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Research paper

Oak loss increases foliar nitrogen, δ^{15}N and growth rates of *Betula lenta* in a northern temperate deciduous forest

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Oak forests dominate much of the eastern USA, but their future is uncertain due to a number of threats and widespread failure of oak regeneration. A sudden loss of oaks (*Quercus* spp.) could be accompanied by major changes in forest nitrogen (N) cycles with important implications for plant nutrient uptake and tree species composition. In this study, we measured the changes in N use and growth rates of black birch trees (*Betula lenta* L.) following oak girdling at the Black Rock Forest in southeastern New York, USA. Data were collected from nine experimental plots composed of three treatments: 100% oaks girdled (OG), 50% oaks girdled (O50) and control (C). Foliar N concentration and foliar ^{15}N abundance increased significantly in the oak-girdled plots relative to the control, indicating that the loss of oaks significantly altered N cycling dynamics. As mineralization and nitrification rates increase following oak loss, black birch trees increase N absorption as indicated by higher foliar N content and increased growth rates. Foliar N concentration increased by 15.5% in the O50 and 30.6% in the OG plots relative to the control, while O50 and OG plots were enriched in ^{15}N by 1.08‰ and 3.33‰, respectively ($P < 0.0001$). A 641% increase in black birch growth rates in OG plots suggests that this species is able to respond to additional N availability and/or increased light availability. The loss of oaks and subsequent increase in black birch productivity may have a lasting impact on ecosystem form and function.

Keywords: black birch, forest disturbance, nitrate reductase, nitrogen cycling, oak girdling, stable isotopes, temperate forest.

Introduction

Over the past century, eastern forests of the USA have experienced the loss of dominant tree species such as the American chestnut (*Castanea dentata* (Marsh.) Borkh.), American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière). Oak trees (*Quercus* spp.) are now considered foundation organisms in eastern US forests, playing critical ecosystem roles such as regulating water yield and quality, carbon storage, N retention, fire regimes and biological diversity (Jones et al. 1998, Foster et al. 2002, Lovett et al. 2002, 2004, Ellison et al. 2005, Templer et al. 2005). However, the future of oak forests is uncertain due to a host of threats including aging canopy trees, climate change, soil acidification, insect herbivory, pathogens and the potential for increased logging (Abrams 1992, Lovett et al. 2006, Cha et al. 2010). One of the most serious potential threats is sudden oak death (SOD), a disease caused by infection of trees with the non-native, pathogenic water mold *Phytophthora ramorum* (Garbelotto and Rizzo 2001, Rizzo et al. 2002). Hundreds of thousands of oak (*Quercus* spp.) and tanoak (*Lithocarnus* spp.) trees have been killed by SOD in California and Oregon (USDA 2005, Meentemeyer et al. 2008), and several eastern species of red and white oaks have been found to be susceptible to the disease in greenhouse trials (Tooley and Kyde 2003, 2007). Oaks are also failing to regenerate through much of their range, primarily due to over-browsing by white-tailed deer, thus shifting forest composition and structure and potentially endangering many of the benefits provided by oak forests (Côté et al. 2004, Rooney and Waller 2003).

Widespread tree mortality can disrupt the tight balance between carbon and N that many forests maintain. Johnson and Edwards (1979) found that an increase in available ammonium following stem girdling caused an increase in nitrification rates, possibly as a result of decreased belowground competition for ammonium between nitrifiers and other heterotrophs. Similarly, Jenkins et al. (1999) found that net N mineralization, nitrification and N turnover increased at sites experiencing hemlock mortality. These findings suggest that oak loss may be accompanied by major changes in forest N cycles with potentially important implications for plant nutrient uptake and tree species composition.

Large forest disturbances may result in a greater availability of both ammonium and nitrate in forest soils and can eventually lead to an N pool enriched in ^{15}N. Leaf $\delta^{15}N$ signatures can be used as integrators 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 (Nadelhoffer and Fry 1994, Robinson 2001, Craine et al. 2009). Because nitrification discriminates against the heavier N isotope, the products of this process (NO_3^- and NO gas) are depleted in ^{15}N. These compounds now relatively rich in ^{14}N are more easily removed from the system via leaching or efflux, leaving behind a ^{15}N-enriched soil N pool, which is reflected in the leaves after uptake (Nadelhoffer and Fry 1994).

Tree species vary in their preferred ratio of ammonium : nitrate uptake and therefore may differ in their growth response to a change in N availability. Black birch (*Betula lenta* L.), a common understory tree at the Black Rock Forest (BRF) in Cornwall, NY, exhibited greater trunk diameter growth than any other species in the first few years, following an oak girdling experiment, compared with trees on unmanipulated control plots (William S. F. Schuster, unpublished data). A substantial black birch growth response has also been found following hemlock decline (Orwig and Foster 1998, Jenkins et al. 1999, Catovsky and Bazzaz 2000, Kizlinski et al. 2002, Stadler 2006, Cobb 2010) and tree harvesting (Smith and Ashton 1993, Kizlinski et al. 2002). Black birch seedlings have also been found to grow larger when nitrate is more readily available (Crabtree 1992, Crabtree and Bazzaz 1992).

