecific stand, there are two to three canopy dominants per treatment. Samples from each individual within a stand were analyzed separately, but we report mean values here. Unfortunately, both sampling days in the Catskills were partly cloudy. We do not expect this confounding factor to influence comparisons between control vs. N-fertilized plots, as foliage from the stands in any given paired plot was collected under the same weather conditions on the same day.

2.4. Foliar NRA vs. root NRA sampling

There can be substantial variation in NRA between different plant parts (Gebauer et al., 1988; Scheurwater et al., 2002). To address differential partitioning of foliage to root NRA between species, on 31st August 2010 we revisited Harvard Forest Site 1 and sampled both foliage and fine roots from each individual tree sampled. To ensure that the foliage and root samples from each tree corresponded with each other, we sampled fine roots by tracing them from the tree trunk to terminal ends of the roots. We sampled from the same species we had sampled in 2009, and collected roots and leaves from three individuals per species.

2.5. Nitrate reductase activity analysis

We placed leaves and roots on ice for a maximum of 9 h before analysis of NRA. We modified the protocol used by Downs et al. (1993) and Algharbi and Hipkin (1984) to assess *in vivo* NRA by measuring foliar and root nitrite production, since nitrite is the intermediate product of nitrate reduction. We rinsed foliar and root samples in deionized water, and cut foliar samples into 5 mm × 5 mm squares and fine root samples into 1 mm segments. We soaked 200 mg of the cut foliar samples in buffered (phosphate buffer, pH 7.0) 40 mM KNO_3 and 1.5% propanol under 64 kPa vacuum for 3 min, and incubated the samples in the dark at 30 °C for 2 h (Downs et al., 1993). For root NRA, we used ~100 mg of the cut fine root samples as there was less total sample mass. We analyzed a portion of the incubation buffer for nitrite concentration, by adding 1 ml each of 1% sulfanilamide in 1:5 HCl and 0.1% n-Napthylethylene Diamine Dihydrochloride (NED). We measured solution absorbance at 535 nm (in 2009 on a Shimadzu 1201 UV spectrophotometer (Pegasus Scientific Inc., Rockville, MD) and in 2010 on a WESTCO SmartChem 200), running true replicates every eight samples. We also dried a subset of the remaining plant tissue in the oven at 65 °C for 48 h to quantify wet to dry mass ratios, and another subset of overstory foliage, on which we performed nutrient and isotopic analyses. We report NRA values as μmol NO_2^- produced per gram dry leaf mass per hour of incubation.

2.6. Foliar elemental and isotopic analyses

We ground foliar subsamples to a fine powder in a ball mill, and analyzed %C, %N, and $\delta^{15}N$ at the Marine Biological Laboratory (MBL) Stable Isotope Laboratory on a Europa ANCA-SL elemental analyzer – with a continuous-flow Europa 20–20 gas source isotope ratio mass spectrometer (2009 samples). Since the fertilizer plots sampled in 2010 have added $\delta^{15}N$, we did not compare $\delta^{15}N$ between fertilized and unfertilized plots. For foliar N, C and P in the fertilization experiments in 2010, we sampled all the foliage collected during the 30th July 2010 sampling at Harvard Forest's Chronic N Addition LTER site, and on both days (10th and 20th August) in the Catskills. We analyzed foliar C and N on Brown University's CE Instruments NC2100 Elemental Analyzer and measured total foliar phosphorus (P) concentration using a modified Kjeldahl digestion and colorimetric analysis on a WESTCO SmartChem 200.

2.7. Statistical analyses

To assess for species differences in NRA under ambient soil conditions, we analyzed the 2009 Harvard Forest samples for effects of site ($n = 3$) and species on NRA, foliar N, C:N, N:P or $\delta^{15}N$ using two-way ANOVA and made pair-wise comparisons using Tukey's HSD. To assess the long-term effects of N-enrichment (via fertilization) on these parameters, we compared species and fertilization treatment in at the Catskill sites using two-way ANOVA and Tukey's

Table 4
Nitrate reductase activity and foliar N at unfertilized Harvard Forest Sites 1–3 (sampled July–August 2009 and 2010). Different letters indicate significant differences ($p < 0.05$) between species. Errors are 1SE.

