

## THE SPATIAL PATTERN OF NITROGEN CYCLING IN THE ADIRONDACK PARK, NEW YORK

BRENDEAN E. McNEIL,<sup>1,2,6</sup> JANE M. READ,<sup>1</sup> TIMOTHY J. SULLIVAN,<sup>3</sup> TODD C. McDONNELL,<sup>3</sup> IVAN J. FERNANDEZ,<sup>4</sup>  
AND CHARLES T. DRISCOLL<sup>5</sup>

<sup>1</sup>*Department of Geography, Maxwell School of Citizenship and Public Affairs, Syracuse University, Syracuse, New York 13244 USA*

<sup>2</sup>*Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706 USA*

<sup>3</sup>*E & S Environmental Chemistry, 2161 Northwest Fillmore Avenue, Corvallis, Oregon 97330 USA*

<sup>4</sup>*Department of Plant, Soil, and Environmental Sciences, University of Maine, Orono, Maine 044569 USA*

<sup>5</sup>*Department of Civil and Environmental Engineering, Syracuse University, Syracuse, New York 13244 USA*

**Abstract.** Maps of canopy nitrogen obtained through analysis of high-resolution, hyperspectral, remotely sensed images now offer a powerful means to make landscape-scale to regional-scale estimates of forest N cycling and net primary production (NPP). Moreover, recent research has suggested that the spatial variability within maps of canopy N may be driven by environmental gradients in such features as historic forest disturbance, temperature, species composition, moisture, geology, and atmospheric N deposition. Using the wide variation in these six features found within the diverse forest ecosystems of the 2.5 million ha Adirondack Park, New York, USA, we examined linkages among environmental gradients and three measures of N cycling collected during the 2003 growing season: (1) field survey of canopy N, (2) field survey of soil C:N, and (3) canopy N measured through analysis of two 185 × 7.5 km Hyperion hyperspectral images. These three measures of N cycling strongly related to forest type but related poorly to all other environmental gradients. Further analysis revealed that the spatial pattern in N cycling appears to have distinct inter- and intraspecific components of variability. The interspecific component, or the proportional contribution of species functional traits to canopy biomass, explained 93% of spatial variability within the field canopy N survey and 37% of variability within the soil C:N survey. Residual analysis revealed that N deposition accounted for an additional 2% of variability in soil C:N, and N deposition and historical forest disturbance accounted for an additional 2.8% of variability in canopy N. Given our finding that 95.8% of the variability in the field canopy N survey could be attributed to variation in the physical environment, our research suggests that remotely sensed maps of canopy N may be useful not only to assess the spatial variability in N cycling and NPP, but also to unravel the relative importance of their multiple controlling factors.

**Key words:** *Adirondack Park; atmospheric nitrogen deposition; foliar nitrogen; forest disturbance; functional trait; hyperspectral remote sensing; nitrogen cycling; spatial variability.*

### INTRODUCTION

Ecologists are increasingly called upon to make accurate predictions of ecosystem processes such as carbon (C) sequestration, forest productivity, and ecosystem nitrogen (N) retention at spatial scales ranging from landscape (i.e., hundreds of hectares) to global (Galloway 1998, Goodale et al. 2002, Aber et al. 2003). Predictions of ecosystem processes at these broad scales typically must account for not only the strong but poorly understood spatial variability in N cycling, but they also must discriminate among the effects of multiple factors (e.g., species composition, climate, atmospheric N deposition) that control N cycling. Here we present results of a case study suggesting that

information contained within remotely sensed maps of canopy N (i.e., mass-based concentration of N in a forest canopy) can help ecologists overcome both of these major challenges.

Remote sensing of canopy N provides a means to assess spatial patterns in net primary production (NPP) and N cycling with high spatial resolution (i.e., 30 × 30 m pixels) at landscape to regional scales (Ollinger et al. 2002, Smith et al. 2002, Ollinger and Smith 2005). It also presents an opportunity to identify potential causal agents through assessment of spatial patterns. A map of canopy N reflects the interactions among many dynamic ecosystem processes (Ollinger and Smith 2005), including recovery from historic disturbance (Goodale and Aber 2001, Latty et al. 2004), response to atmospheric N deposition (McNeil et al. 2007), and climatic variability (Reich and Oleksyn 2004, Wright et al. 2005). Thus if it were possible to identify the controls on the spatial patterns of canopy N, maps of canopy N could serve as invaluable tools to test fundamental ecological assump-

Manuscript received 21 February 2007; revised 13 July 2007; accepted 5 September 2007. Corresponding Editor: M. Friedl.

<sup>6</sup> Present address: Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706 USA. E-mail: bmcneil@wisc.edu

tions and to assess ecosystem response to global change (cf. Reich 2005). The objective of this paper is to identify the relative contributions of factors controlling the spatial pattern of N cycling across the large, complex, temperate forested landscape of the Adirondack Park in northern New York State, USA. This is accomplished by analysis of both field and remotely sensed data.

*Controls on forested ecosystem N cycling by tree species, environment, and humans*

Several recent studies have provided overviews of the relationships among environmental controls (e.g., N deposition, climate, hydrological pathways, disturbance history) and numerous plant, soil, and surface water-based measures of forested ecosystem N cycling (Fenn et al. 1998, Aber et al. 2003, Driscoll et al. 2003b). However, the relative importance of these environmental controls on the spatial pattern of canopy N has not been elucidated. Our rationale for focusing on canopy N as a measure of forested ecosystem N cycling is twofold. First, since the dynamics of forested ecosystem N cycling are thought to be ultimately driven by biotic demand for N, canopy N has been suggested as perhaps the “best” indicator of forested ecosystem N cycling (Aber et al. 1998). Second, canopy N is unique among other measures of forested ecosystem N cycling in that it can be assessed via hyperspectral remote sensing instruments (Ollinger et al. 2002).

Variability in canopy N results from the differing N resource investments made by individual trees (i.e., foliar N). Trees adjust foliar N according to (1) the functional traits of the tree species, (2) the environment experienced by the tree, and (3) the effects of humans on that environment. Plant functional trait strategies fall along a “global leaf-economics spectrum” ranging from species investing large amounts of N to achieve high production rates in short-lived leaves having low leaf mass per area (LMA) to species investing low amounts of N but sustaining lower production rates in long-lived leaves having high LMA (Wright et al. 2004). Within most forest environments, niche differentiation allows for substantial variation in the functional-trait strategies of tree species (Rees et al. 2001). As a result, interspecific variation in foliar N may be as large locally (e.g., within a 30 × 30 m forest plot or image pixel) as it is across continental or global scales (Reich et al. 1997, Poorter and De Jong 1999, Wright et al. 2004).

Despite important fundamental differences in the *magnitude* of foliar N investment, plant species can be expected to physiologically acclimate or genetically adapt foliar N in response to their environment (Aerts and Chapin 2000). A given plant species may increase foliar N in order to increase production under increased soil N availability or it may increase it to compensate for suboptimum growing conditions. One well-established compensatory effect is that foliar N tends to be higher in colder environments (van den Driessche 1974, Yin 1993, Körner 1999, Oleksyn et al. 2002, Reich and Oleksyn

2004, Han et al. 2005). Similarly, plants may exhibit a compensatory increase in foliar N in response to reduced moisture availability (van den Driessche 1974, Vitousek et al. 1992, Wright et al. 2001, 2003). Alternatively, increased temperature and moisture availability can increase rates of decomposition and nutrient cycling, resulting in increased foliar N within canopy trees (Austin and Vitousek 1998, Ollinger and Smith 2005). However, high moisture availability can also increase ecosystem N loss via denitrification, thereby reducing N availability, and likely resulting in canopy trees decreasing their foliar N (Groffman et al. 1992).

Canopy N may also be affected by localized variations in tree species composition and geologic substrate. As tree species differ in their characteristic magnitude of foliar N investment, the relative abundance of species in the canopy could directly influence variability in measurements of canopy N made in a field plot or with hyperspectral remote sensing. Species composition is also known to affect rates of N cycling and thus affect the N available to each tree (Ollinger et al. 2002, Lovett et al. 2004). Geologic composition controls mineral nutrient availability (e.g., phosphorus, calcium) that may limit or co-limit photosynthetic production. Since the investment of N and other nutrients into a leaf is governed by stoichiometric constraints (Sterner and Elser 2002, McGroddy et al. 2004, Reich and Oleksyn 2004, Han et al. 2005), soil limitation of certain mineral nutrients can be accompanied by a reduction in canopy N.

Human actions may increase canopy N through emissions associated with fossil fuel combustion and agricultural activity and the ensuing deposition of N from the atmosphere (see reviews by Aber et al. 1998, Fenn et al. 1998, Gunderson et al. 1998). Conversely, human actions may also decrease canopy N through forest disturbance. While tree species in temperate forests have evolved adaptations to natural disturbances such as large windstorms (Carlton and Bazzaz 1998, Cooper-Ellis et al. 1999), anthropogenic forest disturbances that result in the loss of large quantities of N from the site, such as logging, conversion to agriculture, and fire associated with slash from logging may leave a legacy that can be seen up to centuries later in reduced foliar N (Goodale and Aber 2001, Latty et al. 2004). These effects of human actions upon canopy N underscore the fact that canopy N responds to soil N availability (van den Driessche 1974, Aerts and Chapin 2000). However, the strong coupling of canopy N and rates of soil N cycling (Ollinger et al. 2002) suggests that measurement of soil N properties per se is likely to have little added value in explaining spatial patterns in canopy N.