Further consideration must be given to the effects of disturbance on the hydrology of the system, which can have a controlling effect on both the availability of N sources and on carbon gain through photosynthesis. The integrated leaf water use efficiency (WUE) may reflect canopy disturbance, theoretically decreasing with increasing post-disturbance water availability since change in stomatal conductance affects water loss more than carbon gain (reviewed in Chaves et al. 2004). However, it is possible that a decreased WUE may be partially offset by the effect of increased N uptake on photosynthetic capacity, the effect of increased light availability on carbon gain and/or changes in evaporative demand. Water use efficiency can be estimated from the leaf stable carbon isotope composition ($\delta^{13}C$) based on fractionation by Rubisco (the main carbon-fixing enzyme) and the ratio of the concentrations of CO_2 inside and outside (C_i/C_a) of the leaf (Farquhar et al. 1982, 1989, Farquhar and Richards 1984), and will be considered here for its role in the ecohydrologic response of the canopy to disturbance.

We hypothesize that changes in N availability caused by widespread oak mortality in an oak-dominated forest will have significant impacts on N use and growth rates of black birch trees at BRF. In order to test this prediction, we measured concentration and isotopic signature of foliar N and C (%N, $\delta^{15}N$, %C and $\delta^{13}C$), nitrate reductase activity (NRA) and growth of young black birch trees in replicated oak-girdled and control plots.

Experimental methods

Study site

This study was conducted at the BRF, a 1550 ha preserve located in Cornwall, NY in the Hudson Highlands Region of southeastern New York State. The study plots are located on the north slope of Black Rock Mountain (41.45°N, 74.01°W). Black Rock Forest 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* L.) dominate the canopy, while the understory is dominated by red maple (*Acer rubrum* L.). On the study site, the predominant non-oak trees are red maple (28%), black gum (*Nyssa sylvatica* Marsh.; 22%), black birch (*B. lenta* L.; 20%) and sugar maple (*Acer saccharum* Marsh.; 16%). Air temperatures are strongly seasonal ranging from a mean of −2.7 °C in January to 23.4 °C in July and the average annual precipitation is 1200 mm (NOAA 2002). The soils are mostly medium-textured loams, with granite gneiss bedrock or glacial till parent material at 0.25–1 m depth (Olsson 1981). Site index ranges from poor to good with soils generally acidic and low in nutrients (Lorimer 1981).

The forest was colonized by English settlers in 1700 and has been repeatedly logged with some portions converted to agriculture and pastureland until it was abandoned around 1900. In 1928, the forest became a research forest, and in 1989 BRF was bought from Harvard University and established as part of a consortium of educational and research institutions (Schuster et al. 2008).

Experimental design

In order to explore the potential ecosystem-level consequences of the loss of oaks, an oak-girdling experiment was implemented in 2008 at BRF. The experimental design includes four treatments replicated in three blocks along the north slope of

Black Rock Mountain: 100% oaks girdled (OG; affecting 74–78% of plot basal area (BA)), 50% oaks girdled (O50; 32–38% of BA), 100% non-oaks girdled (NO; 15–37% of BA) and control (C) (Figure 1). The girdling treatment mimics the impact of pathogens like SOD on cambium and phloem function by blocking the translocation of carbon between leaves and roots, generally causing mortality within 1–3 years (Noel 1970). The primary focus of the oak-girdling project is to quantify environmental drivers and identify impacts on key forest taxa and higher-level phenomena including energy flow, chemical cycling and biological diversity.

This study utilized 9 out of 12 experimental plots (75 m × 75 m) in a randomized block design grouped by slope position (upper, middle and lower) (Figure 1). The upper slope plots have lower soil water content and are more steeply sloped than the lower slope (24% vs. 15–16%; William S. F. Schuster, unpublished data). Our study included all plots except for the three NO plots. Notch girdling (Noel 1970) was performed during the summer of 2008, when a chain saw was used to make a 5 cm deep incision at breast height around the circumference of the tree. The cut penetrated from the bark through the phloem and the cambium, preserving most of the xylem. Trees with a diameter at breast height (DBH) <2.54 cm were left untouched.

Sampling

Five black birch trees with a DBH of ~2–6 cm were selected within each of the nine study plots, as close as possible to the center of the plot to minimize edge effects. Leaf samples were collected from each tree at three times throughout the growing season on 23–24 May, 4–5 July and 26–27 August 2010.

Nitrate reductase assay

Nitrate reductase activity was measured in black birch leaves in early July and late August. Leaves were collected on two consecutive sunny days between 11 AM and 1 PM in order to ensure the presence of the light-activated nitrate reductase enzyme. All leaves were cut from the middle of the canopy, using a pole pruner. Four leaves from each tree were then hole-punched into 6 mm discs and weighed to produce ~0.2 g of fresh leaf tissue per sample. The samples were analyzed for nitrate reductase activity based on the method of Stewart et al. (1986). Five milliliters 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 allowed to incubate 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.

