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Controls on the Spatial Patterns of Carbon and Nitrogen in Adirondack Forest Soils along a Gradient of Nitrogen Deposition

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We sampled 42 permanent vegetation plots in the Adirondack Mountains, NY to characterize the spatial patterns of, and controls on soil C and N contents. Average C (24 kg m^{-2}) and N (1.1 kg m^{-2}) contents of the combined organic and mineral horizons were high for northeastern U.S. forests. Contrary to our expectations, whole-profile C and N amounts were not different among northern hardwood (NH), spruce-fir (SF), and pine-dominated (PW) plots. Most of the C and N were stored in organic horizons in the high-elevation SF plots, and in the mineral horizons in NH and PW plots. Regression analyses of the pooled set of sites revealed that the factors that explained the most variability in soil C and N contents were different for organic and mineral horizons and differed between forest types. Overall, growing season degree-days (GSDD) was the variable most closely correlated with C and N contents in both organic and mineral horizons, and varying combinations of N deposition, conifer importance, and soil texture were the principal secondary influences. Spruce-fir plots received the most atmospheric N deposition, and multivariate regression tree (MRT) analysis indicated that N deposition rate was the environmental variable that explained the most variation in organic horizon C (sums of squares [SS] explained = 54%) and N (79% SS explained) amounts in these high-elevation stands. However, even in the unlikely case of 100% retention of the atmospheric inputs of N deposited over the past 50 yr, this source only accounted for a small portion of soil N, and the differences in N among the plots along the deposition gradient. It is likely that differences in GSDD accounted for most of the differences in C and N amounts.

Abbreviations: ANPP, annual net primary productivity; D_b, bulk density; GIS, Geographic Information System; GSDD, growing season degree-days; MAP, mean annual precipitation; MRT, multivariate regression tree; *n*, sample size; NEP, net ecosystem productivity; NH, northern hardwood; PW, pine-dominated; s.e., standard error; SF, spruce-fir; SS, sums of squares; T_h, horizon thickness.

Most of the C (51–60%, Dixon et al.,1994; Heath et al., 2003) and N (55–95%, Van Miegroet et al., 1992) in forest ecosystems are in the soil, therefore understanding the spatial controls on forest soil C and N is important. Nitrogen is regarded by most forest scientists as a key growth-limiting nutrient in temperate forests (Vitousek and Howarth, 1991). Consequently, anthropogenic inputs of N to N-limited forests may now be important influences in several areas of eastern North America and are thought by some to be an important component of global change (LeBauer and Treseder, 2008). Temperate and boreal forest soils are potential sinks for atmospheric CO_2 (Lal, 2005) and could prove to be important as global CO_2 levels are expected to rise in the future (IPCC, 2007). The importance of C and N in forest soils to numerous ecosystem goods and services underscores the need to understand the controls on their dynamics and accumulation. Moreover, determining the relative importance of factors that influence the spatial distribution of C and N stored in forest soils can provide useful data for refining soil C and N-cycling models and informing policies regarding land-use change and atmospheric CO_2 mitigation strategies.

Soil properties are controlled by climate, vegetation, parent material, topography, and time; the suite of factors that define the environment of a given location (Jenny, 1980). In eastern U.S. forests, differences in soil C and N pools are likely controlled by differences in topographic position, climate, species composition, soil texture, stand age, and land-use history (McClaugherty et al., 1985; Finzi et al., 1998; Compton and Boone, 2000; Lovett et al., 2004; Guo et al., 2006). Generally, forest soil organic carbon (SOC) pools are larger under coniferous vegetation (e.g., Finzi et al., 1998), in cooler, wetter conditions (Prichard et al., 2000; Guo et al., 2006), at the bottom of slopes (Kulmatiski et al., 2004), and in finer textured soils (Johnson et al., 2009). Additionally, soil C and N dynamics have been shown to vary along an elevation gradient (600–1400 m) in the Adirondacks (Joshi et al., 2003), implying that the climatic and biotic influences related to elevation (e.g., colder temperatures and coniferous vegetation) are likely to be important influences on the spatial pattern of soil C and N pools in this region.

