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High Foliar and Soil Nitrogen Concentrations in Central Appalachian Forests

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ABSTRACT

Regional topography and climate variation yield differences in ecosystem attributes that make spatially scaled estimates of forest productivity challenging. Foliar nitrogen is a primary indicator of forest ecosystem productivity and is used in regional estimates of terrestrial productivity, but this characteristic has not been well described in the Central Appalachian region. Here we describe foliar and soil N variation among species and elevations at two spatial scales in the Central Appalachian region: (1) across the Elklick watershed in the Fernow Experimental Forest and (2) across the state of West Virginia. We found higher foliar N concentrations at both scales than those previously reported for other temperate forest regions. Canopy and soil nitrogen concentrations were also much greater in the Fernow than generally observed across West Virginia. Soil N concentrations in the Fernow were two times greater than those observed across West Virginia. Species-related differences were observed at both spatial scales, but were not always consistent. Canopy N ranges are generally consistent across elevations throughout the state of West Virginia, but should be scaled according to species-related elevation effects for studies that estimate productivity differences in response to harvest or changing species composition. The incongruence of foliar and soil N concentrations at the Fernow Experimental Forest are not explained by elevation or species composition, but are likely a consequence of greater historical N and H^+ deposition relative to the surrounding West Virginia region.

Key words: soil nitrogen; foliar N; Central Appalachian; West Virginia; hardwood species; spatial variation; ecosystem scaling; canopy N; eastern U.S. hardwood forests; topography; Fernow Experimental Forest.

INTRODUCTION

Regional estimates of productivity are closely related to canopy foliar nitrogen concentrations that drive maximum photosynthetic rates and carbon assimilation. Central Appalachian forests have been included in regional estimates of terrestrial carbon sequestration, but descriptions of the nutrient status in this part of the eastern U.S. are few (Boggs and others 2005; Adams and others 2006) and usually limited to fine-scale watershed studies (Adams and others 2006). Boggs and others (2005) observed greater foliar N concentrations in the Virginia region of the Central Appalachian mountains relative to the surrounding forested region and several recent studies have described trends in foliar and soil characteristics that are linked to atmospheric N deposition gradients (Aber and others 2003; Boggs and others 2005; Pregitzer and others 2008). The Central Appalachian region has a history of high N deposition, and the level of N deposition in

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West Virginia is at the extreme end of the regional range (Ollinger and others 1993; US EPA 2002; US EPA 2006). West Virginia is also heavily forested with economically valuable timber species that may soon be harvested by private landowners. Many ecosystem models use foliar N as a surrogate for productivity and carbon sequestration (Running and Gower 1991; Aber and Federer 1992; Landsberg and Waring 1997) but topographic variation and species composition introduce complexity to such nutrient concentrations that may confound responses to elevated levels of N deposition.

Spatially resolved descriptions of ecosystem N balances in the West Virginia region of the Appalachian Mountains are lacking. Several studies have described foliar nitrogen and ecosystem productivity for the larger Appalachian Region (McNulty and others 1994; Smith and others 2002; Pan and others 2004), but increased spatial resolution of foliar and soil N concentration for West Virginia relative to the surrounding region should help improve modeled estimates of forest productivity in the eastern U.S. Studies that compare productivity estimates derived from foliar N measurements at varied spatial resolutions have concluded that substantial error can be introduced by ignoring small-scale N variation (Reich and others 1999b; Pan and others 2004). Most of the foliar N measurements that are used to parameterize productivity models in the Central Appalachian region were made in N-limited ecosystems (Field and Mooney 1986; Reich and others 1992). Over the past 50 years, N deposition in the Central Appalachian Mountains has been higher than the amounts deposited in many New England and Southern Appalachian sites that have extensive foliar N datasets (Ollinger and others 1993; US EPA 2002; US EPA 2006). The Fernow Experimental Forest in Parsons, West Virginia, is located in a region of the Central Appalachian Mountains with especially high historical rates of N deposition and shows signs of N saturation (Peterjohn and others 1996; Gilliam and others 2001; US EPA 2002). Thus, the range of foliar and soil N concentrations in West Virginia may extend outside the range of observations in other eastern U.S. forests (Nadelhoffer and others 1999; Lovett and others 2002).

Spatial variation in ecosystem characteristics has long presented a challenge for estimating regional and global terrestrial productivity (Houghton 2003). The intensity of land use and concentrations of atmospheric pollutants vary with topographic changes and add a dimension of complexity to forest ecosystem characteristics. Nitrogen deposition and other environmental factors, such as temperature and precipitation, in mountainous regions are likely to vary with elevation (Ollinger and others 1993) even within short distances. Aber and others (2003) documented foliar N of sugar maple trees across an elevation gradient by pooling data from several study sites in the northeastern United States, but included only two sites in the Central Appalachian Mountains that were located substantially south of the other 157 sites. The degree of variation in foliar N with elevation may differ across latitudes and has been given very little attention in the Central Appalachian region.

Forests dominate the landscape of West Virginia, making this state an important component of the mature forest land in the Central Appalachian Mountains. The high diversity of tree species and the significant elevation range (200–1,400 m) in West Virginia provides a model for examining the interactive effects of species and elevation on foliar N in the Central Appalachian Mountains. The objective of our study was to compare the effects of species and elevation on foliar and soil N concentrations in temperate deciduous forests at two spatial scales, the watershed scale and the statewide scale. We investigated foliar N variation across a range of elevations in a mature forested watershed in the Fernow Experimental Forest and compared these trends to measurements made across the larger range of elevations throughout the state of West Virginia. In particular, we were interested in whether leaf N at the top of the forest canopy varies with elevation and species at both spatial scales, whether variations in soil N also exist along the same elevation gradient, and whether the effect of elevation is consistent between the two spatial scales.