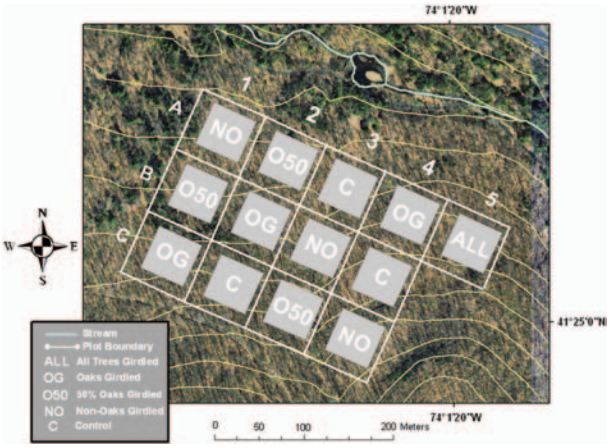

Figure 1. Map of the north slope study plots in the BRF, Cornwall, NY, USA, depicting the layout of the experimental plots and treatments.

The amount of nitrite in the solution was calculated using colorimetric analysis. One milliliter of the reaction mixture was pipetted out and 1 ml sulphanilic acid plus 1 ml α-naphthyl ethylenediamine dihydrochloride (NED) were added and mixed in a vortex mixer. Tubes were incubated for an additional 20 min at room temperature and absorbance was 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:

$$\mathrm{NRA} = \frac{\mathrm{nmol\ NO_2^-}}{\mathrm{ml}} \times \frac{5\,\mathrm{ml\ solution}}{\mathrm{leaf\ fresh\ weight\ (mg)}}$$

δ^{13}C, %C, δ^{15}N and %N

In late May, early July and late August, four leaves from each tree were collected as described above, oven-dried at 60 °C and subsequently ground to a fine powder (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, δ^{13}C, %N and δ^{15}N. Isotopic analysis was performed using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA, USA) followed by a continuous flow isotope ratio mass spectrometer (Delta PlusXP, ThermoFinnigan, Bremen, Germany). Samples were referenced against concurrently run corn and acetanilide standards. The precision (SD) of internal standards was ±0.08‰ (acetanilide) and ±0.03‰ (corn) for the δ^{13}C analysis, and ±0.30‰ (acetanilide) and ±0.08‰ (corn) for the δ^{15}N analysis. National Institute of Standards and Technology (NIST) peach was used for quality control (NIST 1547) with a precision (SD) of ±0.01‰ for δ^{13}C and ±0.05‰ for δ^{15}N. Nitrogen isotope data are reported as δ^{15}N values, which express foliar $^{15}N:^{14}N$ ratios relative to the ratio of $^{15}N:^{14}N$ in atmospheric N_2. $\delta^{15}N\ (‰) = (R_{sample}/R_{atm} - 1) \times 1000$, where $R_{atm} = 0.0036765$ and the $\delta^{15}N$ of atmospheric N_2 by definition is 0.0‰. Similarly, $\delta^{13}C$ values represent the ratio of $^{13}C : ^{12}C$ in leaf tissue relative to the ratio of $^{13}C : ^{12}C$ in atmospheric CO_2.

Specific leaf area and light availability

Specific leaf area (SLA) was calculated for four leaves from every tree at every sampling period. Leaf area was measured with a LiCor Leaf Area Meter (Li-3000, LiCor, Lincoln, NE, USA), and leaves were then oven-dried at 60 °C and their dry weight was used to calculate SLA. Light availability was measured once at each tree on a cloudy day using hemispheric photographs and gap light index (GLI) was calculated using Gap Light Analyzer v2.0 (Frazer et al. 1999).

Birch growth

Within the center 25 m × 25 m subplot of each experimental plot, the DBH of all black birch trees larger than 2.54 cm was measured annually from July 2007 to July 2010. Allometric equations were used to compute aboveground biomass (Brenneman et al. 1978).

Statistical analysis

Data were analyzed using an analysis of covariance for each of the three response variables: NRA, %N and $\delta^{15}N$. Stepwise model selection was used to add and remove variables in the models to solicit only those variables that are statistically significant for explaining variation. Specific leaf area light availability and slope position were found to be highly correlated, so only slope position was used as a covariate with the predictor variables oak-girdling treatment and sampling month. No significant difference was found in NRA or $\delta^{15}N$ measurements between the different sampling periods, so these data were pooled. However, sampling month was found to be a significant factor in foliar %N and was therefore included in the model. To meet the assumptions of normality required for analysis of variance (ANOVA), %N values were raised to the –1/2 power, $\delta^{15}N$ values were raised to the 3/4 power and $\delta^{13}C$ values were raised to the 1/2 power after adding a constant to make all isotope values positive. Tukey's honestly significant difference (HSD) test values were used to determine significance among the categorical values in each ANOVA. Results with $P < 0.05$ were accepted as statistically significant. Stepwise model selection was conducted using statistical software program R version 2.9.2 (R Foundation for Statistical Computing, Vienna, Austria, 2009) and all other analyses were completed in JMP version 8.0.2 (SAS Institute Inc., Cary, NC, USA, 2009).