Species	Sunlit canopy NRA (2009) ($\mu mol\ NO_2^-\ g^{-1}\ day^{-1}$)		Understory NRA (2009) ($\mu mol\ NO_2^-\ g^{-1}\ day^{-1}$)		Foliar NRA: root NRA (2010)	Foliar %N (2009) (%)		Foliar $\delta^{15}N$ (2009) (‰)	
Betula lenta	0.44 ± 0.03	a	0.39 ± 0.10	a	13.34 ± 4.27	2.74 ± 0.24	a	−2.9 ± 0.7	a, b
Betula papyrifera	0.52 ± 0.07	a	–	–	19.03 ± 19.44	2.27 ± 0.26	a, b	−2.7 ± 0.4	a, b
Fagus grandifolia	0.17 ± 0.04	b	0.11 ± 0.03	b	6.13 ± 2.58	2.46 ± 0.39	a, b	−2.3 ± 0.6	a
Quercus spp.	0.09 ± 0.02	b	0.14 ± 0.04	b	27.16 ± 43.56	2.66 ± 0.22	a	−2.0 ± 0.6	a
Acer rubrum	0.05 ± 0.01	b	0.05 ± 0.04	b	4.63 ± 5.54	2.11 ± 0.19	b	−4.0 ± 0.5	b

Table 5
Overstory foliar nitrate reductase activity in the Catskill Mountains (sampled August 2010). Different letters indicate significant differences ($p < 0.05$) between species. Errors are 1SE.

Species	Replicates (no. of paired-plots)	Control plot ($\mu mol\ NO_2^-\ g^{-1}\ day^{-1}$)	N fertilized plot ($\mu mol\ NO_2^-\ g^{-1}\ day^{-1}$)	Significance between species	Fertilization effect on NRA
Betula alleghaniensis	3	0.31 ± 0.06	0.37 ± 0.12	a	No effect ($p = 0.57$)
Fagus grandifolia	3	0.09 ± 0.05	0.09 ± 0.07	b	No effect ($p = 0.79$)
Acer saccharum	2	0.07 ± 0.01	0.04 ± 0.03	b	Negative ($p = 0.02$)
Tsuga canadensis	1	0.01	0.01	–	–

HSD. The Harvard Forest fertilizer experiment is unreplicated ($n = 1$ plot for each treatment) and we chose not to count individual trees within the treatment as replicates. Thus we report here summary statistics for each plot, but do not attempt to access the significance of those differences.

In order to test for short-term changes in NRA associated with pulses of fertilizer additions (e.g. the effects of fertilization events over the course of a growing season, rather than long-term changes associated with over a decade of fertilization relative to control), we repeatedly sampled foliage from *Betula*, *Quercus* and *Acer* trees 0, 4 and 8 days since an application of fertilizer at Harvard Forest. We used repeated measures MANOVA to ask whether time since fertilization affects NRA and whether that effect varies by genus (*Betula, Quercus* and *Acer*).

Finally, we tested for the influence of NRA on a plant's ability to respond to fertilization by calculating foliar %N, C:N, and N:P response ratios (Elser et al., 2007). We calculated response ratios for the two low N Harvard Forest plots and all the plots in the Catskills, as they receive the same amount of fertilization. We asked whether this response ratio (RR_x) was dependent on genus using a one-way ANOVA with pairwise comparisons using Tukey's HSD. We used JMP 8.0 (SAS Institute Inc., NC, USA) for all statistical analyses.

3. Results

3.1. Nitrate reductase activity and foliar chemistry in unfertilized forests

In the background of low soil N at Harvard Forest, *in vivo* NRA in canopy leaves was significantly higher in *B. lenta* and *B. papyrifera* than the other species ($p < 0.0001$), with rates of 0.44 ± 0.02 and 0.52 ± 0.04 $\mu mol\ NO_2^-\ g^{-1}\ h^{-1}$, respectively (Table 4). NRA was not significantly different between *F. grandifolia*, *Quercus* spp. and *A. rubrum* (0.17 ± 0.02, 0.09 ± 0.01 and 0.05 ± 0.01 $\mu mol\ NO_2^-\ g^{-1}\ h^{-1}$, respectively, $p > 0.05$). As in the overstory, *B. lenta*'s average NRA in the understory (0.39 ± 0.10 $\mu mol\ NO_2^-\ g^{-1}\ h^{-1}$) was significantly higher ($p = 0.002$) than the other species within the understory (Table 4). Site was not a determinant of foliar NRA in either the overstory ($p = 0.86$) or understory ($p = 0.71$). On 31 August 2010, we resampled Site 1 to compare foliar to root NRA ratios in individuals. As we have only one replicate (one site), we cannot statistically test whether the difference between species was significant. However, if we were to assume each individual tree is a replicate, the trend in foliar NRA between species was the same as what was found the year before: *Betula* species had significantly higher foliar NRA than *A. rubrum* ($p = 0.0008$), but not *F. grandifolia* and *Quercus* spp. Difference in root NRA between species was not significant ($p = 0.42$), and root NRA was consistently lower – in some cases 10× lower – than foliar NRA in a given tree (Table 4).