METHODS

"Fine-Scale" Watershed Study

Measurements along local elevation gradients were conducted in the Fernow Experimental Forest (Fernow), a 1900 ha subsection of the Monongahela National Forest near Parsons, West Virginia. The Fernow is within the Appalachian Plateau of the Central Hardwood region and is classified as mixed mesophytic according to Braun (1950). This region was extensively logged between 1903 and 1911 (Trimble 1977) and has been managed by the U.S. Forest Service since 1915 (Schuler 2004). Research and forest monitoring efforts were initiated in 1933 (Schuler 2004) but portions of the forest have regenerated naturally over the past 100 years. The climate that accompanied this regeneration period was moist and cool with an average maximum temperature of 15°C and about 146 cm of rainfall spread evenly throughout the year (Kochenderfer 2006).

We established three transects southeast of Elklick Run that traverse relatively unmanaged sections of the Fernow and sampled 30 m radius circular plots at three elevations ranging from 550 to 1090 m (1800–3650 ft). Similar slopes and aspects were maintained along each transect to minimize the variation that may occur as a result of topographic differences other than elevation (Fekedulegn and others 2002). At least five species of dominant canopy trees were identified and marked for sampling in each plot. The species sampled included *Acer saccharum* ($n = 12$), *Betula lenta* ($n = 10$), *Fagus grandifolia* ($n = 11$), *Liriodendron tulipifera* ($n = 12$), *Prunus serotina* ($n = 8$), and *Quercus rubra* ($n = 8$). A 12-gauge semi-automatic shotgun was used to collect small twigs with canopy leaves attached from the tree tops. Each leaf sample was cut into 2.3 cm^2 disks, dried for 48 h at 65°C, and weighed so that leaf mass per unit area ($\mathrm{LM}_{\mathrm{area}}$, g m^{-2}) could be calculated. Carbon and N content of all dried leaf samples were analyzed with a Carlo Erba CN elemental analyzer (Fison Inst., Milan, Italy).

Soil samples were collected from the A horizon at three locations within 2 m of the base of each canopy tree using a 1.9 cm diameter soil corer. The depth of each core was recorded to estimate sample volume. All three soil samples for each individual tree were consolidated, dried for 48 h at 65°C, and weighed. Bulk density was calculated as the mass of soil in a given volume. The carbon and N content of dried soil samples were analyzed using Dumas combustion in a Carlo Erba CN elemental analyzer (Fisons Instr., Milan, Italy).

‘‘Broad-Scale’’ Statewide Study

The broad-scale portion of this study was conducted by sampling four ‘‘mega-transects’’ that traverse a range of elevations (~200–1,400 m) found in the state of West Virginia. All of the mega-transects run west to east across the state with an average distance between sites of 80 km. All sites were mature, closed-canopy deciduous forests with canopy trees at least 30 cm in diameter at breast height. The top 10 most abundant tree species in the state were identified from U.S. Forest Service records (Griffith and Widmann 2003) and canopy foliage from the tops of trees was collected from at least five of these dominant canopy species at each sampling site using a 12-gauge semi-automatic shotgun. The species sampled included *Acer rubrum* ($n = 23$), *A. saccharum* ($n = 23$), *Carya* spp. ($n = 34$), *F. grandifolia* ($n = 21$), *Fraxinus americana* ($n = 7$), *L. tulipifera* ($n = 33$), *P. serotina* ($n = 19$), *Quercus alba* ($n = 31$), *Q. rubra* ($n = 38$), and *Tilia americana* ($n = 11$). Leaf disks were cut, dried for 48 h at 65°C, and weighed so that $\mathrm{LM}_{\mathrm{area}}$ could be calculated.

Soil samples were collected from the A horizon at four locations within 2 m of the base of each tree using a 1.9 cm diameter soil corer. Litter and humus were not sampled. The four soil samples from each tree location were combined, dried for 48 h at 65°C and weighed. The bulk density of the soil was calculated as the mass per volume of soil. All dried soil and leaf tissue samples were analyzed using Dumas combustion in a Carlo Erba CN autoanalyzer (Fisons Instr., Milan, Italy) to measure carbon and N content.

Data Analysis

Many of the species sampled in the Fernow watershed were also sampled at sites across the state but there was not complete overlap of all species at both spatial scales. Thus, we examined datasets from the watershed and statewide scales separately for interactive and main effects of elevation and species on leaf and soil characteristics using a 2-way mixed model ANOVA (SAS-JMP software). If significant differences were detected, then analysis of variation among treatment groups was further assessed with Tukey-Kramer HSD tests.

To assess the spatial variation of topographic N concentration patterns, we conducted a test of the consistency of N changes with elevation at the two spatial scales. Because we were interested in spatial variation of generalized ecosystem traits, we lumped all species together for this analysis. We tested the consistency of foliar and soil nitrogen trends with elevation between the statewide and watershed scales using a 2-way ANCOVA with spatial scale as a main effect and elevation as a covariate (SAS-JMP software; Cary, North Carolina). These trends were synthesized by generating a 3-dimensional surface graph in SigmaPlot (San Jose, California) that represents the running average of soil and foliar N with elevation changes at the two spatial scales.