Results

Birch growth

There was an average relative increase of 641% in aboveground biomass of black birch between July 2007 and July 2010 in the OG plots compared with the control plots (Figure 2). During these first 3 years of the experiment there was an 11.1 ± 1.3% increase in aboveground black birch biomass in the control plots compared with an 82.4 ± 20.0% increase in the OG plots (Figure 2). When only half of the oaks were girdled, the relative increase in aboveground biomass was only 121% compared with the growth on the control plots (from 11.12 ± 1.29% to 24.61 ± 1.83%). While the three treatments differed significantly ($P < 0.00001$), there was an additional slope position effect with saplings on the lower slope growing less than those located on the middle and upper slopes ($P < 0.05$, data not shown).

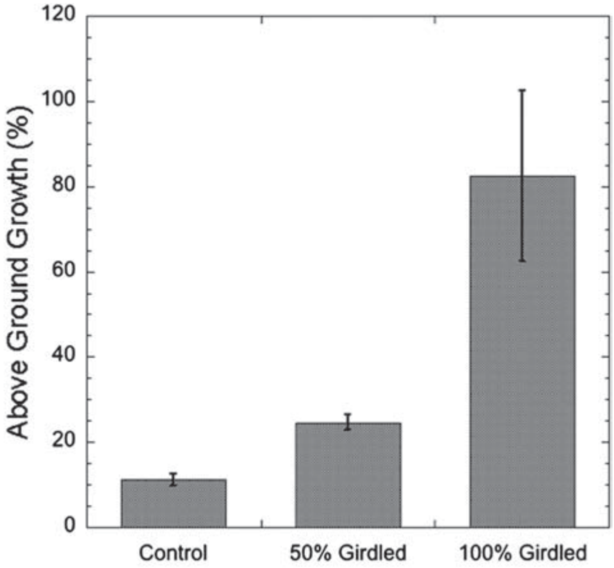

Figure 2. Percent growth in aboveground biomass from July 2007 to July 2010 of all black birch trees larger than 2.5 cm DBH in the central 25 m × 25 m area of each experimental plot. Mean values ± SE for each experimental treatment: control ($n = 44$), 50% oak-girdled ($n = 63$) and 100% oak-girdled ($n = 13$).

Black birch trees on the lower slope were found to have significantly lower SLA ($P < 0.0001$) and experienced a higher light environment ($P < 0.0001$) than trees on the middle or upper slope positions (Table 1). Oak-girdling treatment did not significantly affect the GLI in individual trees ($P = 0.45$). Leaf $C : N$ was 13.5% lower in the O50 and 20.9% lower in the OG plots than in the control ($P < 0.0001$, Table 1). Foliar $\delta^{13}C$ was enriched significantly ($P < 0.0001$) in the OG plots relative to the control and O50 plots (by 4.1% and 4.0%, respectively) (Table 1). Foliar $\delta^{13}C$ also varied significantly between black birch trees at different slope positions ($P < 0.0001$), with the lower slope being significantly higher in foliar ^{13}C abundance than the middle or upper slope.

% Nitrogen

The best predictive model for foliar %N included girdling treatment, month and slope position (Table 2). Mean foliar N

Table 1. Experimental plot and leaf characteristics from the oak removal experiment of BRF, Cornwall, NY, USA. Treatments included: 100% oaks girdled (OG), 50% oaks girdled (O50) and control (C) and were distributed among the plots as in Figure 1. Values shown are means ± SE. Gap light index (GLI) was measured once at each experimental tree and may not be representative of the entire plot ($n = 5$ for each plot). Specific leaf area was calculated for four leaves from each tree at every sampling period ($n = 60$ for each plot). An average value of *C* : *N* and δ^{13}C was calculated for each tree at each sampling period ($n = 15$ for each plot). Within a column, values not connected by the same letter are significantly different (ANOVA with the Tukey HSD test ($P < 0.05$)).

Oak-girdling treatment	Plot	Slope position	GLI (%)	SLA (cm^2/g)	*C* : *N*	δ^{13}C (‰)
C	A3	Lower	6.00 (±0.61) bc	334.0 (±6.92) ab	22.48 (±0.45) ab	−31.53 (±0.13) bc
C	B4	Middle	7.65 (±0.64) b	304.3 (±9.40) b	25.05 (±0.82) a	−32.06 (±0.82) c
C	C2	Upper	7.60 (±0.41) b	326.0 (±7.66) ab	22.16 (±0.41) ab	−31.99 (±0.15) bc
O50	A2	Lower	7.67 (±0.77) b	320.6 (±8.35) ab	20.39 (±0.50) bc	−31.55 (±0.13) bc
O50	B1	Middle	5.65 (±0.43) bc	339.6 (±8.87) ab	20.03 (±0.59) bc	−31.97 (±0.14) bc
O50	C3	Upper	8.16 (±1.58) b	344.3 (±8.22) ab	19.88 (±0.47) bc	−31.92 (±0.12) bc
OG	A4	Lower	17.49 (±2.83) a	244.9 (±16.08) c	20.80 (±1.33) bc	−29.22 (±0.46) a
OG	B2	Middle	6.69 (±1.06) b	321.0 (±15.53) ab	17.76 (±0.76) cd	−31.24 (±0.24) bc
OG	C1	Upper	0.47 (±0.00) c	358.3 (±14.83) a	16.54 (±0.68) d	−31.18 (±0.23) b