Spatial gradients of temperature, precipitation, and atmospheric deposition of N and S exist across the northeastern

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USA (McNulty et al., 1991; Ollinger et al., 1993) and across the Adirondacks (Ito et al., 2002; McNeil et al., 2007). Foliar N concentrations have been shown to increase along the regional east-to-west gradient of increasing wet N deposition in the Adirondacks (McNeil et al., 2007). Similar patterns have also been identified in the southern Appalachians (Boggs et al., 2005). Further, using N deposition gradients, recent investigations have indicated that N deposition is an important influence on the net ecosystem production (NEP) of forests (Magnani et al., 2007; de Vries et al., 2008; Sutton et al., 2008) and may increase C storage in northern forests (Pregitzer et al., 2008).

In addition to the regional gradient, increased cloudwater capture with increasing elevation and the substantial enrichment of NH_4^+ and NO_3^- in cloudwater compared with rain, creates an elevational gradient of N deposition throughout the Adirondacks. Nitrogen deposition rates ~3.0 g N m^{-2} yr^{-1} have been reported (e.g., Miller, 1993) which are nearly six times that of lower elevations (ca. 0.5 g N $m^{-2}yr^{-1}$) in this region. The high end of this range represents some of the highest N deposition rates in North America (Johnson and Lindberg, 1992).

At current rates, the sum of N mineralization and atmospheric N deposition exceeds the vegetation N requirement in Adirondack spruce-fir forests as demonstrated at Whiteface Mt. in the northeastern Adirondacks (Joshi et al., 2003). This raises the question of the fate of the excess N. One alternative is that it is stored in the soil (e.g., Friedland et al., 1991; Johnson, 1992). Another is that the excess N will leach from the soil if these systems have progressed toward N-saturation. Knoepp et al. (2008) showed that stream export of N was greater in high N deposition (>1.2 g N m^{-2} yr^{-1}) sites in the southern Appalachians, suggesting the possibility that temperate forests receiving greater N inputs are showing signs of N saturation. Further, the emission of NO_x and N_2 from soils via denitrification may be yet another important process to consider when evaluating the fate of N in forest ecosystems (e.g., Schlesinger, 2009).

The objectives of this study were to provide estimates of C and N in organic and mineral horizons of well-drained Adirondack forest soils, identify factors that influence soil C and N contents, and assess the relative importance of those factors. We hypothesized that NH and PW soils would have significantly greater amounts of C than SF soils as northern hardwood and pine forests are generally more productive than SF forests in this region. We also hypothesized that the SF plots at the highest elevations, which receive the greatest inputs of atmospheric N, would have significantly greater amounts of soil N and lower C/N ratios than the northern hardwood and pine forests. We used univariate and multivariate regression analysis to relate amounts of forest soil C and N in organic and mineral horizons to potential physical and environmental influences determined from Geographic Information System (GIS) data, plot-level species composition, and modeled estimates of temperature, precipitation and N deposition taken from various sources (Table 1).

MATERIALS AND METHODS

Plots

In 1930 until 1932 Carl Heimburger established a network of >100 sites throughout forests of the Adirondack Mountains. He inventoried herbs, shrubs, and canopy trees to establish forest types, and he described and sampled soils at each site (Heimburger, 1933). In 1984, Andersen (1988) and Johnson et al. (1994), investigating the long-term impacts of acid rain on the pH and Ca content of Adirondack forest soils, established permanent plots at 48 locations sampled by Heimburger.

Table 1. Summary of predictor variables used in this investigation.