*Research problem and approach*

Despite the wealth of studies available to describe the individual roles that tree species, the environment, and humans each play in controlling canopy N and forested ecosystem N cycling, very little is known about how

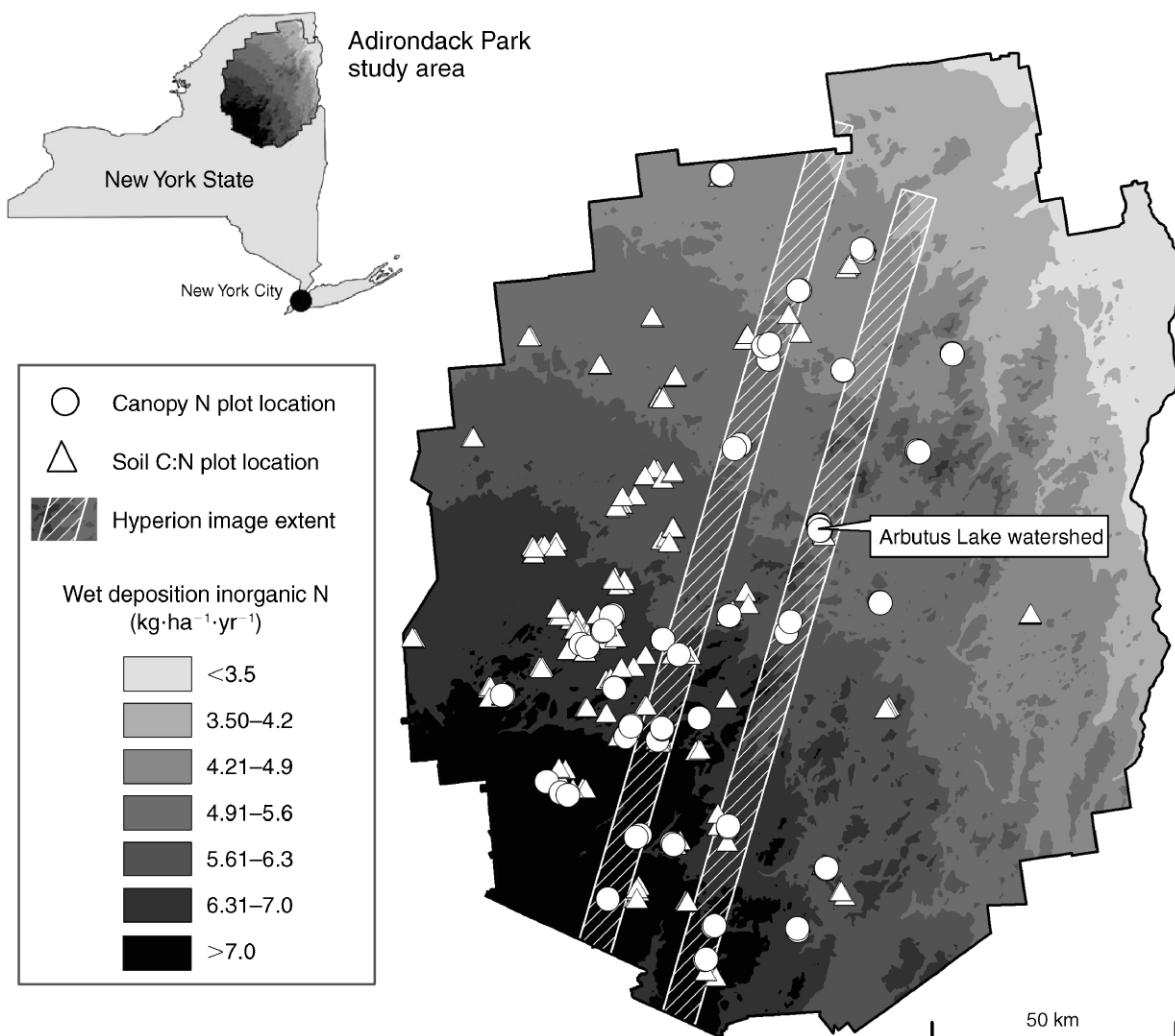


FIG. 1. Sampling locations shown over the gradient of atmospheric N deposition within the Adirondack Park study area, New York, USA. The labeled Arbutus Lake watershed is shown in Fig. 3.

these factors interactively produce the spatial patterns of N cycling evident within landscape-scale and regional-scale (i.e., 10 km to 10<sup>8</sup> km<sup>2</sup>) maps of remotely sensed canopy N. The Adirondack Park of northern New York State (Fig. 1) is an ideal place to study the roles played by species, environment, and humans in controlling spatial variability in N cycling within northern temperate forests. Its complex, mountainous, 2.5 million ha landscape is home to a diversity of species. There are well-documented patterns of historic logging and human-caused forest fires (McMartin 1994, APA 2001, McNeil et al. 2006), and portions of the park receive among the highest rates of N deposition in North America (National Atmospheric Deposition Program [NADP; NRSP-3] data, NADP Program Office, Champaign, Illinois, USA). The park's forests presently retain the majority of N inputs from atmospheric deposition (Ito et al. 2005) and thereby help mitigate problems of N pollution (Driscoll et al. 2003b) that could affect the acid

neutralizing capacity of upland surface waters and the N status of estuaries of the Hudson and St. Lawrence rivers.

We evaluated relationships among the dependent variables of canopy N (measured in the field and via remote sensing) and soil C:N ratio and six independent variables: (1) atmospheric N deposition, (2) forest disturbance history, (3) moisture availability, (4) species composition, (5) geologic setting, and (6) temperature (Fig. 2). This approach incorporates variation among all the major spatial controls on N cycling identified by Aber et al. (2003). We removed the potentially confounding factor of interannual variation by collecting all field and remotely sensed data within the height of the 2003 growing season. Previous studies in the northeastern United States have shown foliar N to vary by as much as 25% between years (Magill et al. 2000). This variation may have confounded recent attempts, based on data collected in different years, to uncover

possible spatial patterns of foliar N in the northeastern United States (Aber et al. 2003). Finally, our approach makes extensive use of a Geographic Information System (GIS; Fig. 2) as a means to assess variation in the spatial controls on N cycling (see McNeil et al. 2005). Coupled with the spatially explicit measurements of N cycling provided by remotely sensed maps of canopy N and field surveys of canopy N and soil C:N, these aspects of our approach enable us to conduct a holistic assessment of spatial pattern at a regional scale.

## METHODS

### *Study area*

Each of our two field measurements of N cycling (canopy N and soil C:N) were independently collected and do not share coincident sample locations. However, these surveys were similar in that they minimized temporal variability and were each designed to encompass the spatial variability present within the statistical population of the forests of the Adirondack Park (McNeil et al. 2005, 2007, McNeil 2006, Sullivan et al. 2006). Field studies were largely confined to the Adirondack Long Term Monitoring program (ALTM; Driscoll et al. 2003a), Environmental Monitoring and Assessment Program (EMAP; Larson et al. 1994), and Direct Delayed Response Program (DDRP; Church et al. 1989) watersheds. The remote sensing canopy N data provide continuous coverage of the study area within the image extents (Fig. 1).

Bedrock geology, surficial geology, and soil GIS data layers available from the Adirondack Park Agency (APA 2001) reveal several general patterns of geologic and edaphic variation. In most locations, thin Spodosols with fine sandy loam texture have developed from basal till overlaying bedrock geology of Middle Proterozoic-aged granitic gneiss. Most bedrock types have a poor ability to buffer inputs of acidity; however, there are prominent areas of more highly weathered bedrock types where the granitic gneiss is interlayered with metasedimentary rock. Soils are generally thinner at higher elevations. In lowland areas draining directly into the Hudson and St. Lawrence Rivers, sandy soils overlay glacial outwash deposits, and more loamy soils have developed from ablation till. Elevations range from <300 m in river valleys on the periphery of the park to mountain peaks rising to elevations between 900 m and 1500 m. The region is characterized as humid continental with short, cool summers and long, cold winters. Average total annual precipitation within the park ranges from 1560 mm in the southwest to 780 mm in the northeast. Mean July temperature varies from 18° to 21°C. Mean January temperatures range from -11° to -8°C.

From its inception in 1892, the early years of the Adirondack Park's history included a documented mixture of clear-cut and selective-cut logging (McMartin 1994). Selective-cut logging was almost always for spruce, and amounted to ~25% biomass removal from

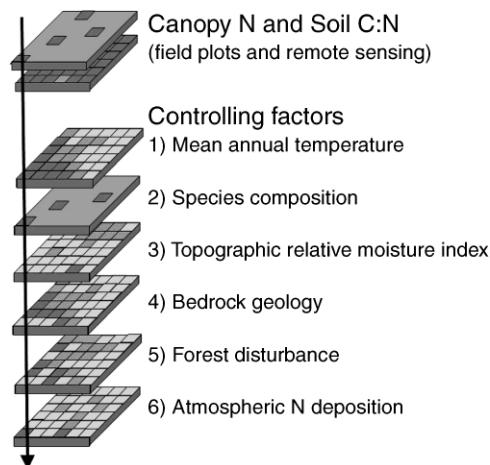


FIG. 2. Schematic of GIS-based research approach for studying the spatial pattern of N cycling.

the Adirondack forest (Pinchot 1898, McMartin 1994, McNeil et al. 2006). Although fire is typically rare in these northern hardwood forests (Bormann and Likens 1979), many large fires were ignited along logging railways and fueled by the slash from logging during several especially droughty years of the early 20th century (McMartin 1994, Jenkins and Keal 2004). The spatial pattern of these logging-related forest disturbances during the late 19th and early 20th centuries is well documented (APA 2001). Subsequent to this period of logging-related forest disturbance, several natural disturbances have occurred, including large windstorms in 1950 and 1995 and an ice storm in 1998 (Millward and Kraft 2004). Varied edaphic, geologic, climatic, and disturbance influences have resulted in a variable mosaic of species composition. The majority of the upland landscape is northern hardwood forest, grading into boreal and subalpine spruce/fir forests above ~760 m elevation (McMartin 1994). Spruce/fir forests are also common in poorly drained lowland areas throughout the park (Jenkins and Keal 2004).