Table 2. Best-fit model summaries and effect tests for predicting leaf N characteristics in the nine plots from the oak removal experiment at the BRF, Cornwall, NY, USA.

Model response variable	Model				Model parameters	Parameter		
	R2	Degrees of freedom	*F* ratio	*P* value		Degrees of freedom	*F* ratio	*P* value
%N	0.54	14	10.21	<0.0001	Girdling treatment	2	46.19	<0.0001
					Slope position	2	6.26	<0.005
					Month	2	6.00	<0.005
					Girdling Treatment × Month	4	2.57	<0.05
					Girdling Treatment × Slope	4	3.96	<0.005
δ^{15}N	0.84	4	172.77	<0.0001	Girdling treatment	2	342.18	<0.0001
					Slope position	2	3.36	<0.05
NRA	0.30	13	2.48	0.01	Slope position	2	4.48	0.01

concentration was 2.02 ± 0.03%, 2.34 ± 0.03% and 2.64 ± 0.07% in the C, O50 and OG plots, respectively ($P < 0.0001$). Sampling period was a significant factor, with black birch foliar %N significantly lower in July than in May or August ($P < 0.01$). Leaf N was 15.5% greater in the O50 and 30.6% greater in the OG plots than in the control ($P < 0.0001$). Leaf %N was positively correlated to SLA ($P < 0.0001$) and light ($P < 0.005$).

Slope position was also a significant factor in predicting foliar %N ($P < 0.005$); leaves from the top of the slope had significantly higher N content than those from the bottom of the slope. There were significant interaction effects between slope position and girdling treatment ($P < 0.01$) and between month and girdling treatment ($P < 0.05$). Black birch foliage in the OG plots showed a stronger decrease in %N from May to July than the other girdling treatments and a less significant increase from July to August than the other girdling treatments (Figure 3).

δ^{15}N

In addition to changes in the bulk N concentration, there were significant changes in the isotopic signature of the leaf N in the treatment plots. The best predictive model for foliar δ^{15}N included only girdling treatment and slope position; month sampled was not a significant predictive variable (Table 2). Foliar δ^{15}N was significantly different between oak-girdling treatments, with O50 and OG plots increasingly enriched in ^{15}N ($P < 0.0001$, Figure 4). Mean foliar δ^{15}N was −3.25 ± 0.07‰, −2.17 ± 0.08‰ and 0.08 ± 0.12‰ in the C, O50 and OG plots, respectively. Foliar δ^{15}N also varied significantly between black birch trees at different slope positions ($P < 0.05$), with the lower slope being significantly lower in foliar ^{15}N abundance than the middle of the slope (Figure 4).

Nitrate reductase activity

The best predictive model for foliar NRA included only slope position (Table 2). Black birch trees on the lower slope had less NRA than those on the middle or upper slope, regardless of treatment ($P = 0.01$). Trees on the lower slope also showed a clear trend of increasing foliar NRA with an increasing level of oak girdling (Figure 5).

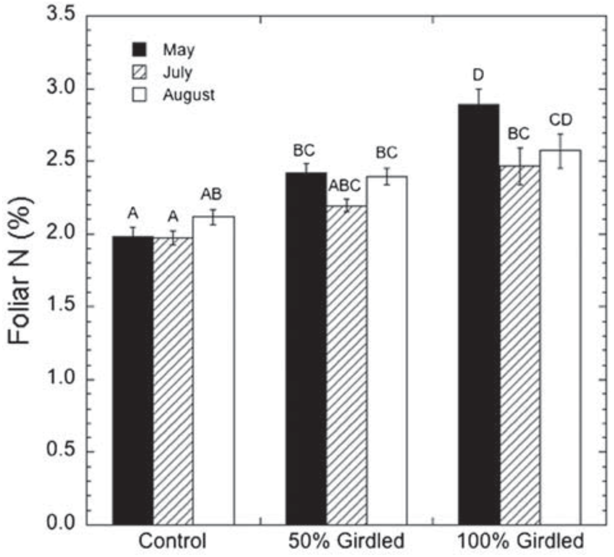

Figure 3. Foliar N content by mass (mean ± SE) for black birch leaves collected on each experimental treatment at each sampling time. Fifteen trees per treatment type were sampled three times, spaced evenly throughout the growing season in late May, early July and late August ($n = 135$). Values not connected by the same letter are significantly different (ANOVA with the Tukey HSD test ($P < 0.05$)).