Predictor variable	Mean (Range)	Description	Data source
Climate			
Growing season degree-days	1690 (722–2361)	Index of mean daily air temperature and growing season length (O'Neill and DeAngelis, 1981): GSDD = (mean daily temperature)*(the number of days with a mean temperature > 0°C)	Temperature data from the DAYMET Climate Model (Thornton et al., 1997) available at www.daymet.org
Mean annual precipitation	123 (96–156)	Mean precipitation between 1980 and 2003 (cm yr^{-1})	DAYMET Climate Model (Thornton et al., 1997) available at www.daymet.org
N deposition	0.9 (0.4–3.1)	Total inorganic nitrogen in wet deposition (g N $m^{-2}yr^{-1}$) for plots below ~600 m, and in wet + dry for plots above ~600 m. (dry deposition inputs below 600 m are comparatively small)	Ito et al., 2002; McNeil et al., 2007 scaled using Miller, 1993 for plots > 600 m
Parent Material			
% Silt + Clay	21 (7–44)	Relative amount (%) of silt + clay-sized mineral material determined according to Bouyoucous (1930)	Heimburger, 1933
Rock volume	0.01 (0.0001–0.04)	The volume of rock (m^3) in a given excavation mineral layer	Field measurements, this study
Organisms			
Conifer importance	58 (0–100)	Importance of conifers at each site: (relative density + relative basal area)/2 (Forrester et al., 2003)	Bedison, *unpublished data*
Forest type	categorical	Forest vegetation type (NH, P, SF) stratified by codominant vegetation and elevation	Bedison et al., 2007
Topography			
Elevation	693 (305–1325)	Elevation (m) determined with GPS receivers at each site	Field measurements, this study
Slope	8.4 (0–27)	Slope of each site determined from a digital elevation model (DEM)	Adirondack Park Agency, 2001
Soil Depth	categorical	Depth of soil as either shallow (lithic contact below organic or thin mineral horizons) or deep (bottom of pit was reached before bedrock)	Field measurements, this study
Aspect	categorical	Exposure (N, S, E, W) determined from a DEM	Adirondack Park Agency, 2001

Bedison et al. (2007) found 42 of those plots in 2004/05, remeasured the trees, and recorded the locations with global positioning system (GPS) receivers.

The plots were located within the 2.5-million-hectare Adirondack Park, NY (Fig. 1). This mountainous region is characterized by considerable relief (ca. 1600 m), cold, snowy winters and cool, wet summers. The sites used in this study were located on unmanaged public lands accessible by hiking trails. Because of Heimburger's objectives, these plots represented a range of NH, subalpine SF and PW forests that are typical of the region. Sites were either logged in the late 19th/early 20th century (some of the NH plots), never logged (high-elevation SF and some NH sites), or were established on post-agricultural land (several of the pine sites). Most NH and SF stands were uneven-aged, however some PW sites were even-aged.

The three forest types represented in this investigation; NH (*n* = 20), red/white pine-dominated (PW, *n* = 10) and SF (*n* = 12), were differentiated by species composition and occur at different elevations (Bedison et al., 2007). Northern hardwood plots were dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britton). Red spruce (*Picea rubens* Sarg.) was the most important associated conifer in this forest type. Pine-dominated stands were characterized by white pine (*Pinus strobus* L.) and/or red pine (*Pinus resinosa* Ait.) and had a variety of associated hardwood species that occurred in limited amounts. The SF forests sampled in this study were characterized by red spruce, balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* var. *cordifolia* (Marsh.) Regel) and were at elevations ≥800 m (Bedison et al., 2007).