The park's airshed includes the industrialized Ohio Valley and major east coast urban centers, resulting in high rates of atmospheric inorganic N deposition ( $\text{NO}_3^- + \text{NH}_4^+$ ; Driscoll et al. 2003a). The spatial pattern of N deposition generally decreases from southwest to northeast (Ito et al. 2002; National Atmospheric Deposition Program [NADP; NRSP-3] data, NADP Program Office, Champaign, Illinois, USA; Fig. 1), and the magnitude of this gradient is only slightly smaller than the N deposition gradient across the entire northeastern United States (Ollinger et al. 1993).

### *Fieldwork and laboratory analyses*

We conducted all fieldwork during the peak summer growing season of 2003 and found no significant relation between sample date and canopy N or soil C:N (Sullivan et al. 2006, McNeil et al. 2007). In both the canopy N

and soil C:N field surveys, we measured the latitude, longitude, and elevation of each plot centerpoint with a survey-grade global positioning system (GPS) unit ( $\pm 1$  m accuracy). Field protocols included measurements of plot species composition and either canopy N or soil C:N. In plots measured for canopy N, we assessed the area-based relative canopy abundance of each species in the  $30 \times 30$  m plot using a camera-based point-quadrat canopy survey (Smith and Martin 2001). We converted the area-based relative canopy abundance to mass-based canopy abundance using leaf mass per area (LMA) values measured for each species in the nearby White Mountains of New Hampshire by Smith and Martin (2001). In plots measured for soil C:N, we used a metric wedge prism to make genus-level measurements of the relative basal area of species in each plot (Avery and Burkhart 1994).

For measurements of canopy N, we collected leaf material from one to five (typically three) individuals of each species encountered in the canopy survey by shooting down and combining leaves from two to four canopy heights on each tree (Smith and Martin 2001). Each foliage sample was oven-dried at  $60^\circ\text{C}$  in the laboratory for 48 h and ground to pass through a 1-mm mesh screen. Samples were analyzed for foliar N using the carbon, hydrogen, nitrogen (CHN) combustion method, maintaining quality control checks (duplicates, standards, blanks) within 5% error of expected values. Foliar N measurements from individual trees were averaged to obtain a plot-average foliar N value for each species in each plot. As described for all 75 field plots in the Supplement, canopy N was calculated as the weighted mean of species foliar N measurements, determining relative weights for each species in the plot by its mass-based canopy abundance (Smith and Martin 2001).

Soil samples were collected in both the O horizon and upper 10 cm of the mineral B horizon (Sullivan et al. 2006). Soil C:N data in the O and B horizons were positively correlated ( $R^2 = 0.41$ ,  $P < 0.0001$ ,  $n = 176$ ). We use C:N data from the O horizon since they had stronger relationships with environmental variables. Samples were transported in coolers to the laboratory, air dried, sieved (6 mm for O horizon, 2 mm for B horizon), homogenized with a rifle splitter, and oven-dried (O horizon at  $70^\circ\text{C}$ , B horizon at  $105^\circ\text{C}$ ) prior to determination of C and N concentrations with a CHN combustion analyzer.

#### *Remote sensing analysis*

Prior to our 2003 field season, we requested Hyperion (Ungar et al. 2003) hyperspectral remote sensing images to be taken over watersheds targeted for canopy N collections. While image collections during our July and August field collections were unsuccessful due to cloud cover, we obtained two relatively cloud-free images on 9 September and 11 September 2003 and downloaded the

$185 \times 7.5$  km Hyperion images (see Fig. 1 for image extents) as Level 1R radiometrically corrected data.

In preparation for the calibration of image spectral data to our canopy N field data, we performed preprocessing routines to correct for the spectral "smile" and along-track "striping" that result from the push-broom design of the Hyperion instrument (Datt et al. 2003, Goodenough et al. 2003). We then did atmospheric correction (Atmospheric CORrection Now, Version 5, Mode 1.5 pb, Analytical Imaging and Geophysics, Boulder, Colorado, USA), image geometric correction (root mean square error [RMSE]  $< 10$  m relative to New York State Digital Orthophoto Program images; *available online*),<sup>7</sup> cloud masking, and band subsetting to obtain 113 usable bands of image reflectance data (McNeil 2006). We extracted reflectance spectra from the 28 pixels containing the spatial coordinates of the plot centerpoints that were within image extents and not masked by clouds. We note that previous studies have either spectrally smoothed (e.g., via derivative transformation) or spatially smoothed (e.g., by averaging spectra in a  $2 \times 2$  pixel window) extracted image data (e.g., Townsend et al. 2003). However, we chose to retain the empirical advantage afforded by original unsmoothed reflectance data extracted from a single pixel. We correlated the 28 canopy N measurements and the corresponding 113 bands of reflectance data using a four-factor partial least squares (PLS) regression model ( $R^2 = 0.93$ ,  $P < 0.0001$ , root mean square error of prediction [RMSEP] =  $0.28\%$  N; McNeil 2006). After applying the PLS calibration equation to all nonclouded, forested pixels in the image, we created our remotely sensed canopy N data set by extracting a random sample of 1836 pixel locations, representing 15% of the nonspatially autocorrelated pixels within the entire canopy N map (McNeil 2006).

#### *Independent variables*

We used field and GIS data to measure the spatial distribution of six of the major spatial controls on N cycling (Aber et al. 2003): (1) mean annual temperature, (2) forest species composition, (3) topographic relative moisture availability, (4) surficial and bedrock geology, (5) forest disturbance history, and (6) atmospheric N deposition (Fig. 2; data in Supplement). In addition to examining metadata accuracy statements of each GIS data layer (APA 2001), we assessed spatial data quality (e.g., positional and attribute accuracy; Guptill and Morrison 1995) of all input and derived GIS layers by visually comparing descriptions of sample locations against our field notes and independent data layers (e.g., USGS Digital Raster Graphics; USGS 1998).

We used a multiple regression model and the GPS or image coordinates to estimate mean annual temperature (Ito et al. 2002) at each sample location.

<sup>7</sup> ([www.nysgis.state.ny.us](http://www.nysgis.state.ny.us))

We measured species composition for all field plots. The species abundance information from the canopy N field plots enabled us to classify species composition at the species alliance level of the National Vegetation Classification System (FGDC 1997). For pixels sampled within the remotely sensed canopy N map, we classified forest type using the 1992 USGS National Land Cover Data set (NLCD; Vogelmann et al. 2001), lumping the class of “woody wetlands” into coniferous forest since there was no significant difference in canopy N between these two classes in our field sample.

We used the Topographic Relative Moisture Index (TRMI; Parker 1982) to describe the purely topographic variation that occurs independently of the coincident precipitation and N deposition gradient in our study area (Fig. 1). We calculated the TRMI from mosaicked and sink-filled USGS quadrangle digital elevation model data, using ArcGIS GRID (Environmental Systems Research Institute [ESRI], Version 9.0, Redlands California, USA) to derive the four data layers (i.e., slope aspect, slope configuration, relative slope position, and slope steepness) used to assign a TRMI value to each pixel, with zero representing the most xeric sites and 60 representing the most mesic (Parker 1982, Wilds 1996, McNeil 2006).

We evaluated the effects of bedrock and surficial geology using GIS layers from the Adirondack Park Agency (APA 2001). These data layers contain information on the bedrock type, surficial rock type, and a four-category classification of the acid sensitivity of each bedrock type (APA 2001). For statistical analyses, we treated the surficial and bedrock layers as categorical data, and the acid sensitivity classes as four-category ordinal data.

Using a digitized map of historic disturbance prior to 1916 (APA 2001), historic accounts (McMartin 1994), and GIS models describing the spread of logging into the region (McNeil et al. 2006), we developed an ordinal index for testing the hypothesis that canopy N values would decrease and soil C:N values would increase with increasing severity of forest disturbance prior to 1916 (Goodale and Aber 2001, Latty et al. 2004). This index classifies each sample location into one of four categories, ordered from least to most severe disturbance history: (1) old growth, (2) selectively cut, (3) clear-cut, and (4) clear-cut and burned. We also evaluated a more coarse classification made by grouping categories 1 and 2 into a class called *moderately disturbed* and categories 3 and 4 into a class called *severely disturbed*. According to APA GIS data (APA 2001) and historical information (Jenkins and Keal 2004), many of our sample locations were affected by a 1950 blowdown and salvage logging event. We statistically treated this catastrophic wind and forest harvest event (Cooper-Ellis et al. 1999) as an ordinal three-category variable: severe (50–100% of canopy loss), moderate (25–50% of canopy loss), and undisturbed. Our study sites were largely unaffected by more recent natural disturbances of a 1995 blowdown

TABLE 1. Variability in measures of N cycling explained by spatial controls.

Spatial control	Data	Field canopy N	Image canopy N	Soil C:N
Forest type	c	0.77	0.29	0.35
Temperature	s	ns	0.02	ns
N deposition	s	ns	0.003	ns
Pre-1916 logging and fire	c	ns	0.007	ns
1950 blowdown and salvage cut	c	ns	0.008	ns
Topographic moisture availability (TRMI)	s	0.19	0.08	ns
Bedrock geology	c	ns	0.08	ns

Notes: Values are  $R^2$  results obtained from ANOVA for categorical (c) data or regression for scalar (s) data. Results not significant at  $P < 0.05$  are labeled “ns.” All other values are significant at  $P < 0.001$ .

and a 1998 ice storm (APA 2001, Millward and Kraft 2004; also see Supplement).