At these unfertilized sites, foliar NRA did not correlate with our measures of foliar N economy (Table 4). Foliar %N in *B. lenta* (2.7 ± 0.1%) was significantly higher ($p = 0.007$) than in *A. rubrum* (2.1 ± 0.0%), but not significantly different from *B. papyrifera*, *F. grandifolia* or *Quercus* spp. Foliar C:N ratio was significantly different ($p = 0.01$) between *B. lenta* (22:1) and *A. rubrum* (28:1), but not with the other species (data not shown). Foliar $\delta^{15}N$ in *A. rubrum* (−4.0 ± 0.3‰) was significantly depleted than those of *F. grandifolia* or *Quercus* spp. (−2.3 ± 0.3‰ and −2.0 ± 0.3‰, respectively), but not significantly different from the two *Betula* species.

3.2. Response of NRA and foliar chemistry to fertilization

We found no significant effect of fertilization on NRA in the Catskills (where we have true replication; Table 5) or at Harvard Forest (if we consider each tree a replicate; Fig. 2). In both locations, *Betula* exhibited the highest NRA in both unfertilized and fertilized plots, and *Acer* the lowest. Despite slight differences in light environment between sampling days, we found similar values for NRA within genera between the two regions. Not surprisingly, N fertilization led to higher foliar %N and N:P, and decreased C:N. However the response ratio (RR_x) was not significantly influenced by genus or species (Nested ANOVA $p > 0.1$ and 0.05 in genus and species, respectively; for $RR_{\%N}$ and $RR_{N:P}$; Table 6). *Betula* and *Acer*, which had the highest and lowest NRA, respectively, had nearly identical $RR_{\%N}$, $RR_{C:N}$ and $RR_{N:P}$. *Quercus* had the smallest response to fertilization for $RR_{\%N}$ and $RR_{N:P}$.

To test for the effect of time since fertilization on NRA, we measured foliar NRA on three different days with different times since fertilization at Harvard Forest. Foliar NRA was dependent on genus ($p < 0.0001$) and time since fertilization ($p < 0.001$), with a significant time x genus interaction (Wilks Lambda $p < 0.001$). *Betula* showed a 38% decrease in NRA between the day of fertilization and 8 days post-fertilization, whereas *Quercus* and *Acer* showed no significant trend in NRA with time (Fig. 2). However, NRA of *Betula* on the day of, and 4 days after, fertilization was not significantly different from NRA in the control plot (if we were to use trees as replicates p is >0.05). Even the anomalously low NRA values for *Betula* 8 days post fertilization were not markedly different from its range in the control plot (Fig. 2).

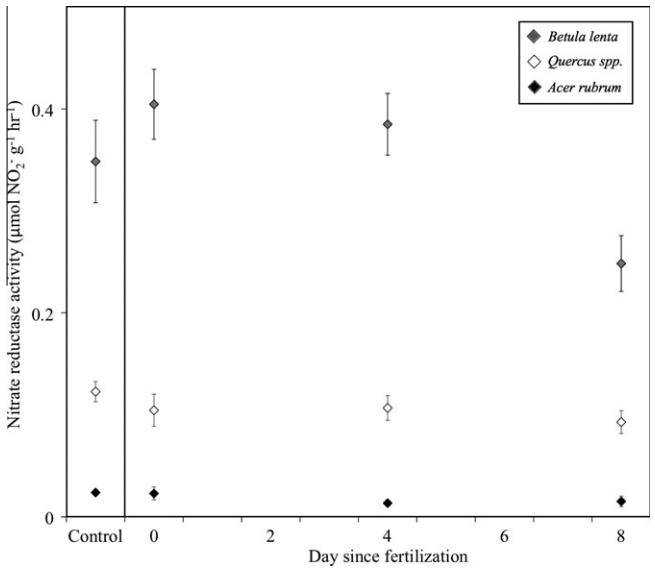

Fig. 2. Overstory foliar NRA from trees in control and N fertilized plots at different times post-fertilizer application at the Chronic N Addition LTER site, Harvard Forest (sampled summer 2010). Control plots were sampled on all 3 days, the mean for each species is presented here. Error bars are 1SE.