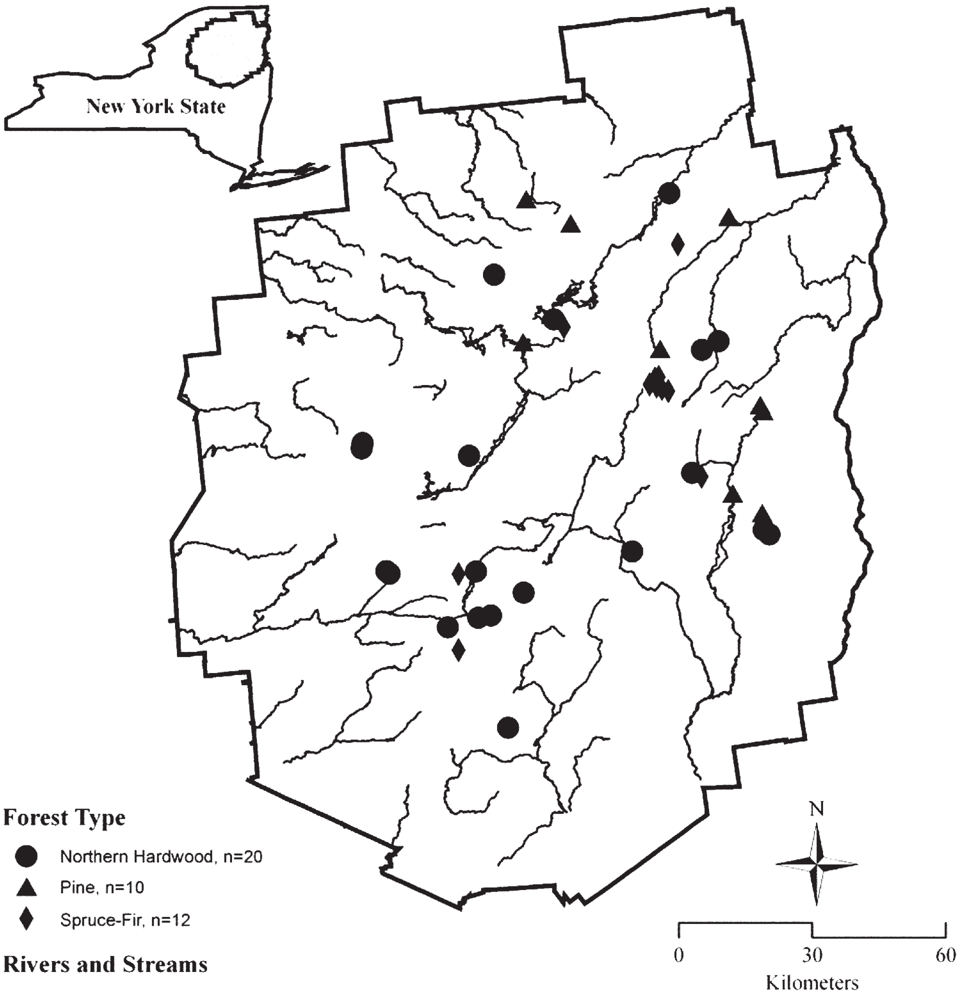

Fig. 1. Location of 42 Adirondack forest sites used in this investigation.

Soils throughout the Adirondack Mountains vary from thin with frequent bedrock outcrops to deep and sandy (April et al., 2004). These soils mantle gneisses, metasedimentary rocks and, in the High Peaks region, anorthosite. Parent material, where soils developed on unconsolidated sediments, is either glacial till or coarse-textured glacio-fluvial sediments deposited during the Wisconsinan glaciation (April et al., 2004; Johnson et al., 1994). Northern hardwood forests dominate on fine and medium-textured soils at low-to-moderate elevations (≤900 m; McGee, 2001). Pines compete best on excessively drained coarse sands and gravels of either fluvial or deltaic origin which occur at the lowest elevations across the landscape (Cook et al., 1952). At higher elevations (900–1500 m), SF forest soils are either entirely organic with a shallow, lithic contact or have thin mineral horizons derived from glacial till beneath a deep forest floor.

As the sites were selected in the early 1930s based on vegetation and drainage class, (Heimburger, 1933), the plot locations cannot be considered random. Therefore, we confine our conclusions to the set of plots sampled in this investigation. However, we are unaware of any reasons why this set of plots is different from a stratified random sample of mature Adirondack northern hardwood, SF, and PW forests on well-drained sites.