Finally, we used a multiple regression model (Ito et al. 2002, McNeil et al. 2007) and the GPS or image coordinates to estimate the total inorganic N in wet deposition at all sample locations. This N deposition model does not assess the spatial pattern of N inputs from dry, fog, or cloudwater forms of atmospheric N deposition (McNeil et al. 2007). While this limitation likely has little effect on the regional spatial pattern of total N deposition, it may cause underpredictions for coniferous forests and at high elevations where dry and cloud forms of deposition are likely to make up a larger component of the total N deposition (Weathers et al. 2006).

#### Statistical methods

We used univariate regression for continuous independent variables and ANOVA for ordinal or categorical independent variables as means to identify the amount of variation in canopy N or soil C:N that could be explained by each spatial control. Given the known differences in the dynamics of N cycling among forests of different species composition (Lovett and Rueth 1999, Ollinger et al. 2002, Lovett et al. 2004), we considered that relationships between spatial controls and N cycling may differ among particular forest types or species alliances. Accordingly, we stratified all three data sets by forest type and the field canopy N data set by species alliance, and we repeated all analyses. Only two alliances, spruce/fir ( $n = 13$  plots) and sugar maple/yellow birch/American beech ( $n = 24$  plots), had sufficient sample size and distribution across the environmental gradients in the Adirondack Park to merit analysis. Finally, we used stepwise multiple regression to identify the combined explained variation of independent variables and to identify interactive effects between multiple variables (e.g., forest type, N deposition, TRMI). We performed all statistical analyses using the JMP-IN software package (SAS Institute, Version 5.1, Cary, North Carolina, USA).

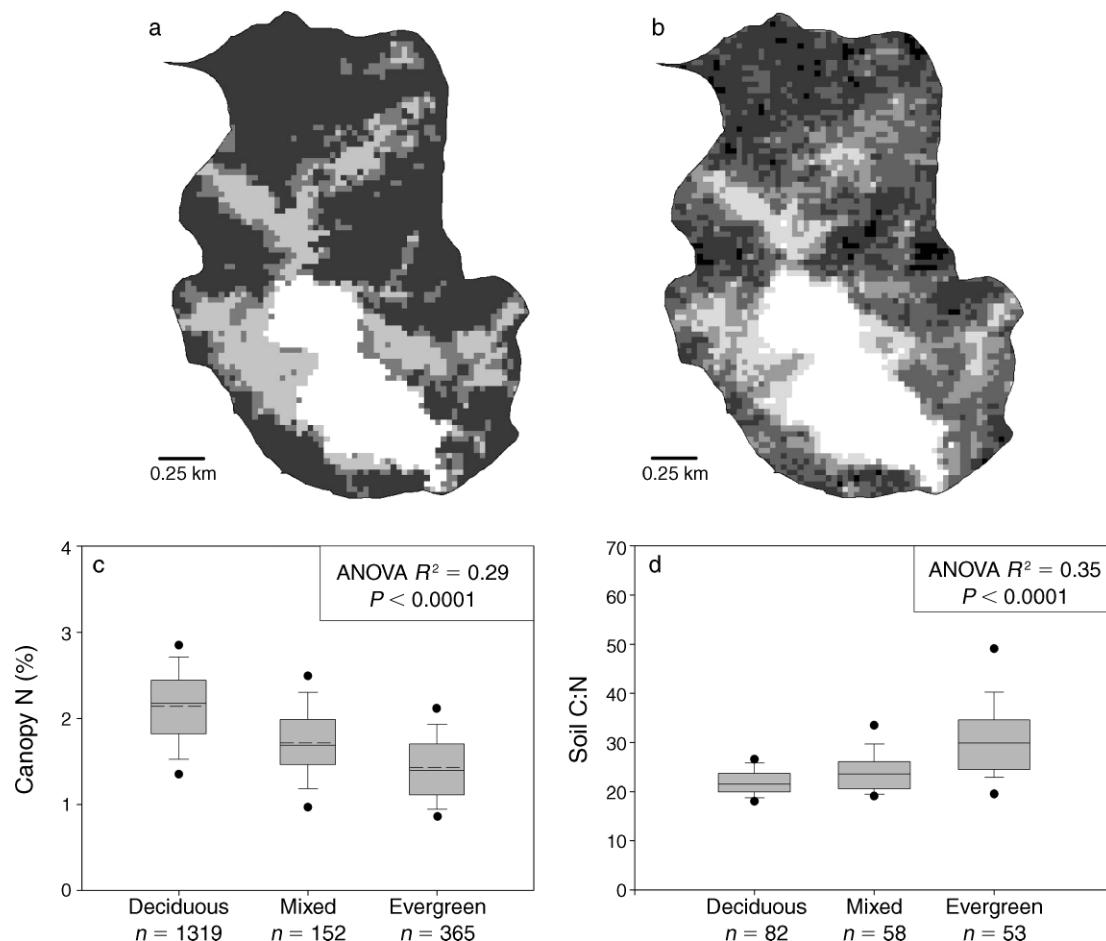


FIG. 3. Relationships between forest type and N cycling in the Arbutus Lake watershed (see Fig. 1 for location). As shown cartographically in panels (a) and (b), and graphically in panels (c) and (d), deciduous forests [dark shades in panel (a)] have higher canopy N [dark shades in panel (b)] and lower soil C:N. Boxes in (c) and (d) describe the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and points the 5th and 95th percentiles. The solid line within each box is the median; the dashed line is the mean.

## RESULTS

**Overview.**—Of the environmental variables considered, only forest type explained more than one-fourth of the variability in canopy N or soil C:N (Table 1). Forest type was particularly effective for explaining variability in field measurements of canopy N (77% of variability explained). About one-third of the variability was explained by the forest type for both remotely sensed canopy N and soil C:N. TRMI was also an important predictor of field canopy N (19% of variation explained; Table 1). Other environmental variables considered were weakly associated with remote sensed estimates of canopy N (Table 1).

Interpretation of these results should consider the different sample sizes, statistical distributions, and sample design of the three dependent variables (i.e., soil C:N, field canopy N, remotely sensed canopy N). The field canopy N data set was drawn from the statistical population of Adirondack forest ecosystems following a

stratified random design and exhibited a bimodal distribution of canopy N (McNeil 2006). In contrast, the remote sensing data set was drawn using a purely random design within the image extents and had a normal distribution of canopy N data (McNeil 2006). We note that these two datasets are not completely independent, as 28 of the 75 field plots were used to calibrate the remote sensing data. Here we focus our analysis primarily on the remotely sensed canopy N data set because of its larger sample size and normal distribution. Nevertheless, results were qualitatively similar between the field and remotely sensed canopy N data sets.

**Forest type.**—The spatial pattern of N cycling was strongly related to forest type (Fig. 3), which explained 29% of the spatial variability of canopy N in the remote sensing data set and 35% of the spatial variability in O horizon soil C:N (Fig. 3c, d, Table 1). It is noteworthy that forest type explained substantially more of the variability in canopy N within the field data set

(ANOVA,  $R^2 = 0.77$ ,  $P < 0.0001$ ) than in the remote sensing data set. The discrepancy in the amount of explained variance is likely to be largely related to differences in sample size and statistical distributions, but also may have been affected by inaccuracies introduced by the remote sensing algorithms used in classifying forest type (Vogelmann et al. 1998, Zhu et al. 2000). Inclusion of a finer level of forest type classification, based on 12 species alliances rather than three forest types, had only a marginal improvement (i.e., 5% of variance) in explaining the spatial variation in the field canopy N data set. Moreover, alliances within the same forest type did not differ significantly in their mean canopy N.

*Climate and N deposition.*—Precipitation, temperature, and N deposition covary along the latitudinal, longitudinal, and elevational gradients in the Adirondack Park, but N deposition overwhelms climatic variation in its effect along the latitude and longitude gradients, and N deposition and temperature likely interact to affect N cycling along the elevational gradient (McNeil 2006, McNeil et al. 2007). Remotely sensed canopy N and soil C:N exhibited the expected relationships with N deposition (i.e., positive with canopy N, negative with soil C:N), but they were very weak (Table 1). Furthermore, N deposition was positively related to O horizon total soil N across the 193 soil sample locations ( $R^2 = 0.13$ ,  $P < 0.0001$ ), a finding that was consistent within deciduous ( $R^2 = 0.11$ ,  $P = 0.002$ ) and coniferous ( $R^2 = 0.16$ ,  $P = 0.003$ ) forest types. The mixed forest type showed a nonsignificant positive trend.

*Moisture availability.*—We found significant relationships between canopy N and TRMI, such that canopy N was higher in drier locations with a low TRMI (Table 1). This result appears to support the hypothesis that canopy trees may increase foliar N as a compensation for a lack of soil moisture availability (van den Driessche 1974, Vitousek et al. 1992, Wright et al. 2001, 2003), but multiple regression analyses suggested the presence of collinearity among forest type and TRMI.

*Multiple regression analyses.*—Forest type was the first variable selected in the stepwise multiple regressions for both canopy N and soil C:N dependent variables. For the analysis of the remotely sensed canopy N data set, TRMI was the only variable that satisfied our specified model entrance requirements (effect significant at  $P < 0.05$ ; contribute  $>3\%$  of explained variance), and contributed an additional 5% of explained variance (adjusted  $R^2 = 0.34$ ). However, neither TRMI nor any other variable was selected in the analysis of the field canopy N and soil C:N data sets.