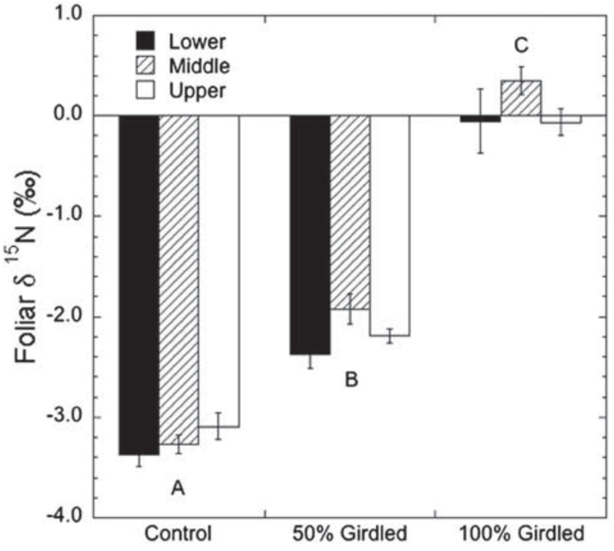

Figure 4. Foliar δ^{15}N signatures ($^{0}/_{00}$) for black birch leaves collected from each experimental treatment (at each slope position). Mean values with error bars (SE) for 15 trees per treatment sampled three times throughout the growing season ($n = 135$). Among girdling treatments, values not connected by the same letter are significantly different (ANOVA with the Tukey HSD test ($P < 0.05$)).

Discussion

One of the most apparent biological responses to oak girdling at BRF has been an increase in the growth rate of black birch trees on the oak-girdled plots compared with the control plots. Once a minor component of northern hardwood forests, black birch is now increasing in density over most of its range as a result of partial cutting of the overstory (Ward and Stephens 1996) and hemlock decline (Kizlinski et al. 2002), and has become a common component of forest regeneration in southern New England (Kittredge and Ashton 1990). In this study, we found that oak loss has important effects on N use in black birch trees and, in conjunction with increased light penetration into the canopy, affects the trees' growth. Furthermore, we suggest that these changes may lead to a widespread alteration of ecosystem form and function.

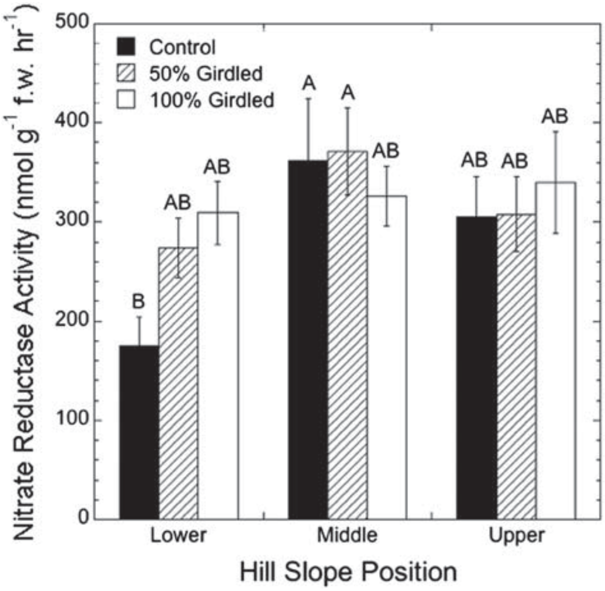

Figure 5. Black birch foliar NRA levels (nanomoles of NO_2 produced per hour per gram fresh leaf weight) for each experimental treatment at each slope position. Mean values with error bars (SE) for 15 trees per treatment sampled three times throughout the growing season ($n = 135$). Values not connected by the same letter are significantly different (ANOVA with the Tukey HSD test ($P < 0.05$)).

Nitrogen availability

Girdling blocks the flow of carbon from tree leaves to roots, which forces the roots to utilize stored reserves of carbon to survive and within about three years starves the roots to the point of mortality (Edwards and Ross-Todd 1979). The mycorrhizal fungi that depend upon these carbon pools experience declines in their productivity, growth and survival as well (Johnson and Edwards 1979). With fewer trees taking up N and increased decaying biomass belowground (roots and mycorrhizal fungi), girdling increases belowground N availability. We hypothesized that the cascade of events resulting from these responses increased available N and led to the increased growth rates of black birch trees in oak-girdled forest stands.