RESULTS

Species and Elevation Effects at the Watershed Scale (Elklick Watershed)

In the Elklick watershed of the Fernow Experimental Forest, there was no significant effect

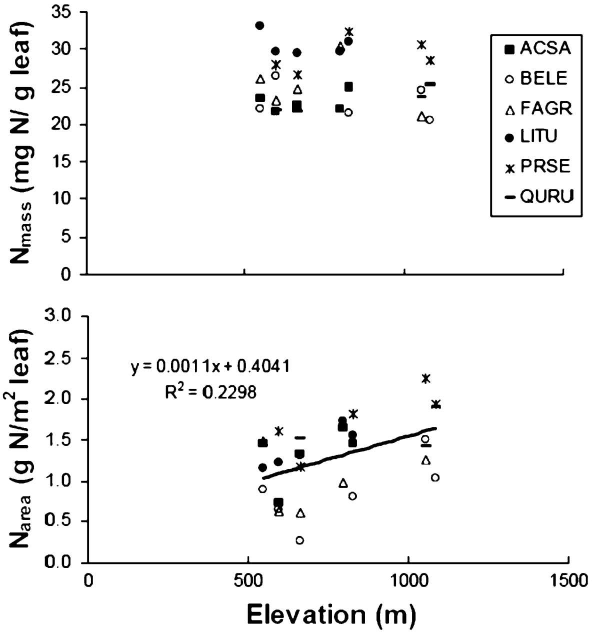

Figure 1. Comparison of trends in mass based foliar [N] (N_{mass}, top panel) and area based foliar [N] (N_{area}, bottom panel) in the Fernow Experimental Forest (Fernow). Each data point represents a plot mean for a tree species including *Acer saccharum* (ACSA), *Betula lenta* (BELE), *Fagus grandifolia* (FAGR), *Liriodendron tulipifera* (LITU), *Prunus serotina* (PRSE), and *Quercus rubra* (QURU). A line is fitted to show the relationship of N_{area} to elevation.

of elevation on foliar N_{mass} ($F_{elev} = 1.32$, $P_{elev} = 0.2555$), but foliar N_{area} increased with elevation ($F_{elev} = 9.16$, $P_{elev} = 0.0040$) (Figure 1). This change was paralleled by increases in soil C:N (Table 1) and was similar among all of the tree species that we sampled ($F_{spp\times elev} = 0.44$, $P = 0.8186$). Despite the similarity in species responses to elevation, there were differences in mean foliar N concentrations among species (Figure 2; N_{area}: $F_{spp} = 4.88$, $P_{spp} = 0.0012$; N_{mass}: $F_{spp} = 9.39$, $P_{spp} < 0.0001$). *P. serotina* foliage had the highest overall N_{area}, almost 100% greater than that observed in the *F. grandifolia* leaves. *F. grandifolia* leaves also had the lowest LM_{area} of all species sampled in the Fernow, although not significantly less than *P. serotina*. *Q. rubra* had the highest LM_{area} with 83% greater LM_{area} than that of *F. grandifolia* leaves. In addition to the effect of tree species on LM_{area} ($F_{spp} = 4.64$, $P = 0.0016$), increasing elevation was correlated with an LM_{area} increase ($F_{elev} = 7.48$, $P = 0.0088$) that was similar for all species ($F_{spp\times elev} = 0.56$, $P = 0.7318$). Variation in N_{mass} due to species was more modest (Figure 2; $F_{spp} = 9.39$, $P < 0.0001$) than species differences in LM_{area} and N_{area}. *A. saccharum* leaves had the lowest N_{mass} and *L. tulipifera* leaves had the highest N_{mass} (32% greater than *A. saccharum*).

There were significant differences in soil C:N ratios and bulk density with elevation in the Fernow Experimental Forest (Table 1). Soil C:N increased with elevation ($F_{elev} = 56.13$, $P_{elev} < 0.0001$) and bulk density decreased with elevation ($F_{elev} = 5.47$, $P_{elev} = 0.0213$). There were no significant effects of tree species on any of the soil variables in the Fernow watershed but the bulk density change with elevation was driven mostly by the differences observed in soils associated with *Q. rubra* trees (Table 1; $R^2 = 0.72$, $P = 0.0002$). BELE was the only tree species in the Fernow with foliar N_{mass} that was correlated soil N.

Species and Elevation Effects at the Statewide Scale (West Virginia)

At the statewide scale, the effects of elevation on both N_{area} and N_{mass} differed by species (Figure 3; N_{area}: $F_{elev\times spp} = 2.23$, $P_{elev\times spp} = 0.0203$; N_{mass}: $F_{elev\times spp} = 5.24$, $P_{elev\times spp} < 0.0001$). For five of the ten species sampled across the state, variation in N_{mass} was partially explained by elevation (Figure 4). Foliar N_{mass} of *Q. alba* showed the strongest response to the statewide elevation gradient, increasing 65% over 655 m in elevation ($R^2 = 0.44$). In contrast, N_{mass} of *A. saccharum* leaves was affected by elevation but increased by only 16% over 1,100 m in elevation. Among the 10 species sampled across West Virginia, those with the highest correlation between N_{area} and elevation were *A. rubrum*, *A. saccharum*, and *Q. alba* (Figure 4). The change in LM_{area} with elevation also differed by tree species ($F_{elev\times spp} = 2.3261$, $P = 0.0153$). LM_{area} of *A. rubrum* increased the most with elevation, paralleling the change in N_{area}, but LM_{area} of *Carya* spp. declined with elevation whereas the remaining species showed very little response to elevation.