*Analyses stratified by species alliance.*—We observed a significant relationship between canopy N and N deposition within plots sampled within the spruce/fir species alliance (Fig. 4), but not the sugar maple/yellow birch/American beech alliance. This result adds canopy

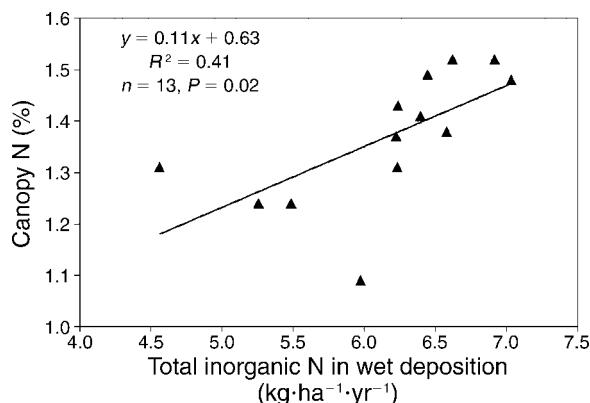


FIG. 4. Relationship between canopy N and N deposition for field plots sampled within a spruce-fir species alliance.

N evidence to previous findings that rates of N cycling within spruce/fir forests increase along the regional gradient of N deposition in the northeastern United States (McNulty et al. 1991).

## DISCUSSION

### *Species functional traits and the spatial pattern of N cycling*

Consideration of our results left us with several important questions. Why is forest type the dominant control on the spatial pattern of N cycling (Fig. 3)? Why was the spruce/fir species alliance the only forest type where we observed a strong N cycling response to the gradient of N deposition (Fig. 4)? Spruce/fir forests are unique among Adirondack forest types because their canopy biomass is almost exclusively dominated by two species that do not differ greatly in foliar N (Fig. 5). Thus we suspected that these unique results obtained within the spruce/fir association (Fig. 4) could be indicative of a broader connection between the foliar N of tree species and the spatial pattern of N cycling.

As has been observed worldwide (Wright et al. 2004), the mean foliar N of each major canopy species in our study was very closely related to its leaf mass per area (LMA;  $R^2 = 0.95$ ,  $P < 0.0001$ ; Fig. 5 inset). Whereas the statistical strength of the relationship between LMA and foliar N (Fig. 5 inset) is partly due to the separation of broadleaf deciduous and needleleaf evergreen functional groups along the  $x$ -axis (LMA), the relationship is similar for the wide variation in mean LMA and mean foliar N within the needleleaf evergreen functional group (Fig. 5 inset). These functional trait relationships are driven by powerful evolutionary forces that shape the functional trait strategies of plant species (Reich et al. 1990). In turn, the proportional canopy abundance of these evolved species differences in functional traits can directly affect the N cycle (Hobbie 1992, Finzi et al. 1998, Lovett et al. 2004, Townsend et al. 2007) by creating a positive feedback whereby the functional traits of a species modify the localized cycling of N

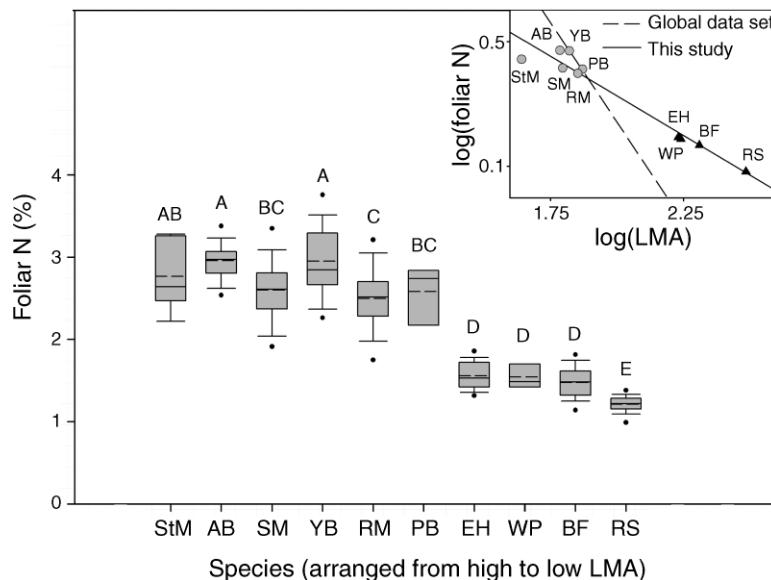


FIG. 5. Interspecific variation in foliar N is related to leaf mass per area (LMA). Species are listed in order of declining mean LMA (as measured by Smith and Martin [2001]) and are abbreviated as: StM (striped maple, *Acer pensylvanicum*,  $n = 10$  plots), AB (American beech, *Fagus grandifolia*,  $n = 52$  plots), SM (sugar maple, *Acer saccharum*,  $n = 37$  plots), YB (yellow birch, *Betula alleghaniensis*,  $n = 34$  plots), RM (red maple, *Acer rubrum*,  $n = 30$  plots), PB (paper birch, *Betula papyrifera*,  $n = 7$  plots), EH (eastern hemlock, *Tsuga canadensis*,  $n = 25$  plots), WP (white pine, *Pinus strobus*,  $n = 7$  plots), BF (balsam fir, *Abies balsamea*,  $n = 24$  plots), and RS (red spruce, *Picea rubens*,  $n = 42$  plots). Box plots are as in Fig. 3. Different letters above each box denote statistically different means ( $P < 0.05$ ). The inset shows the standardized major axis regression between the log mean foliar N and log mean LMA of the 10 species, as compared with a similar analysis on a global data set compiled by Wright et al. (2004).

toward the evolutionary benefit of the species (Grime 2001, Daufresne and Hedin 2005, Chapman et al. 2006). In particular, the litter input of canopy N is perhaps the most important factor controlling rates of decomposition, and therefore N availability (Melillo et al. 1982, Lovett et al. 2004, Chapman et al. 2006, Parton et al. 2007). Thus, consideration of the mean foliar N of each species as an evolved functional trait (see e.g., Reich et al. 2003, Garnier et al. 2004, Mouillot et al. 2005, McGill et al. 2006) that affects the plant–soil cycling of N provides a solid theoretical basis for separating two independent components of variability in N cycling: (1) *interspecific variability*, or the variability in N cycling caused by the proportional abundance of species functional traits in the canopy biomass; and (2) *intraspecific variability*, or the variability in N cycling caused by each species responding to environmental stimuli by adjusting its resource investments (e.g., foliar N) about its evolved functional traits (e.g., mean foliar N).

#### *Interspecific variability in N cycling*

We isolated the interspecific component of variability in N cycling by recalculating canopy N at each field plot based on the relative canopy abundance (see Supplement for data) and mean foliar N (Fig. 5) of each species. We labeled the result of this recalculation the species-mean canopy N. A regression of the species-mean canopy N against the field-measured canopy N

revealed that 93% of the variation in field-measured canopy N could be attributed to the interspecific component of variability in canopy N (Fig. 6a). We noted that the calculation of species-mean canopy N ( $x$ -axis of Fig. 6a) is not independent of the field-measured values ( $y$ -axis), since the mean of each species is developed from the same field data. However, when we calculated species-mean canopy N values from any random half of the data set and applied these independent means to the calculation of species-mean canopy N on the other half of the data set, the regression against field-observed values was virtually identical (i.e.,  $R^2$ , slope, intercept) to the one shown in Fig. 6a.

The relationship of soil C:N and species-mean canopy N (Fig. 7a;  $R^2 = 0.37$ ) provides additional and independent support for the hypothesis that the spatial pattern in N cycling in forests of the Adirondack Park is largely controlled by the proportional abundance of species functional traits. Relative to the finding of Ollinger et al. (2002) that canopy N could explain 65% of the variability in soil C:N within the forests of New Hampshire's White Mountains, the relationship between species-mean canopy N and soil C:N (Fig. 7a) is surprisingly strong. First, the finding of Ollinger et al. (2002) was based on canopy N and soil C:N field measurements taken at the same sample locations, whereas we compared soil C:N measurements with predictions of canopy N made using species means developed from different plot locations. Second, species