Table 6
Response ratio (RR_x = value in treatment/value in control) of the different genera found at both Harvard Forest and the Catskills. For each case, data for genera found in a certain site were averaged to come up with a plot mean response ratio. There were no significant differences between species for any of the response ratios except for $RR_{C:N}$ between *Acer* and *Quercus* (Tukey's HSD, $p = 0.013$, $n = 4$ for *Betula* and *Fagus*, $n = 3$ for *Acer* and $n = 2$ for *Quercus*). Genera are ranked from top to bottom in order of mean NRA. Errors are 1SE.

Genus	$RR_{\%N}$	$RR_{N:P}$	$RR_{C:N}$
Betula	1.13 ± 0.10	1.25 ± 0.32	0.91 ± 0.05
Fagus	1.09 ± 0.05	1.49 ± 0.66	0.91 ± 0.04
Quercus	1.02 ± 0.05	1.12 ± 0.46	1.02 ± 0.02
Acer	1.17 ± 0.07	1.38 ± 0.27	0.86 ± 0.05

4. Discussion

The consistency of NRA for a given genus, across different locations and fertilization regimens, suggests that NRA is relatively invariant in these groups. Harvard Forest and the Catskills sites have been fertilized for 22 and 13 years, respectively, and thus the trees within the 65-year-old Harvard Forest plots have been fertilized for almost a third of their lifetime. It is thus surprising that, for a given species, the levels of foliar NRA does not differ between control and fertilized plots, as we saw an increase in KCl-extractable ammonium and nitrate in the top 10 cm of soil in the High N treatment plot at Harvard Forest (data not shown), as has been reported elsewhere (Magill et al., 2000). In addition, both Harvard Forest and Catskill fertilization plots show trends towards increased NO_3^- consumption (Venterea et al., 2004; Christenson et al., 2009). We also saw no variation in NRA across the Harvard Forest landscape in 2009. Taken together, these data suggest that foliar NRA, at least for the species studied, is species-dependent and is insensitive to soil N availability. If this is true, it is unlikely that anthropogenic N deposition will lead to increased expression of foliar NRA.

Betula has the highest NRA among the genera sampled in this study; and it may be that *Betula* has the advantage of high NRA earlier on in ontogeny that we were not able to perceive in the mature forest. *B. lenta* seedlings have a preference for obtaining a substantial (~35%) proportion of their N from nitrate, and *B. papyrifera* and *B. alleghaniensis* seedlings are capable of assimilating nitrate and ammonium at equal capacity (Crabtree and Bazzaz, 1993). While there is a cost to reducing nitrate rather than using ammonium (Gutschick, 1981), this cost may be compensated by the increased access to nitrate afforded by high NRA early in tree development, especially in high light environments. The *Betula* species we studied tend to grow well after a disturbance, such as treefalls, fires and landslides (Forcier, 1975; Perala and Alm, 1990; Walters et al., 1993) that can lead to elevated N (and nitrate) availability (Foster et al., 2003). The trend of seeing high NRA in early successional species is also consistent with recent findings in the tropics (Aidar et al., 2003).

The idea that NRA can vary during ontogeny as well as across phylogeny has been proposed by Andrews (1986), and is supported by a comparison of our results with those of Downs et al. (1993). Using the same *in vivo* assay for NRA as we used here, Downs et al. (1993) found that with fertilization of 50 kg NO_3^- ha^{-1} $year^{-1}$, *A. rubrum* seedlings had foliar NRA of ~1 μmol NO_2^- g^{-1} h^{-1}. This is more than double the NRA of any of the mature hardwoods in our study, and more than 10× the values we found for mature *A. rubrum* (Table 4). Comparing their data to ours suggests substantial variation in NRA between seedlings and mature trees, but as Downs et al. measured NRA in fertilized potted seedlings, while we measured NRA of our mature trees in the field, we recognize the need for a more thorough test of this assertion. We did not observe large differences in NRA between overstory and 1–5 m tall understory tress of the same species at the three unfertilized sites (Sites 1–3, Harvard Forest), but it is possible that NRA is highest very early in plant development. This may explain why we did not find a correlation between NRA and our admittedly incomplete indicators of tree nitrogen use strategy.