Changes in soil properties with elevation were less apparent at the statewide scale than those observed in the Fernow watershed (Table 1). There were significant increases in the percentage of soil C and soil N along the West Virginia elevation gradient (%C: $F_{elev} = 18.62$, $P_{elev} < 0.0001$; %N: $F_{elev} = 17.03$, $P_{elev} < 0.0001$) that were consistent among tree species (%C: $F_{spp} = 1.20$, $P_{spp} = 0.2933$; %N: $F_{spp} = 1.12$, $P_{spp} = 0.3472$). The increases in C and N with elevation were proportional such that elevation had no effect on C:N (Table 1). There were, however, differences in C:N ratios among soils associated with different tree species across West Virginia ($F_{spp} = 3.7108$, $P_{spp} = 0.0002$), and

Table 1. Soil Properties of the A Horizon Collected at the Base of Canopy Trees in the Elklick Watershed of the Fernow Experimental Forest (a) and along Statewide West Virginia Transects (b)

Study site	Tree species	*n*	Soil %N[+]		Soil %C[+]		Soil C:N		Bulk density	
			Mean	Std. err.	Mean	Std. err.	Mean	Std. err.	Mean	Std. err.
(a)										
Fernow	*Acer saccharum*	29	0.540	0.036	5.426	0.580*	10.280	0.768*	0.548	0.036
Fernow	*Betula lenta*	18	0.480	0.024	5.302	0.533*	11.154	1.144*	0.722	0.064
Fernow	*Fagus grandifolia*	25	0.505	0.032	4.960	0.548*	10.178	0.847*	0.583	0.045
Fernow	*Liriodendron tulipifera*	20	0.490	0.032	4.261	0.455	8.523	0.513*	0.652	0.049
Fernow	*Prunus serotina*	18	0.571	0.049	6.464	1.055*	11.070	1.167*	0.597	0.054
Fernow	*Quercus rubra*	17	0.564	0.057*	8.279	1.362*	14.009	1.416*	0.532	0.069**
(b)										
West Virginia	*Acer rubrum*	23	0.273	0.029	4.522	0.556	15.97	0.6686	1.039	0.113
West Virginia	*Acer saccharum*	23	0.270	0.031*	4.043	0.467*	14.91	0.472	1.039	0.062
West Virginia	*Carya spp.*	34	0.247	0.028*	3.385	0.313*	14.95	0.4009	1.059	0.075
West Virginia	*Fagus grandifolia*	21	0.219	0.023*	4.053	0.493*	18.31	0.6293	0.967	0.041
West Virginia	*Fraxinus americana*	7	0.242	0.042	3.313	0.660	13.4	0.7038	1.357	0.141
West Virginia	*Liriodendron tulipifera*	33	0.279	0.021	4.541	0.483	15.85	0.6897	1.067	0.076
West Virginia	*Prunus serotina*	19	0.322	0.059*	4.268	0.527	15.69	0.7938	0.982	0.053
West Virginia	*Quercus alba*	31	0.262	0.028	4.517	0.515	17.14	0.8041	0.957	0.051
West Virginia	*Quercus rubra*	38	0.264	0.032	4.391	0.489	17.87	0.8299	1.114	0.052
West Virginia	*Tilia americana*	11	0.292	0.029	4.142	0.447	14.31	0.9846	0.850	0.060

Linear regression on elevation is significant ($\alpha = 0.05$) and the relationship is positive.

***Linear regression on elevation is significant ($\alpha = 0.05$) and the relationship is negative.*

[+] *For samples collected in West Virginia data were log transformed prior to statistical analysis to attain normal distribution. Means shown represent the original dataset.*

this was in contrast to observations made in the Fernow. Soils surrounding *F. grandifolia* and *Q. rubra* trees had significantly higher C:N ratios than soils around *Carya* spp. and *A. saccharum* trees according to a Tukey HSD test ($\alpha = 0.05$, $Q = 3.1970$). No differences in soil bulk density were observed among species or elevation ($P > 0.05$) across the statewide transects. There was a significant correlation or trend between foliar N_{mass} and soil N for five of the tree species studied at the statewide scale (ACSA: $P = 0.0156$, FRAM: $P = 0.0344$, LITU: $P = 0.0782$, QURU: $P = 0.0594$, BELE: $P = 0.0053$).

Elevation Trends in N at Two Spatial Scales

The last objective was to determine how foliar and soil trends vary with spatial scale, regardless of species differences. To address the degree to which ecosystem characteristics are conserved as the geographic area of interest increases, we contrasted elevation-related trends in foliar and soil N and C at the watershed and statewide scales.

The effect of elevation on N_{area} of the forest canopy varied at the two spatial scales ($F_{scale \times elev} = 17.34$, $P < 0.0001$). Overall, N_{area} was 33% greater across West Virginia than in the Fernow. In the Fernow, N_{area} increased with elevation but this change was not observed across West Virginia (Figure 5). Similarly, LM_{area} increased with elevation in the Fernow but not across West Virginia ($F_{scale \times elev} = 23.06$, $P < 0.0001$) (Figure 5). Mass-based C and N concentrations of canopy leaves were significantly different between the two spatial scales (%C: $F_{scale} = 158.12$, $P < 0.0001$; N_{mass}: $F_{scale} = 14.41$, $P = 0.0002$) but there were no effects of elevation observed on these two variables. This analysis suggests that elevation changes in foliar chemistry that are observed for individual species, as shown in Figure 4, are inconsequential for ecosystem trends. The mean percentage of C observed in the Fernow was 7% greater than leaf C measured across the state of West Virginia. Mean N_{mass} was 12% greater in the Fernow than the statewide mean (Figure 2).