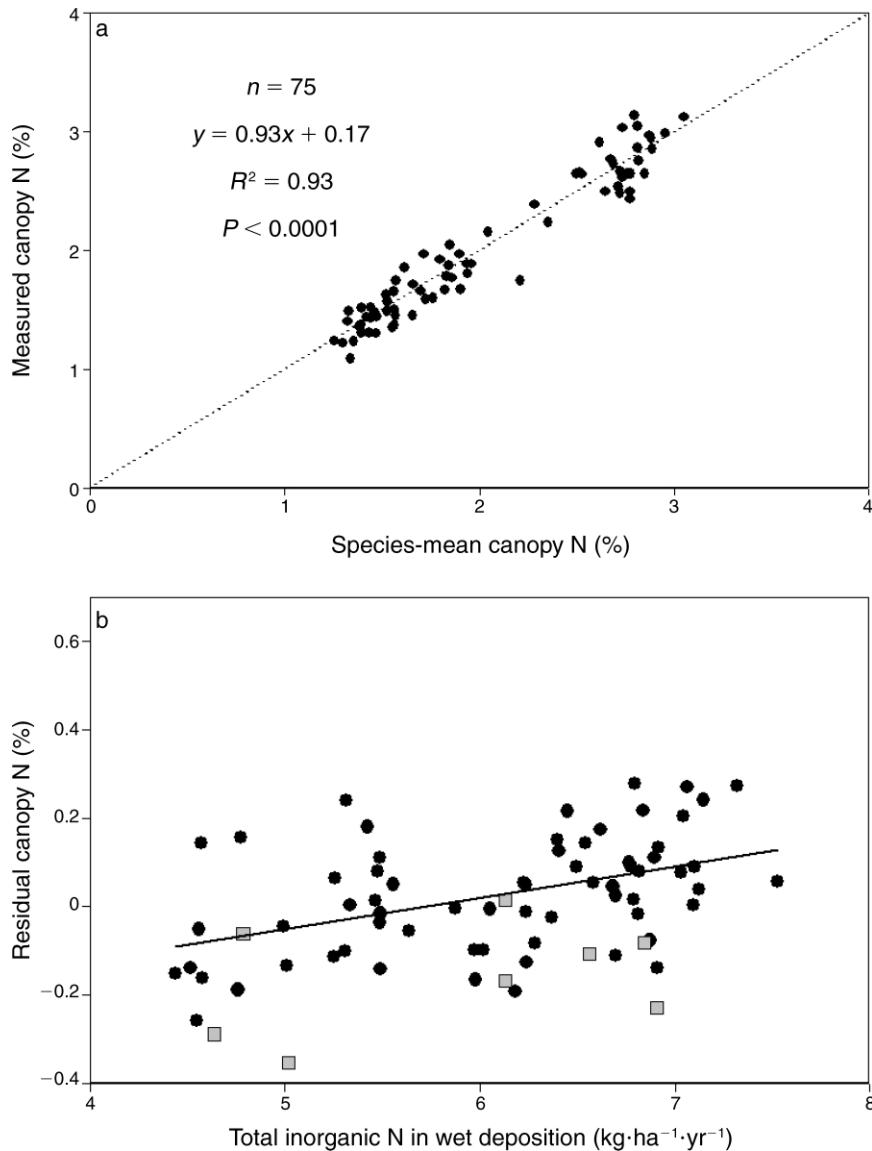


FIG. 6. (a) Interspecific and (b) intraspecific components of spatial variability in field-measured canopy N. Panel (a) shows that the combination of species-specific mean foliar N values and species relative abundance ( $x$ -axis; see Fig. 5 and Supplement for data) accounts for 93% of spatial variability in field-measured canopy N. Panel (b) visualizes an analysis of the residuals from (a) against independent variables of N deposition and historic disturbance. Together these variables account for 40% of the residual variation, or an additional 2.8% of total spatial variability in field-measured canopy N. For (b) the univariate regression with N deposition,  $R^2 = 0.22$  ( $P < 0.0001$ ). For the ANOVA among severely disturbed plots (gray squares) and moderately disturbed plots (black circles),  $R^2 = 0.25$  ( $P < 0.0001$ ).

were only identified in the field to the genus level for plots in the soil C:N survey, introducing noise into the determination of species-mean canopy N. Despite these sources of noise, these data provide independent support for the important role played by species functional traits in structuring the spatial pattern of N cycling in the Adirondack Park. More generally, the regressions in Figs. 6a and 7a add to a growing body of literature identifying the important interrelationships of species functional traits (e.g., foliar N, LMA) and the spatial heterogeneity of ecosystem processes (Reich et al. 2003,

Garnier et al. 2004, Dijkstra et al. 2006, McGill et al. 2006, Shipley et al. 2006).

#### *Intraspecific variability in N cycling*

We isolated the intraspecific component of variability in N cycling by regressing the residuals from the interspecific analyses (Figs. 6a and 7a) against the six independent variables used in our analysis (Fig. 2). Results from this analysis indicate the average foliar N response of individual species to spatial variability in environmental variables. We emphasize that this is an

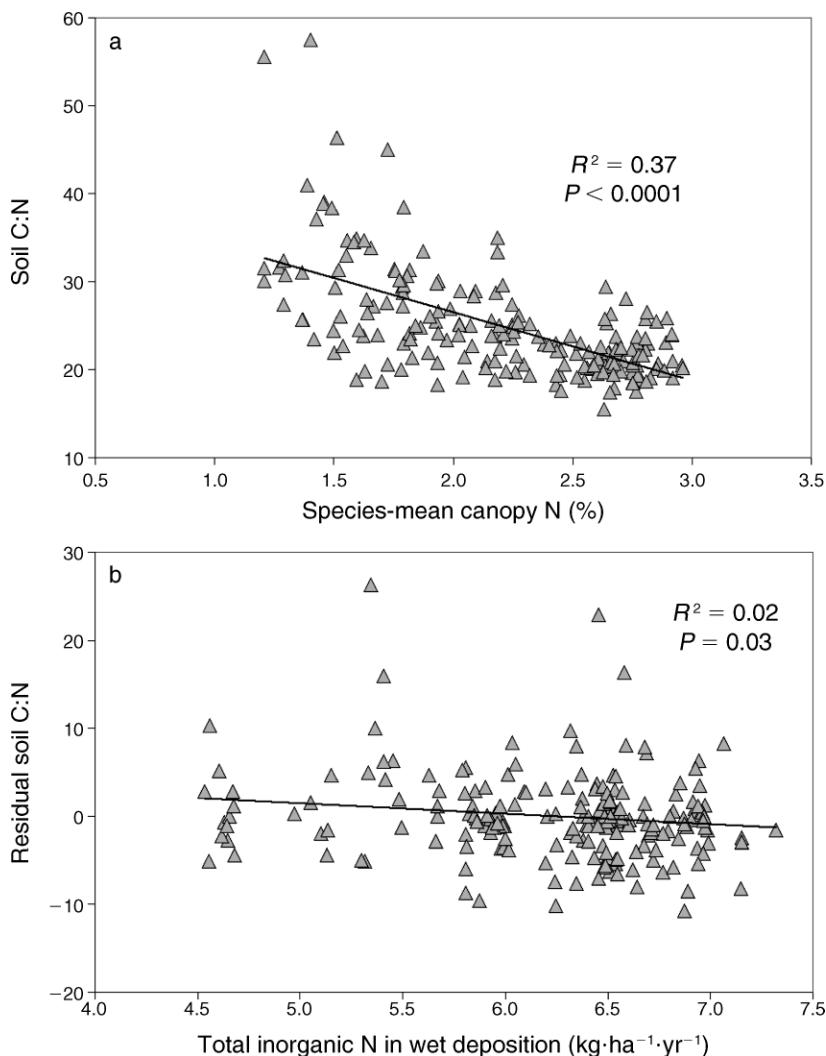


FIG. 7. Inter- and intraspecific components of spatial variability in organic horizon soil C:N. Similar to the analysis in Fig. 6, panel (a) shows that the combination of species-specific mean foliar N values and species relative abundance ( $x$ -axis) accounts for 37% of the spatial variability in organic horizon soil C:N. Panel (b) visualizes an analysis of the residuals from (a) against the independent variable of N deposition, revealing that N deposition accounts for an additional 2% of the spatial variability in organic horizon soil C:N.

average response, because the magnitude of foliar N response to N deposition and other environmental gradients can vary widely among species with different functional traits (McNeil 2006, McNeil et al. 2007). Nevertheless our data indicate that, on average, forest tree species in the Adirondack Park adjust their foliar N in response to the two anthropogenic factors, N deposition and historic forest disturbance (Fig. 6b). It is notable that a relationship with soil moisture availability, as measured by the Topographic Relative Moisture Index (TRMI), was *not* detected within this residual analysis. This result suggests that the explained variation attributed to moisture availability within our original analysis (Table 1) was subsumed within the interspecific variation caused by the distribution of species abundances along environmental gradients of

soil moisture availability (Canham et al. 2006). The responses to N deposition and historic forest disturbance exhibited the expected patterns. Foliar N was higher (i.e., positive residuals in canopy N) in locations that receive higher N deposition ( $R^2 = 0.22$ ,  $P < 0.0001$ ; Fig. 6b). Locations that were severely disturbed (i.e., clear-cut or clear-cut and burned) had significantly lower foliar N (i.e., negative residuals in canopy N) than those locations with that were moderately disturbed (i.e., selective-cut or old growth; ANOVA,  $R^2 = 0.26$ ,  $P < 0.0001$ ; Fig. 6b). Multiple regression results suggested that the anthropogenic gradients of N deposition and disturbance together explained 40% of the residual variance, or 2.8% of the spatial variation in the field-measured canopy N data set. The standardized beta coefficients for N deposition and the 1916-era logging-

related disturbance events were roughly equivalent ( $-0.39$  and  $-0.43$ , respectively), suggesting that N deposition and 1916-era logging-related disturbance each account for about 1.4% of the spatial variability in canopy N.

Our data also indicate that the foliar N response to N deposition is aligned with the intraspecific response of soil C:N ratios to N deposition (Fig. 7b). The residuals about the relationship of soil C:N to species-mean canopy N (i.e., residuals from Fig. 7a) indicate the expected response (Aber et al. 2003) of lower soil C:N in areas of higher N deposition (Fig. 7b). This response ( $R^2 = 0.02$ ; Fig. 7b) was not as strong as that observed in the canopy N data set ( $R^2 = 0.22$ ; Fig. 6b). This may have been due in part to imprecision in determining the species-mean canopy N for the soil C:N plot locations and in part to other factors (e.g., soil disturbance) that disrupt direct correlation among canopy and soil-based indicators of N cycling (Ollinger et al. 2002, Aber et al. 2003).

The observed effects of N deposition and historic disturbance have important implications for the N dynamics of Adirondack forests. First, the finding that N deposition has significant effects that are visible in canopy N (Fig. 6b) and soil C:N (Fig. 7b) adds important support to other assessments that concluded that N deposition is altering the N status of forests in the region (Aber et al. 2003, Ito et al. 2005, McNeil et al. 2007). In addition, the observation that historic disturbances have left a nutrient cycling legacy visible in these plot-scale data adds to the mounting body of literature documenting the lasting effects of human actions upon the N cycle of forested ecosystems in the northeastern United States (e.g., Goodale and Aber 2001, Foster and Aber 2004, Latty et al. 2004).