Soil Sampling and Analysis

In the summers of 2005 and 2006, quantitative soils pits (Hamburg, 1984; Huntington et al., 1988) were excavated at each of the 42 permanent plots. Loose leaf litter (Oi horizon) was cleared away and all rocks, roots, and soil to the bottom of the rooting zone were removed from a 0.5 m × 0.5 m pit and weighed. Organic horizons (Oe, Oa) were subsampled. Mineral soil was subsampled as 0 to10, 10 to 20, and 20+ cm to a depth where no more roots were visible in the excavation. Though the boundary between organic and mineral soil can be unclear, nearly all the soils we sampled were either Spodosols (Haplorthods) or Histosols (Folists) and the organic horizons were easily identified. Typically, a black, greasy Oa horizon was underlain by a coarse-textured, albic E horizon, thus making the delineation between organic and mineral soil clear. Further, in sites where mineral soil was present, a majority of the profiles contained an E horizon which was always found within the 0- to 10-cm layer.

Air-dry soils were sieved through metal screens based on horizon designation (Oe, 5 mm; Oa, 2 mm; mineral, 1 mm) according to the procedures of Heimburger (1933) and Andersen (1988) so valid comparisons of a variety of soil properties could be made in related investigations. Samples were then ground and analyzed for total %C and %N by combusting 3 to 5 mg in an elemental analyzer using standard procedures (Carlo-Erba NA 1500 C/N Analyzer, Fisons Instruments, Beverly, MA). For each organic horizon or mineral layer, C and N concentrations were converted to C and N amounts using the bulk density (D_b) of the sieved, air-dry soil and the horizon/layer thickness (T_h). Results are reported on an oven-dry-weight basis which was obtained by drying subsamples at 95°C for 12 h as Heimburger (1933) did.

Predictor Variables and Statistical Analyses

We explored the relationships between forest soil C and N contents of organic and mineral horizons and 11 potential predictor variables known to influence soil properties (e.g., Jenny 1941): (a) *climate*: GSDD, mean annual precipitation (MAP), inorganic N deposition; (b) *parent material*: % silt + clay, rock volume; (c) *organisms*: conifer importance, forest type; and (d) *topography*: elevation, slope, aspect, and in the case of SF sites, soil depth. The data source and a description of each variable are provided in Table 1.

Elevation was not considered as a predictor variable in MRT analyses (described below) because it does not directly control C or N content in soils. Rather, we used climatic variables that were correlated with elevation (and with each other) in this investigation (e.g., GSDD, MAP, N deposition) as possible influences on forest soil C and N storage. As forest type is also related to elevation (Bedison et al., 2007), we used conifer importance (the average of relative density and relative basal area of conifers at each plot), a variable that captured differences in forest composition but was not significantly correlated with elevation in this network of plots (Spearman's $\rho = 0.18$, $P = 0.27$), as a possible biologic influence. Conifers were present throughout the plots in this investigation and were a potential influence on soil C and N as conifer litter generally has a higher lignin/N ratio than NH litter (e.g., Scott and Binkley, 1997) which slows decomposition rates (Melillo et al., 1982).

We used the predictor variables in univariate linear regression analyses to explain variability in C and N contents in organic and mineral horizons (to the bottom of the rooting zone), and in the whole-profile (combined organic and mineral horizons). One site, which contained an unusually large rock near the bottom of the pit, was omitted from the mineral soil and whole-profile analyses as the calculated C and N amounts for that plot were physically implausible. A Tukey-Kramer test was used to determine differences in C and N contents and the C/N ratio where categorical data (i.e., forest type, aspect) were used. Carbon and N contents were $\log_{10}$ transformed where the data did not meet the requirements of normality. A Wilcoxon's signed-ranks test was used where pair-wise comparisons of soil C and N involved zeroes. Correlation between predictor variables was determined with a Spearman's Rank Correlation test. The data were analyzed with JMP (v 7.0.1, SAS Institute, Cary, NC) and statistical significance was evaluated at $P \leq 0.05$.