The magnitude of change in soil N with elevation was similar at both spatial scales ($F_{elev} = 6.69$, $P = 0.0101$) but the mean soil N in the Fernow was 97% greater than the mean soil N_{mass} across West Virginia ($F_{scale} = 125.31$, $P < 0.0001$). Soil C concentrations were not affected by elevation in the same manner as soil N at the two spatial scales

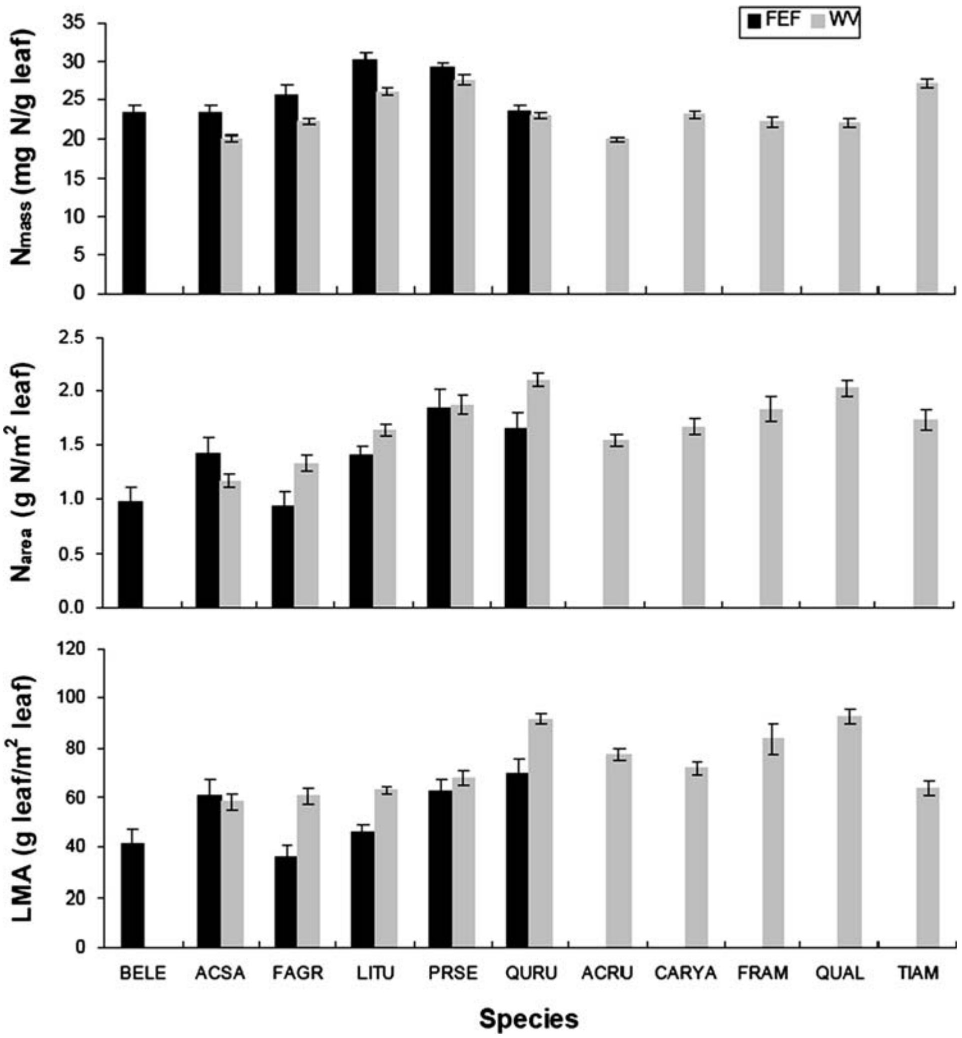

Figure 2. Foliar [N] on a mass basis (N_{mass}), foliar [N] on an area basis (N_{area}), and leaf mass per area (LMA) of 11 hardwood tree species (BELE: *Betula lenta*, ACSA: *Acer saccharum*, FAGR: *Fagus grandifolia*, LITU: *Liriodendron tulipifera*, PRSE: *Prunus serotina*, QURU: *Quercus rubra*, ACRU: *Acer rubrum*, CARYA: *Carya* spp., FRAM: *Fraxinus americana*, QUAL: *Quercus alba*, TIAM: *Tilia Americana*) in the Fernow Experimental Forest (Fernow) in *black* and across West Virginia (WV) in *gray*. *Error bars* represent standard error.

($F_{scale\times elev} = 25.78$, $P < 0.0001$). Soil C_{mass} increased more with elevation in the Fernow than across the state such that soil C:N changed with elevation in the Fernow, but not across the West Virginia elevation gradient ($F_{scale\times elev} = 65.48$, $P < 0.0001$). Differences in soil bulk density were also evident between the two spatial scales as bulk density decreased with elevation in the Fernow while remaining relatively constant across elevations throughout the state of West Virginia ($F_{scale\times elev} = 6.05$, $P = 0.0144$).

There are contrasting trends in foliar and soil N with elevation gradients at the two spatial scales. The interactive effects of species and elevation on foliar N prevent a simplified model of soil and foliar N trends with elevation, but there is a consistent increase in foliar and soil N with elevation across West Virginia (Figure 6). Soil and foliar N trends in the Fernow deviate drastically from this pattern (Figure 6).