Declines in soil respiration have been detected as a result of oak girdling on the north slope of BRF (Levy-Varon et al. 2012), providing strong evidence of mycorrhizal and root mortality in the girdled plots. Furthermore, soil samples taken before and after oak girdling in a pilot study at BRF show an increase in nitrate and ammonium levels in the girdled stands indicating that more N is available for plant uptake (Jerry M. Melillo and William S. F. Schuster, unpublished data). Our results further support this hypothesis as we found that, despite seasonal variation and slope position, black birch foliage on oak-girdled plots had a significantly higher N content than foliage on control plots. Correspondingly, black birch leaf *C* : *N* decreased significantly on oak-girdled plots. Foliar $\delta^{13}C$ is known to correlate with WUE in C_3 plants (Farquhar and Richards 1984, Farquhar et al. 1989) and was significantly higher in black birch trees growing on the OG plots and on the lower slope, ranging from -32.06 ± 0.82 to -29.22 ± 0.46‰ overall. The highest foliar $\delta^{13}C$ (-29.22 ± 0.46‰) was measured on the oak-girdled plot located at the lowest slope position. This is a plot that would not be expected to experience increased water limitation but rather should have the highest water availability due to downslope transport and the lack of competition from the overstory trees, an assertion that is confirmed by direct measurements of soil moisture reported in Levy-Varon et al. (2012). Together this evidence indicates that none of the trees were water-stressed.

Light penetration into the canopy increases after tree mortality and undoubtedly interacts with increased N abundance to affect birch growth. Light is directly involved in photosynthetic carbon fixation, which is well correlated to leaf N (Field and Mooney 1986), linking both N and light to tree growth. Light is also necessary to activate the nitrate reductase enzyme and create the large amount of reductant used to reduce NO_3^- and create amino acids, which can eventually be incorporated into photosynthetic proteins. Oak girdling increased light availability at the plot level in the BRF experiment (William S. F. Schuster, unpublished data), which is consistent with the increased growth of black birch. However, we found that the GLI measured at the individual birch trees we sampled was highly variable and not significantly higher on oak-girdled plots than on control plots. This was likely because the sampled trees were in the understory and may have been shaded by mature non-oak trees that remained standing. Similarly, SLA values of the sampled leaves did not decrease consistently with oak girdling (Table 1). As a result, we conclude that it is highly likely that light and N are interactively affecting tree growth in the girdled plots, but caution that direct evidence of a causal relationship is needed.

The root and mycorrhizal mortality that results from oak girdling provides an increase in belowground organic N to a previously N-limited system. Because mycorrhizal fungi retain ^{15}N-enriched N under N-limited conditions (Hobbie and Colpaert 2003), the decay of the oaks' ectomycorrhizal fungal mycelia may release N with a high $\delta^{15}N$ signature, which is likely absorbed by the black birch trees and reflected in the leaf $\delta^{15}N$ values. In addition, the N released by girdling can increase the N mineralization rate and the inorganic N availability (Johnson and Edwards 1979). The increase in available inorganic N ultimately leads to an increase in nitrification, making more soil nitrate available for plant uptake (Jenkins et al. 1999). Because nitrifying bacteria discriminate against the heavier N isotope, the products of nitrification (NO_3^- and N_2O gas) are depleted in ^{15}N. These ^{15}N-depleted compounds are more mobile than ammonium and easily removed from the system via leaching or gaseous efflux (Nadelhoffer and Fry 1994) and as this N leaks out of the system, the soil and vegetation N pools become enriched in ^{15}N. Furthermore, as fractionations during N transformations are no longer substrate limited, their expression becomes more pronounced, resulting in higher $\delta^{15}N$ values following large forest disturbances (Nadelhoffer and Fry 1994).

Because N transferred to plants by mycorrhizal fungi is depleted in ^{15}N (Hobbie et al. 2000), foliar $\delta^{15}N$ may also increase with increased N availability if the proportion of N acquired by plants, supplied by fungi, decreases or if the proportion of N taken up by fungi that is transferred to the host plants increases (Hobbie and Colpaert 2003). It is possible that the black birch trees in this study became less dependent on ectomycorrhizal fungi for N acquisition after oak girdling and subsequent increases in soil N, and as a result their foliage became enriched in ^{15}N (Hobbie and Colpaert 2003, Craine et al. 2009).

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). For example, foliar $\delta^{15}N$ values have been found to be positively correlated with N availability in surface soil (Garten and Miergroet 1994). Garten (1993) also found a correlation between foliar ^{15}N abundance and net nitrification potential in soil and suggested that measurements of foliar $\delta^{15}N$ in non-N-fixing plants may help to identify the position of forests along a gradient from N deficiency to N saturation.

Many studies have demonstrated the relationship between changes in the N cycle 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 clear-cutting (Pardo et al. 2002), 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). Our foliar ^{15}N data indicate that the girdled plots are enriched relative to the control plots by a difference of 3‰, which is consistent in magnitude with similar studies (Pardo et al. 2002). Consistent with Garten (1993), we did not find significant seasonal variation in foliar $\delta^{15}N$. However, Garten (1993) found foliar enrichment of $\delta^{15}N$ in valley bottoms, which we did not find on our study slope.