We also used MRTs to determine combinations of variables that split the sites into groups that had different C and N amounts (JMP, v 7.0.1, SAS Institute, Cary, NC). This analytical technique has been used previously to delineate factors that influence soil C and N amounts in the Yale-Myers Forest (Kulmatiski et al., 2004) and in the Green Mountains, VT (Johnson et al., 2009). It is used here to assess the relative importance of predictor variables related to soil C and N contents.

Multivariate regression tree analysis is a powerful non-parametric statistical technique that is able to capture higher-order interactions which are not well-represented in simple linear models and utilizes both continuous and categorical data. It uses a least squares splitting criterion based on predictor variables (De'ath and Fabricius, 2000; Kulmatiski et al., 2004). This binary splitting approach minimizes the within-group SS while maximizing the between groups SS for a given level in the tree (De'ath, 2002). Each terminal node (leaf) can thus be characterized by the multivariate mean of its sites and the environmental values that define it (De'ath, 2002). Each split in the tree is represented as a branch which is labeled with the amount of variability explained by that particular split. Each group is identified by the splitting criterion, the group mean and sample size. Terminal nodes were maintained at $n \geq 5$, thus groups where $n \leq 9$ were not split further. Further, trees were pruned when splits in the data resulted in ecologically implausible trends. Though MRT techniques can be used for predictive modeling (e.g., Breiman et al., 1984; Vayssières et al., 2000), we used this analytical procedure as an exploratory tool to assess the relative influence of predictor variables in explaining variability in C or N storage.

RESULTS

Regional Forest Soil Carbon and Nitrogen Storage

The average C and N stored in organic horizons (combined Oe and Oa horizons) across all forest types was 7.1 ± 1.0 kg m^{-2} and 304 ± 43 g m^{-2}, respectively (values represent mean ± 1 s.e.). Overall, a majority of the organic horizon C (5.6 ± 1.0 kg m^{-2}, 79%) and N (238 ± 41 g m^{-2}, 80%) were stored in Oa horizons, though relative contributions of Oe and Oa horizons varied with forest type (Table 2). Average mineral soil pool sizes were 17.3 ± 2.5 kg C m^{-2} and 805 ± 113 g N m^{-2}. About half of the mineral horizon C

Table 2. Mean C (kg m^{-2}) and N (g m^{-2}) storage and C/N ratio measurements (± 1 standard error) for Oe, Oa, total organic (Oe + Oa), 0–10 cm, 10–20 cm, 20+ cm, total mineral, and whole-profile soils sampled in northern hardwood (NH), spruce-fir (SF) and pine-dominated (PW) plots.

	Forest type								
	Northern Hardwood			Pine			Spruce-Fir		
Horizon	C	N	C/N	C	N	C:N	C	N	C:N
	kg m^{-2}	g m^{-2}							
Oe	1.3 ± 0.1	59.6 ± 5.9	21.3 ± 0.4	1.6 ± 0.2	59.0 ± 9.1	27.5 ± 1.4	1.9 ± 0.5	84.1 ± 21.5	22.6 ± 1.1
Oa	4.5 ± 1.0	187.7 ± 37.6	23.4 ± 1.0	0.8 ± 0.6	39.1 ± 30.7	24.9 ± 4.1	11.4 ± 2.0	486.2 ± 88.5	23.9 ± 1.4
Total Organic	5.8 ± 1.0	247.3 ± 38.2	22.9 ± 0.8	2.4 ± 0.7	98.1 ± 34.6	27.1 ± 1.6	13.3 ± 2.1	570.3 ± 92.1	23.3 ± 1.2
0–10 cm	5.3 ± 0.4	246.3 ± 19.1	22.1 ± 0.9	7.3 ± 1.5	350.9 ± 69.9	22.1 ± 1.7	3.1 ± 1.1	126.8 ± 42.3	23.7 ± 3.6
10–20 cm	4.6 ± 0.4	203.7 ± 9.9	22.5 ± 1.3	4.4 ± 0.7	206.0 ± 37.1	20.7 ± 0.9	2.1 ± 1.2	88.2 ± 44.2	21.0 ± 4.0
20+ cm	12.8 ± 4.9	615.3 ± 192.4	20.4 ± 1.4	8.0 ± 1.4	383.1 ± 116.0	18.7 ± 1.5	1.0 ± 1.0	41.8 ± 41.8	23.7 ± na†
Total Mineral	22.7 ± 4.8	1065.3 ± 186.4	21.5 ± 1.2	19.7 ± 2.4	940.0 ± 156.2	28.6 ± 7.2	6.2 ± 2.5	256.8 ± 106.8	24.0 ± 3.6
Whole-Profile	28.5 ± 4.8	1312.6 ± 179.7	21.7 ± 1.1	22.1 ± 2.4	1038.1 ± 164.8	25.8 ± 4.1	19.5 ± 2.1	827.1 ± 77.8	23.7 ± 1.4