DISCUSSION

Dominant tree species in the Elklick watershed of the Fernow Experimental Forest have higher mass-based foliar and soil nitrogen concentrations than has often been observed in the surrounding Appalachian regions (Table 2; Martin and Aber 1997; Mitchell and others 1999; Reich and others 1999a; Ollinger and others 2002; Ollinger and Smith 2005). Furthermore, foliar and soil N patterns at the broad scale in this study (across the state) do not accurately reflect patterns observed in the Fernow (Figure 6). A high proportion of mid-elevation sites (from ~550 to 1100 m) in the Fernow relative to the larger West Virginia region contribute to a parabolic appearance of N_{mass} across elevation gradients (Figure 5). In addition, the incongruence between N trends (of both leaves and soil) in the Fernow and the rest of the state is not explained by species-driven variation in N (Figure 2). These results indicate that something

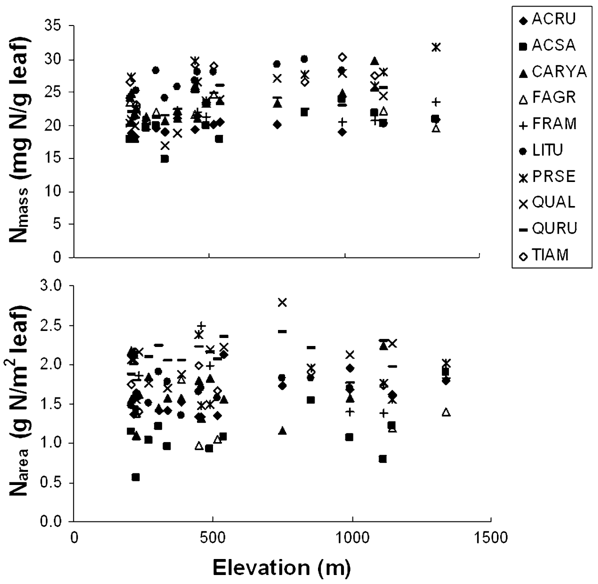

Figure 3. Mass based foliar [N] (N_{mass}, top panel) and area based foliar [N] (N_{area}, bottom panel) in West Virginia (WV). Each data point represents a plot mean for a tree species (BELE: *Betula lenta*, ACRU: *Acer rubrum*, ACSA: *Acer saccharum*, CARYA: *Carya* spp., FAGR: *Fagus grandifolia*, FRAM: *Fraxinus americana*, LITU: *Liriodendron tulipifera*, PRSE: *Prunus serotina*, QUAL: *Quercus alba*, QURU: *Quercus rubra*, TIAM: *Tilia americana*).

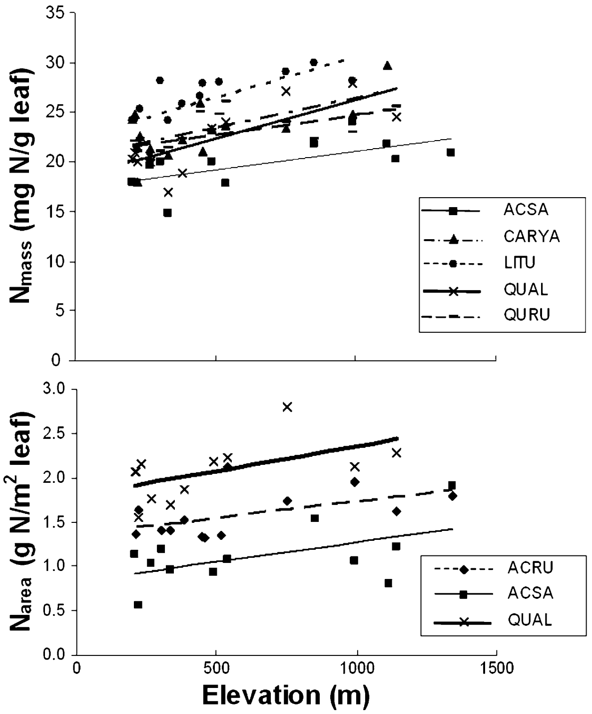

Figure 4. Elevation effects on foliar [N] of canopy hardwood species growing along an elevation gradient in West Virginia. Only those species with foliar N that is correlated with elevation (a subset from Figure 3) are shown [species × elevation effect on N_{mass}: $F = 5.2415$, $P < 0.0001$; species × elevation effect on N_{area}**: $F = 2.2297$, $P = 0.0203$; species × elevation effect on LMA: $F = 2.3261$, $P = 0.0153$] (ACSA: *Acer saccharum*, ACRU: *Acer rubrum*, CARYA: *Carya* spp., LITU: *Liriodendron tulipifera*, QUAL: *Quercus alba*, QURU: *Quercus rubra*). N_{area} was log transformed for normal distribution, but data shown are true plot means.

other than species and elevation is causing the different foliar chemistry observed in the Fernow and one cause is likely to be atmospheric N deposition.

Nitrogen deposition associated with anthropogenic pollutants has been implicated as a cause for biogeochemical differences among regions (Ollinger and others 1993; Lovett and Rueth 1999; Nadelhoffer and others 1999; Aber and others 2003). There are only limited N deposition data available for West Virginia and, although they are consistent with the trends we observed here, a finite conclusion cannot yet be made. The few datasets that exist indicate that historical N deposition rates have been much greater in Parsons, West Virginia, where the Fernow is located, than N deposition in the surrounding region (US EPA 2006). Data averaged since 1978 from a CASTNET site (US EPA 2006) in Giles County, Virginia (along the southern border of West Virginia) reveal inorganic N deposition (including wet and dry) was 78% greater in Parsons than that observed at the southern edge of the state.