#### *Prospects for remotely sensed maps of canopy N*

This research demonstrates that as much as 95.8% of the spatial variability in canopy N (Fig. 6) and 39% of the variability in soil C:N (Fig. 7) can be directly attributed to measured variability within the physical environment. Moreover, our analyses suggest that the spatial pattern of N cycling in the Adirondack Park is primarily structured by the proportional abundance of species functional traits in the canopy biomass, and secondarily influenced by anthropogenic environmental gradients of N deposition and historic disturbance. These conclusions highlight a valuable new application of remotely sensed maps of canopy N. In particular, these maps present an exciting opportunity to identify the controls on N cycling and net primary production (NPP) by relating the spatial pattern of canopy N to underlying environmental gradients. The possibility to extend this opportunity to other forested environments is considerable. Hyperspectral imagery is increasingly available to ecologists via commercial instruments and through existing (i.e., Hyperion [Ungar et al. 2003]) and AVIRIS [Green et al. 1998]) and planned National

Aeronautics and Space Administration (NASA) missions. Moreover, one recent study presented a generalized algorithm that enables researchers to forgo field calibration and directly map canopy N from AVIRIS and Hyperion imagery collected over tropical, temperate, and boreal forest environments (M. E. Martin, L. Plourde, S. Ollinger, M.-L. Smith, and B. E. McNeil, *unpublished manuscript*).

Future research along several fronts will help enhance the use of remotely sensed maps of canopy N as tools to help identify the controls on N cycling and NPP in forest ecosystems. First, our data indicate that remote sensing-based studies seeking to identify ecosystem responses from canopy N may require a much more stringent level of accuracy in the detection of canopy N than the oft-cited (e.g., Coops et al. 2003, Smith et al. 2003, Townsend et al. 2003) level of  $<0.5\%$  N (Schimel 1995). While the exact level of accuracy will depend on the specific response to be detected, and the forest system in question (e.g., a forest dominated by a single functional type may have less confounding interspecific variability), our field-based measurements suggest that detecting ecosystem responses to N deposition in the Adirondack Park would require a root mean square error (RMSE) level of accuracy of  $<0.16\%$  N (RMSE of regression in Fig. 6a).

Second, since the proportional abundance of species functional traits in the canopy biomass appears to be a primary control on the spatial pattern canopy N, our study suggests that harnessing the information content latent within remotely sensed maps of canopy N may require concomitant advances in the ability to measure the proportional abundances of species functional traits within image pixels (see e.g., Plourde et al. 2007). Such remotely sensed maps of species abundance or functional trait abundance will not only enable proper assessment of the interspecific component of spatial variability in N cycling, but will also enable examination of the foliar N responses to environmental gradients. This last point is especially important given our previous findings suggesting that functional traits also control the degree to which foliar N of species will increase or decrease in response to environmental stimuli (McNeil 2006, McNeil et al. 2007).

Finally, and perhaps most important, robust use of remotely sensed maps of canopy N as a repeatable measure of spatial and temporal variability in ecosystem N cycling will require an enhanced understanding of its ecotypic and temporal variability. We minimized both these sources of variability within our study by sampling within a single growing season and within a well-defined physiographic region. Yet we have substantial reasons to believe that temporal variability is particularly important to consider. In addition to previous studies documenting large interannual variability in foliar N (e.g., Magill et al. 2000), our measurements of canopy N in 2003 were as much as 20% higher than subsequent remeasurements at several field plots in 2004 (B. E.

McNeil, unpublished data). Future research addressing these poorly understood forms of variation in canopy N will further enhance the vast ecological information that may now be garnered from remotely sensed maps of canopy N.

## ACKNOWLEDGMENTS

We appreciate the field, laboratory, and logistical support of many individuals, including Craig Mackowiak, Mario Monteseoeca, Don Bickelhaupt, Marlene Hall and her staff at the SU Department of Public Safety, Karen Roy and her staff at the Adirondack Lakes Survey Corporation, the office staff and rangers of the New York State Department Environmental Conservation Region Five, the staff at the SUNY ESF Adirondack Ecological Center, members of the Adirondack Park Agency GIS office, and the many private landowners who allowed us to collect samples on their land. We thank Lucie Plourde, Mary Martin, and Marie-Louise Smith for their kind assistance with the remote sensing component of this research. We also appreciate the thoughtful comments of two anonymous reviewers. This study was funded through a generous grant from the W. M. Keck Foundation and through the Environmental Monitoring, Evaluation, and Protection (EMEP) Program of the New York State Energy Research and Development Authority.

## LITERATURE CITED

- Aber, J. D., C. L. Goodale, S. V. Ollinger, M. L. Smith, A. H. Magill, M. E. Martin, R. A. Hallett, and J. L. Stoddard. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *BioScience* 53:375–389.
- Aber, J. D., W. H. McDowell, K. J. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. G. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience* 48:921–934.
- Aerts, R., and F. S. I. Chapin. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30:1–55.
- APA ([New York State] Adirondack Park Agency). 2001. Shared Adirondack Park geographic information CD-ROM. New York State Adirondack Park Agency GIS Office, Ray Brook, New York, USA.
- Austin, A. T., and P. M. Vitousek. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia* 113:519–529.
- Avery, T. E., and H. E. Burkhart. 1994. Inventories with point samples. Page 237 in *Forest measurements*. McGraw-Hill, New York, USA.
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York, New York, USA.
- Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecological Applications* 16:540–554.
- Carlton, G. C., and F. A. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79:1305–1319.
- Chapman, S. K., J. A. Langley, S. C. Hart, and G. W. Koch. 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist* 169:27–34.
- Church, M. R., et al. 1989. Future effects of long-term sulfur deposition on surface water chemistry in the Northeast and Southern Blue Ridge Province: results of the DDRP. EPA/600/3-89/061. United States Environmental Protection Agency, Corvallis, Oregon, USA.
- Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* 80:2683–2696.
- Coops, N., M. L. Smith, M. E. Martin, and S. V. Ollinger. 2003. Prediction of eucalypt foliage nitrogen content from satellite derived hyperspectral data. *IEEE Transactions Geoscience and Remote Sensing* 41:1338–1346.
- Datt, B., T. R. McVicar, T. G. Van Niel, D. L. B. Jupp, and J. S. Pearlman. 2003. Preprocessing EO-1 Hyperion hyperspectral data to support the application of agricultural indexes. *IEEE Transactions on Geosciences and Remote Sensing* 41:1246–1259.
- Daufresne, T., and L. O. Hedin. 2005. Plant coexistence depends on ecosystem nutrient cycles: extension of the resource-ratio theory. *Proceedings of the National Academy of Sciences (USA)* 102:9212–9217.
- Dijkstra, F. A., S. E. Hobbie, and P. B. Reich. 2006. Soil processes affected by sixteen grassland species grown under different environmental conditions. *Soil Science Society of America Journal* 70:770–777.
- Driscoll, C. T., K. M. Driscoll, K. M. Roy, and M. J. Mitchell. 2003a. Response of Adirondack ecosystems to declines in atmospheric deposition. *Environmental Science and Technology* 37:2036–2042.
- Driscoll, C. T., D. Whitall, J. D. Aber, E. W. Boyer, M. Castro, C. Cronan, C. L. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, and S. V. Ollinger. 2003b. Nitrogen pollution in the northeastern United States: sources, effects, and management options. *BioScience* 53:357–374.
- FGDC (Federal Geographic Data Committee). 1997. Vegetation classification standard. Standard FGDC-STD-005. Federal Geographic Data Committee, Vegetation Subcommittee, Reston, Virginia, USA.
- Fenn, M. E., M. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemeyer. 1998. Nitrogen excess in North American ecosystems: a review of predisposing factors, geographic extent, ecosystem responses and management strategies. *Ecological Applications* 8:706–733.
- Finzi, A. C., N. V. Breemen, and C. D. Canham. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* 8:440–446.
- Foster, D. R., and J. D. Aber. 2004. *Forests in time*. Yale University Press, New Haven, Connecticut, USA.
- Galloway, J. N. 1998. The global nitrogen cycle: changes and consequences. *Environmental Pollution* 102:15–24.
- Garnier, E., J. Cortez, G. Billes, M.-L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubrey, A. Bellmann, C. Neill, and J.-P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637.
- Goodale, C. L., and J. D. Aber. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* 11:253–267.
- Goodale, C. L., et al. 2002. Forest carbon sinks in the Northern Hemisphere. *Ecological Applications* 12:891–899.
- Goodenough, D. G., A. Dyk, K. O. Niemann, J. S. Pearlman, H. Chen, T. Han, M. Murdoch, and C. West. 2003. Processing Hyperion and ALI for forest classification. *IEEE Transactions on Geosciences and Remote Sensing* 41:1321–1331.
- Green, R. O., M. L. Eastwood, C. M. Sarture, T. G. Chrien, M. Aronsson, B. J. Chippendale, J. A. Faust, B. E. Pavri, C. J. Chovit, M. Solis, M. R. Olah, and O. Williams. 1998. Imaging spectrometry and the airborne visible infrared imaging spectrometer (AVIRIS). *Remote Sensing of Environment* 65:227–248.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Second edition. John Wiley and Sons, Chichester, UK.
- Groffman, P., J. Tiedje, D. Mokma, and S. Simkins. 1992. Regional scale analysis of denitrification in north temperate forest soils. *Landscape Ecology* 7:45–53.