† only 1 spruce-fir site had 20+ cm mineral soil.

(8.3 ± 2.5 kg m^{-2}, 48%) and N (396 ± 102 g m^{-2}, 50%) were in the 20+ cm layer (Table 2).

The average whole-profile amounts for all sites were 24.4 ± 2.5 kg C m^{-2} and 1.1 ± 0.1 kg N m^{-2}. Considering all sites, there was significantly more C ($P = 0.0005$) and N ($P = 0.0002$) in mineral horizons than in organic horizons. Overall, despite differences in the character and composition of organic and mineral horizons, the mineral horizon C/N ratio (23.9 ± 2.2) was not different from the organic horizon C/N ratio (24.1 ± 0.7).

Relationships between Amounts of Soil Carbon and Nitrogen and Potential Predictor Variables

Biologic Factors

Organic horizon (combined Oe and Oa) C and N contents were significantly different among forest types (Fig. 2). Spruce-fir plots had the most organic horizon C and N while P plots contained the least (Table 2). Mineral horizon C and N contents were significantly lower in SF sites than in either NH or PW plots, which were not significantly different (Fig. 2). On average, NH whole-profile C and N pools were the largest, though they were not significantly different from C and N pools in either SF or PW plots (Fig. 2).

There were significant differences in the vertical distribution of soil C and N among forest types. There was significantly more C and N in mineral horizons than in organic horizons in both NH ($P < 0.0001$) and PW ($P = 0.004$) plots. However, mineral soil C and N amounts were not different from organic horizon pools in SF plots ($P = 0.13$).

The organic horizon C/N ratio was significantly higher in PW plots than in NH plots, but was not different between PW and SF plots (Table 2). There were no significant differences in either the mineral horizon (Table 2) or whole-profile (Fig. 2) C/N ratios among forest types.

Topographic Factors and Parent Material

Linear regression showed a positive relationship between elevation and organic horizon C ($R^2 = 0.34$, $P = 0.0001$) and N ($R^2 = 0.41$, $P < 0.0001$) contents. In contrast, mineral horizon C ($R^2 = 0.13$, $P = 0.03$) content was significantly and inversely correlated with elevation. Neither N content nor the C/N ratio were significantly related to elevation in mineral horizons. As a result, there was no significant relationship between elevation and either whole-profile C or N content or the C/N ratio.

We tested for aspect effects in the pooled set of sites using a Tukey-Kramer test and found that plots with different aspects did not have significantly different C or N content or C/N ratios in either organic or mineral horizons. Likewise, depth to bedrock (designated as either shallow to lithic contact or no lithic contact) and soil texture (i.e., % silt + clay) were not related to any differences in mineral soil C or N content. Excluding one site which had an unusually large rock near the bottom of the pit, rock volume was also not significantly related to either mineral horizon C or N content in the pooled data.

Climate Variables

Plots with a greater number of GSDD had significantly lower organic horizon C and N contents (Fig. 3A and 3B).