Historic records of $[H^+]$ deposition indicate that the Fernow has received more than twice the historic average $[H^+]$ deposition recorded at the Horton Station site near southern West Virginia (US EPA 2006). Large additions of $[H^+]$ to the soil disrupt the cation exchange complexes in the soil and result in cation leaching (Likens and others 1996). The high C and N concentrations in leaf tissue may be caused by the loss of cations such as Ca^+, Mg^+, and K^+ that are normally found at high concentrations in leaves (Mader and Thompson 1969; Likens and others 1998; Schaberg and others 2006). Loss of soil and foliar cations due to acidification has been observed in the Fernow (Adams and others 2006), but the effect of elevation on soil and foliar cation concentrations has not been documented.

There is generally a positive trend in the relationship between soil N and foliar N across the state (Figure 6), but the relative contribution of different species to these general trends provides deeper insight into mechanisms that affect N cycling. Deciduous forests in West Virginia are very diverse because they lie at the boundary of beech–maple–

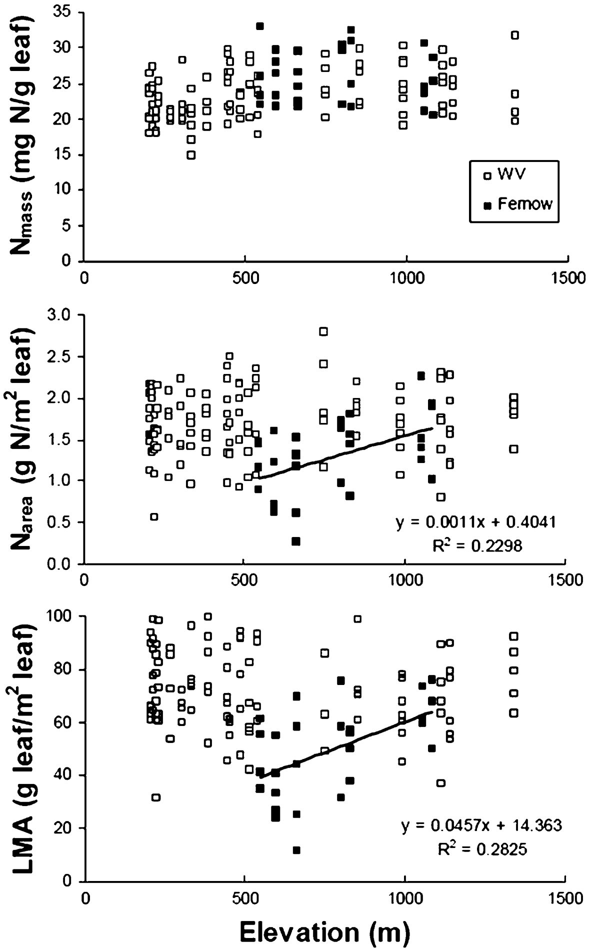

Figure 5. Whole ecosystem trends of foliar [N] on a mass basis (N_{mass}), foliar [N] on an area basis (N_{area}), and leaf mass per area (LMA) at two spatial scales (Fernow Experimental Forest [Fernow] and West Virginia [WV]). Lines are fitted to show the separate relationships of N_{area} and LMA with elevation in the Fernow. Each point represents a plot mean.

birch dominated forest and oak–hickory dominated forest types (Iverson and Prasad 2001). Differences in foliar decomposition rates among species may contribute to variable N turnover and additions to the soil. In sites with fewer maples and greater oak abundance, soil N additions from leaf litter may be slowed by the more recalcitrant oak leaves (McClaugherty and others 1985; Cornelissen 1996). Sugar maple and red oak trees both had foliar [N] correlated with soil [N] and elevation across West Virginia and thus these species may be important determinants of N availability in forest ecosystems. Other studies have also recently concluded that sugar maple is a key tree species associated with nitrogen cycling changes (Lovett and Rueth 1999; Templer and others 2005; Lovett and Mitchell 2004). The higher overall N concentration of soil appears to dilute the species effect in the Fernow where differences in soil [N] among species are lacking.

Previously published values of foliar N_{mass} in forests with species common to our study ranged from 17.6 to 28.8 mg g^{-1} (Table 2; Martin and Aber 1997; Mitchell and others 1999; Reich and others 1999a; Ollinger and others 2002; Ollinger and Smith 2005). The values reported in Table 2 are provided for comparison with the species averages from this study. It should be noted that some of the literature values represent a community of multiple species that is dominated by a species of interest in our study. Generally in the Fernow, species N_{mass} averaged between 23.4 to 30.3 mg g^{-1} with an overall average that is 21% higher than N_{mass} reported by studies listed in Table 2. Mean species-level N_{mass} across West Virginia was 8% higher overall than the literature average. Both C and N concentrations in canopy