In the context of the above mechanisms, the isotopic data suggest a possible increase in nitrification, an increase in the loss of nitrate from the system and a general opening of the N cycle after oak girdling. Furthermore, soil water samples collected by zero-tension lysimeters in the study area showed an increase in total dissolved N and nitrate concentrations after oak girdling (Kathleen C. Weathers and Amanda M. Lindsey, personal communication). Significant nitrate losses after girdling have been found previously by Edwards and Ross-Todd (1979). In addition, Jenkins et al. (1999) concluded that nitrate leaching was likely occurring at sites experiencing increases in net N mineralization, nitrification and N turnover following high tree mortality. Accelerations of N cycling rates have been noted in response to other disturbances as well, including root rot, defoliation, gap formation and clear-cutting (Swank et al. 1981, Matson and Boone 1984, Mladenoff 1987, Waide et al. 1988, Kim et al. 1995). In this study, it appears that oak loss results in an increase in N availability that leads to an increased foliar N content. Several factors may contribute to the observed alteration of the foliar isotopic signature in black birch trees, including release of ^{15}N-enriched N from decaying oak ectomycorrhizal fungi, the general opening of the N cycle and loss of the lighter N isotope, and a possible decrease in black birch reliance on ectomycorrhizal fungi.

Nitrate reductase activity

We predicted that the increased growth of black birch would result from an increase in N availability within oak-girdled plots and that black birch was specifically able to take advantage of the increased amount of nitrate available in the forest soils following oak girdling. Since nitrate reductase is a substrate-inducible enzyme, an increase in available nitrate should be reflected in increased nitrate reductase activity. Other studies have demonstrated correlations between soil nitrate availability and leaf NRA (Taylor et al. 1982, Adams and Attiwill 1982). We hypothesized, but did not find, that this mechanism would contribute to the increased foliar N content in black birch. After the disturbance of oak girdling, the increase in nitrification and subsequent loss of nitrate should lead to an increase in the δ^{15}N of the soil ammonium pool, which may be indicated by the enriched foliar ^{15}N values. Although nitrate production has likely increased, the observed foliar ^{15}N data may also indicate a loss of nitrate from the system, perhaps limiting the nitrate available to plant roots and NRA. Alternatively, several interacting and potentially confounding ecological factors (e.g. hill-slope position, hydrology and changes in the density and species composition of the understory vegetation) may have resulted in significant variation in nitrate availability within and between plots making a trend in NRA difficult to identify.

Black birch trees on the lower slope, which had the lowest overall NRA and foliar %N, did show a trend of increasing NRA with oak girdling. If these trees were most N limited to begin with, the increase in available nitrate after girdling may have had the most impact on trees in those plots, as they also experienced the largest average increase in growth rate. It is also possible that we failed to detect a significant trend because we obtained an incomplete picture of whole plant NRA in *B. lenta*. The enzyme activity fluctuates extensively diurnally (Lillo 1983, Aslam et al. 2001), seasonally (Koyama et al. 2008) and throughout the plant (Black et al. 2002). Among species, nitrate reductase levels vary between leaves, stems and roots (Black et al. 2002). Scientific literature lacks this information regarding *B. lenta*, but other species in the *B.* genus have been shown to reduce nitrate in their leaves (Al Gharbi and Hipkin 1984, Friemann et al. 1991, 1992). However, 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.

Conclusion

Evidence in the form of an enriched ^{15}N foliar signal and increased foliar %N indicates that the loss of oaks from this forest has significantly altered N cycling dynamics. As mineralization and nitrification rates increased, black birch trees increased N absorption as indicated by higher foliar N content. With more N available and accumulating in the leaves, black birch is able to respond to the increased light availability and dramatically increase growth rates. A disturbance like large-scale tree mortality can therefore favor the success of certain species, such as black birch, which are able to respond to additional N by increasing their mechanisms of uptake and use. The incorporation of N into black birch leaves ensures the later return of this N to the soil and its continued cycling within the system. Importantly, through increases in N uptake, black birch will prevent some nitrate leaching from the system, which could otherwise result in soil and water acidification and forest decline. The additional N provides a window of opportunity for rapid growth in the girdled plots, which black birch utilizes to increase productivity. The forests that emerge from these disturbances and the resulting changes in N cycling are likely to bear the imprint of black birch productivity during this time. Oak mortality is a dynamic change that will have significant but difficult-to-predict ecosystem consequences, which are potentially confounded by anthropogenic alterations of N cycling such as atmospheric N deposition.

Our experimental results do not address whether the observed responses are unique to black birch during oak canopy loss or more generally the response of an understory species to canopy disturbance. Our results are, however, consistent with the concept of oak as a foundation species (Lovett et al. 2002, 2004, Templer et al. 2005). The unique foliar and litter properties of some oak species affect carbon and N cycling by producing litter with low decomposition rates (Lovett et al. 2006). Oak leaf litter also leads to soils with low nitrification rates (Finzi et al. 1998, Lovett et al. 2004), low nitrate leaching into streams (Lewis and Likens 2000, Lovett et al. 2002) and high retention of atmospherically deposited N (Templer et al. 2005). If oaks disappear from eastern forests and are replaced by black birch trees with N-rich foliage, the ability of these forests to retain N could be reduced. Pests and diseases are likely to be the primary cause of species composition change in eastern US forests in the next few decades (Lovett et al. 2006), and have the potential to alter nutrient cycling and ecosystem functioning in oak forests.

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Conflict of interest

None declared.

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