- Gunderson, P., B. A. Emmet, O. J. Kjonas, C. J. Koopmans, and A. Tietema. 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. *Forest Ecology and Management* 101:37–55.
- Guptill, S. C., and J. L. Morrison, editors. 1995. *Elements of spatial data quality*. Elsevier Science, Oxford, UK.
- Han, W., J. Fang, D. Guo, and Y. Zhang. 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist* 168:377–385.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7:336–339.
- Ito, M., M. J. Mitchell, and C. T. Driscoll. 2002. Spatial patterns of precipitation quantity and chemistry and air temperature in the Adirondack region of New York. *Atmospheric Environment* 36:1051–1062.
- Ito, M., M. J. Mitchell, C. T. Driscoll, and K. M. Roy. 2005. Nitrogen input–output budgets for lake-containing watersheds in the Adirondack region of New York. *Biogeochemistry* 72:283–314.
- Jenkins, J., and A. Keal. 2004. *The Adirondack atlas*. Syracuse University Press, Syracuse, New York, USA.
- Körner, C. 1999. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer, Berlin, Germany.
- Larson, D. P., K. W. Thornton, N. S. Urquhart, and S. G. Paulson. 1994. The role of sample surveys for monitoring the condition of the nation's lakes. *Environmental Monitoring and Assessment* 32:101–143.
- Latty, E. F., C. D. Canham, and P. L. Marks. 2004. The effects of land-use history on soil properties and nutrient dynamics in northern hardwood forests of the Adirondack Mountains. *Ecosystems* 7:193–207.
- Lovett, G. M., and H. Rueth. 1999. Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient. *Ecological Applications* 9:1330–1334.
- Lovett, G. M., K. C. Weathers, M. A. Arthur, and J. C. Schultz. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* 67:289–308.
- Magill, A. H., J. D. Aber, G. M. Berntson, W. H. McDowell, K. J. Nadelhoffer, J. M. Melillo, and P. Steudler. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. *Ecosystems* 3:238–253.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- McGroddy, M. E., T. Daufresne, and L. O. Hedin. 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology* 85:2390–2401.
- McMartin, B. 1994. *The great forest of the Adirondacks*. North Country Books, Utica, New York, USA.
- McNeil, B. E. 2006. *Spatial variability of foliar nitrogen in the Adirondack Park, NY*. Dissertation. Syracuse University, Syracuse, New York, USA.
- McNeil, B. E., R. E. Martell, and J. M. Read. 2006. GIS and biogeochemical models for examining the legacy of forest disturbance in the Adirondack Park, NY, USA. *Ecological Modelling* 195:281–295.
- McNeil, B. E., J. M. Read, and C. T. Driscoll. 2005. Identifying controls on the spatial variability of foliar nitrogen in a large, complex ecosystem: the role of atmospheric nitrogen deposition in the Adirondack Park, NY, USA. *Journal of Agricultural Meteorology* 60:1157–1160.
- McNeil, B. E., J. M. Read, and C. T. Driscoll. 2007. Foliar nitrogen responses to elevated atmospheric nitrogen deposition in nine temperate forest canopy species. *Environmental Science and Technology* [doi: 10.1021/es062901z].
- McNulty, S. G., J. D. Aber, and R. D. Boone. 1991. Spatial changes in forest floor and foliar chemistry of spruce–fir forests across New England. *Biogeochemistry* 14:13–29.
- Melillo, J. M., J. D. Aber, and J. M. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- Millward, A. A., and C. E. Kraft. 2004. Physical influences of landscape on a large-extent ecological disturbance: the northeastern North American ice storm of 1998. *Landscape Ecology* 19:99–111.
- Mouillot, D., W. Stubbs, M. Faure, O. Dumay, J. A. Tomasini, J. B. Wilson, and T. D. Chi. 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. *Oecologia* 145:345–353.
- Oleksyn, J., P. B. Reich, R. Zytkowski, P. Karolewski, and M. Tjoelker. 2002. Needle nutrients in geographically diverse *Pinus sylvestris* L. populations. *Annals of Forest Science* 59:1–18.
- Ollinger, S. V., J. D. Aber, G. M. Lovett, S. E. Millham, R. G. Lathrop, and J. M. Ellis. 1993. A spatial model of atmospheric deposition for the northeastern U.S. *Ecological Applications* 3:459–472.
- Ollinger, S. V., and M. L. Smith. 2005. Net primary production and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. *Ecosystems* 8:760–778.
- Ollinger, S. V., M. L. Smith, M. E. Marthin, R. A. Hallett, C. L. Goodale, and J. D. Aber. 2002. Regional variation in foliar chemistry and soil nitrogen status among forests of diverse history and composition. *Ecology* 83:339–355.
- Parker, A. J. 1982. The Topographic Relative Moisture Index: an approach to soil-moisture assessment in mountain terrain. *Physical Geography* 3:160–168.
- Parton, W., W. L. Silver, I. C. Burke, L. Grassens, M. E. Harmon, W. S. Currie, J. Y. King, E. C. Adair, L. A. Brandt, S. C. Hart, and B. Fasth. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* 315:361–364.
- Pinchot, G. 1898. *Adirondack spruce: a study of the forest in Ne-ha-sa-ne park, with tables of volume and yield and a working plan for conservative lumbering*. Critic Company, New York, New York, USA.
- Plourde, L. C., S. V. Ollinger, M. L. Smith, and M. E. Martin. 2007. Estimating species abundance in a northern temperate forest using spectral mixture analysis. *Photogrammetric Engineering and Remote Sensing* 73:829–840.
- Poorter, H., and R. De Jong. 1999. A comparison of specific leaf area, chemical composition, and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143.
- Rees, M., R. Condit, M. Crawley, S. W. Pacala, and D. G. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* 293:650–655.
- Reich, P. B. 2005. Global biogeography of plant chemistry: filling in the blanks. *New Phytologist* 168:263–266.
- Reich, P. B., D. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1990. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–1969.
- Reich, P. B., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences (USA)* 101:11001–11006.
- Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences (USA)* 94:13730–13734.
- Reich, P. B., I. J. Wright, J. Cavender-Bares, J. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Sciences* 164(Supplement):S143–S164.

- Schimel, D. S. 1995. Terrestrial biogeochemical cycles: global estimates with remote sensing. *Remote Sensing of Environment* 51:49–56.
- Shipley, B., D. Vile, and E. Garnier. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314:812–814.
- Smith, M. L., and M. E. Martin. 2001. A plot-based method for rapid estimation of forest canopy chemistry. *Canadian Journal of Forest Research* 31:549–555.
- Smith, M. L., M. E. Martin, S. V. Ollinger, and L. Plourde. 2003. Analysis of hyperspectral data for estimation of temperate forest canopy nitrogen concentration: comparison between an airborne (AVIRIS) and a spaceborn (HYPERION) sensor. *IEEE Transactions on Geosciences and Remote Sensing* 41:1–5.
- Smith, M. L., S. V. Ollinger, M. E. Martin, J. D. Aber, R. A. Hallett, and C. L. Goodale. 2002. Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecological Applications* 12:1286–1302.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey, USA.
- Sullivan, T. J., I. Fernandez, A. T. Herlihy, C. T. Driscoll, T. C. McDonnell, N. A. Nowicki, K. U. Snyder, and J. W. Sutherland. 2006. Acid-base characteristics of soils in the Adirondack Mountains, New York. *Soil Science of America Journal* 70:141–152.
- Townsend, A. R., C. C. Cleveland, G. P. Asner, and M. M. C. Bustamante. 2007. Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88:107–118.
- Townsend, P. A., J. R. Foster, R. A. J. Chastain, and W. S. Currie. 2003. Imaging spectroscopy and canopy nitrogen: application to forests of the central Appalachian Mountains using Hyperion and AVIRIS. *IEEE Transactions on Geosciences and Remote Sensing* 41:1347–1354.
- Ungar, S. G., J. S. Pearlman, J. Mendenhall, and D. Reuter. 2003. Overview of the Earth Observing One (EO-1) mission. *IEEE Transactions on Geosciences and Remote Sensing* 41:1149–1159.
- USGS. 1998. National mapping program technical instruction: standards for digital line graphs. 1. General. Washington, D.C., USA. (<http://rockyweb.cr.usgs.gov/nmpstds/dlgstds.html>)
- van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. *The Botanical Review* 40:347–394.
- Vitousek, P. M., G. Aplet, D. R. Turner, and J. J. Lockwood. 1992. The Mauna-Loa environmental matrix: foliar and soil nutrients. *Oecologia* 89.
- Vogelmann, J., T. Sohl, P. V. Campbell, and D. M. Shaw. 1998. Regional land cover characterization using Landsat thematic mapper data and ancillary data sources. *Environmental Monitoring and Assessment* 51:415–428.
- Vogelmann, J. E., S. M. Howard, L. M. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s National Land Cover Data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. *Photogrammetric Engineering and Remote Sensing* 67:650–652.
- Weathers, K. C., S. M. Simkin, G. M. Lovett, and S. E. Lindberg. 2006. Empirical modeling of atmospheric deposition in mountainous landscapes. *Ecological Applications* 16:1590–1607.
- Wilds, S. P. V. 1996. Gradient analysis of the distribution of flowering dogwood (*Cornus florida* L.) and dogwood anthracnose (*Discula destructiva* Redlin.) in western Great Smokey Mountains National Park. Thesis. University of North Carolina, Chapel Hill, North Carolina, USA.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wright, I. J., et al. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography* 14:411–421.
- Wright, I. J., P. B. Reich, and M. Westoby. 2001. Strategy-shifts in leaf physiology, structure, and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Functional Ecology* 15:423–434.
- Wright, I. J., P. B. Reich, and M. Westoby. 2003. Least-cost input mixtures of water and nitrogen for photosynthesis. *American Naturalist* 161:98–111.
- Yin, X. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Canadian Journal of Forest Research* 23:1587–1602.
- Zhu, Z., L. Yang, S. Stehman, and R. Czaplewski. 2000. Accuracy assessment for U.S. Geological Survey regional land-cover mapping program: New York and New Jersey region. *Photogrammetric Engineering and Remote Sensing* 66:1425–1438.

#### SUPPLEMENT

Plot descriptions and calculation of canopy N from foliar N data (*Ecological Archives* A018-012-S1).