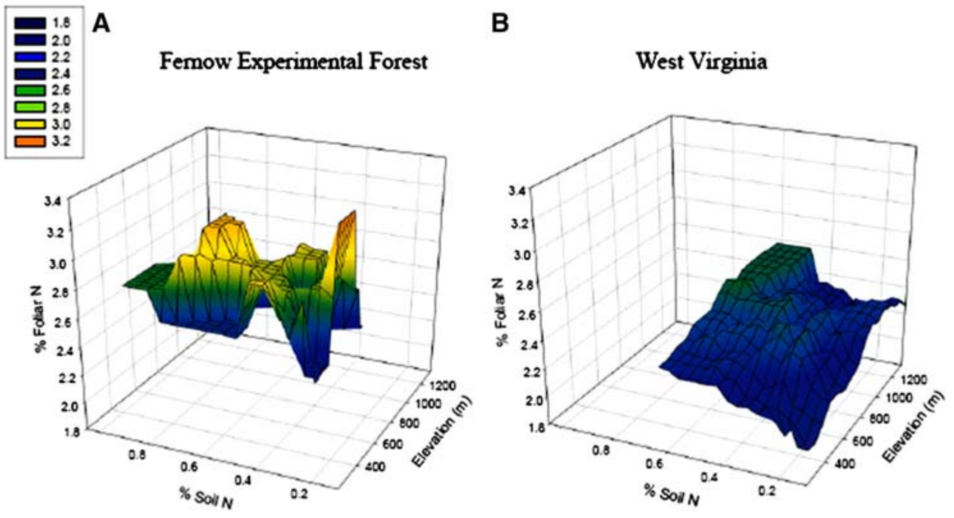

Figure 6. Surfaces represent running averages between data points that are site averages of foliar and soil nitrogen concentration along an elevation gradient in the Fernow Experimental Forest (**A**) and West Virginia (**B**).

Table 2. Published Foliar Nitrogen Concentrations for Overstory Tree Species Common to Central Appalachian Forest

Location	Species	Foliar N (mg N/g leaf)	Source
North Carolina	Basswood	28.8	Mitchell and others 1999
Wisconsin	Basswood dominated$^+$	26.1	Martin and Aber 1997
New Hampshire	Beech dominated$^+$	21.7	Smith and others 2002
New Hampshire	Beech-Birch$^+$	21.3	Ollinger and others 2002
West Virginia	**American Beech**	**23.5**	**This study in Fernow**
North Carolina	Birch species	19.5	Mitchell and others 1999
West Virginia	**Black birch**	**23.5**	**This study in Fernow**
Wisconsin	Black cherry	20.7	Reich and others 1999
Wisconsin	Black cherry	20.7	Reich and others 1995
West Virginia	**Black cherry**	**29.2**	**This study in Fernow**
Wisconsin	Hickory	19.8	Reich and others 1999
Wisconsin	Hickory	19.8	Reich and others 1995
North Carolina	Hickory species	24.5	Mitchell and others 1999
New Hampshire	Maple, beech, birch$^+$	19.8	Ollinger and Smith 2005
North Carolina	Red maple	18.4	Reich and others 1999
North Carolina	Red maple	18.0	Mitchell and others 1999
Wisconsin	Red maple	21.0	Reich and others 1999
Wisconsin	Red maple	19.5	Reich and others 1995
New Hampshire	Red maple dominated$^+$	20.0	Smith and others 2002
Wisconsin	Red maple dominated$^+$	23.7	Martin and Aber 1997
North Carolina	Red oak	28.7	Mitchell and others 1999
Wisconsin	Red oak	21.1	Reich and others 1995
Wisconsin	Red oak dominated$^+$	23.5	Martin and Aber 1997
Massachusetts	Red oak-Red maple$^+$	21.4	Martin and Aber 1997
West Virginia	**Red oak**	**23.5**	**This study in Fernow**
New Hampshire	Sugar maple$^+$	22.7	Ollinger and others 2002
Wisconsin	Sugar maple	18.5	Reich and others 1999
Wisconsin	Sugar maple	17.6	Reich and others 1995
New Hampshire	Sugar maple dominated$^+$	20.6	Smith and others 2002
Wisconsin	Sugar maple dominated$^+$	23.9	Martin and Aber 1997
West Virginia	**Sugar maple**	**23.4**	**This study in Fernow**
Wisconsin	White ash	19.8	Reich and others 1999
Wisconsin	White ash	21.3	Reich and others 1995
North Carolina	Ash species	19.2	Mitchell and others 1999
North Carolina	White oak	23.2	Mitchell and others 1999
Wisconsin	White oak dominated$^+$	24.8	Martin and Aber 1997
North Carolina	Yellow birch	17.8	Reich and others 1999
New Hampshire	Yellow birch dominated$^+$	22.0	Smith and others 2002
North Carolina	Yellow poplar	21.3	Mitchell and others 1999
West Virginia	**Yellow poplar**	**30.3**	**This study in Fernow**

$^+$*Forested plot sampled was dominated by the indicated species but included some other species.*
Bold text identifies data that was measured in this study.

leaves of the Fernow were higher than statewide means suggesting that this particular locality represents the high end of a nitrogen gradient in the state.

Previous studies that have examined foliar N of deciduous tree species in the northeastern U.S. also found that the relationship between foliar N and elevation varied by species (Ollinger and Smith 2005; Aber and others 2003). In a study of the Tibetan Plateau, Luo and others (2005) observed that N_{area} and LM_{area} of conifer species increased with elevation but the relationships of N_{area} and LM_{area} with elevation were not as strong for hardwood species. Although species differences in foliar N were observed at both spatial scales in West Virginia, the response of foliar N to elevation change was more variable among species at the statewide scale. The different patterns in foliar N may in part be explained by soil N transformations. Aber and others (2003) found that nitrification rates were correlated with elevation and this may lead to greater N leaching. Soil C:N is negatively correlated with nitrification rates and nutrient retention (McNulty and others 1991; Lovett and Rueth 1999; Lovett and others 2002; Ollinger and others 2002) and thus the effects of tree species and elevation on soil C:N trends that we present here suggest differential nitrification rates. Further study of soil nitrogen species could clarify the roles that N availability and/or leaching play in soil and foliar N changes with elevation.

CONCLUSIONS

Central Appalachian forests have greater foliar nitrogen concentrations than those observed in the surrounding region. There are inconsistent patterns of foliar and soil chemistry in the Fernow relative to the larger West Virginia region. This incongruence is not explained by species or elevation and is likely a consequence of inputs of N from atmospheric N deposition.

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