While high NRA in *Betula* is consistent with its life history strategy, so is the low NRA in *Acer*. There is a wealth of literature documenting low nitrate affinity in *Acer* spp. (e.g. high nitrate leaching; (Lovett and Mitchell, 2004), high nitrification rates (Lewis and Likens, 2000; Lovett et al., 2002; Ollinger et al., 2002; Venterea et al., 2003), and low nitrate uptake and retention (Rothstein et al., 1996; Templer and Dawson, 2004)). While *Acer* creates soils that are characterized by high nitrification rates and high extractable nitrate, the trees do not appear to take up and use much of the nitrate produced. This may not be disadvantageous, since both *Acer* species in this study are relatively slow growing and succeed in ammonium-dominated forests. However soil acidification caused by high nitrate leaching may have adverse effects for *A. saccharum*, as this species performs poorly on base-poor sites (Lovett et al., 2004).

Nitrate reduction can occur both in the roots and shoots, and it has been suggested that temperate perennial species commonly have higher NRA in the roots than in the shoots under low nitrate concentrations, while the relative importance of shoot NRA increases with increasing soil nitrate concentration (Andrews, 1986). However, we found much higher NRA in leaves than in roots at one of the unfertilized sites at Harvard Forest (Table 4). We also did not find significant differences in root NRA across species. We did not test for root NRA within the fertilizer plots to avoid disturbance to the plots. However, a fertilization study on three tree species (*Eucalyptus regnans*, *E. oblique, Pinus radiata*) seedlings showed evidence for NRA induction in root tissue of all three species, even though it was only induced in the foliar tissue of one of the two genera studied (Adams and Attiwill, 1982). Changes in the N acquisition strategies of fungal communities with N fertilization may have important implications for plant nitrate reduction in the soil as well. Chronic N fertilization has been found to decrease microbial biomass and fungal:bacteria ratios in several long-term N fertilization experiments in northeastern temperate forests, including Harvard Forest (Wallenstein et al., 2006; Frey et al., 2004). We do

not know whether NRA expression by fungi may provide differential access to nitrate across their tree species symbionts.

Whether or not root NRA changes with fertilization, our data do not support our initial hypothesis that high levels of NRA would be advantageous under N enrichment. We expected species with higher NRA to have higher foliar %N and lower C:N than species with lower NRA, under the assumption that species with higher NRA are able to tap into pools of N that low NRA species do not. We also expected species with higher NRA to have significantly lower foliar $\delta^{15}N$ signatures than that of species with lower NRA, as nitrate has a lower $\delta^{15}N$ signature than ammonium (Pardo et al., 2006). Thus we expected *Betula* to exhibit the strongest fertilization response, and *Acer* the weakest, since they bracket the range of NRA seen in our study (Table 4). However, foliar metrics of nutrient availability in *Betula* and *Acer* responded virtually identically to N fertilization (%N + 15%, N:P + 30%, C:N–10%; Table 6). The only significant response to fertilization was a lowering of C:N in *Acer*, which was significantly lower than the C:N response of *Quercus*, a genus of intermediate NRA. These data suggest that the N economy of species (as measured by our few proxies) may not be substantially influenced by the ability to produce nitrate reductase.

This assertion should only be viewed as preliminary, however, since our characterization of the N economy of these trees was based on a few simple measures (%N, C:N, N:P). Other metrics such as canopy N content or nutrient resorption efficiency may be a more robust measure of tree nutrient status (Vitousek, 1982; McGroddy et al., 2004). A comparative study of N-cycling characteristics between the monospecific Catskill stands found that *B. alleghaniensis* has significantly lower nitrogen resorption efficiency than *Quercus* spp., *F. grandifolia* or *A. saccharum* (Lovett et al., 2004), consistent with *Betula* having access to additional N through its production of NRA. *Quercus* spp. and *F. grandifolia* showed intermediate, and *A. saccharum* the highest N resorption (Lovett et al., 2004), consistent with the idea that even under N enrichment, the lack of NRA may force *A. saccharum* to cycle N relatively conservatively. Thus we cannot rule out the possibility that generic differences in NRA will play a role in determining species success under continued N enrichment, and only assert here that we see little evidence for this link based on the metrics of N status we measured.

5. Conclusions

Our data suggest that there are strong species-level constraints on mature tree foliar NRA in northeastern temperate forests. Contrary to our original hypothesis, NRA was unaffected by soil N availability, and did not correlate by several metrics of response to fertilization. However, it is possible that an analysis of NRA in seedlings, rather than mature trees, would provide a different answer. It is also possible that our metrics of N cycling (%N, C:N, N:P, $\delta^{15}N$) were not sufficient to document the advantages conferred to species that produce higher NRA. Given our dataset, however, we find no evidence that the differences in NRA between northeastern temperate hardwoods will substantially affect their relative competitive ability under continuing anthropogenic N deposition.

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