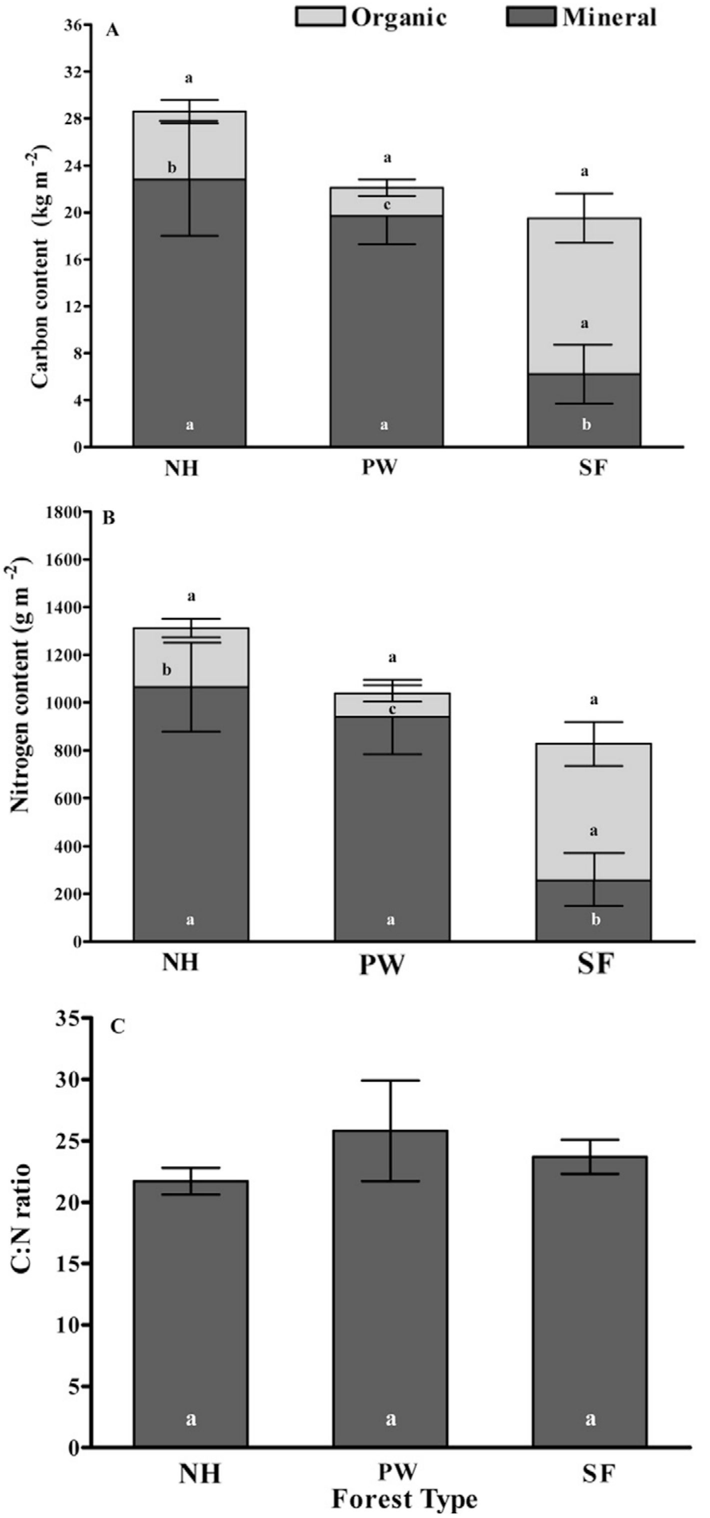

Fig. 2. Mean organic horizon (Oe + Oa) and (A) total mineral C and (B) N storage and whole-profile C/N ratio (C) (±1 standard error) measurements for northern hardwood (NH), spruce-fir (SF), and pine woods (PW) sites sampled in this investigation. Bars within the same soil stratum not connected by the same letter are significantly different. Letters above each bar represent differences in whole-profile C and N storage.

However, the influence of GSDD on mineral horizon C and N amounts was not significant, though the trend was positive (Fig. 3D and 3E). As a result, there was not a significant relationship between GSDD and whole-profile C or N content in the pooled set of plots. Further, plots with a longer, warmer

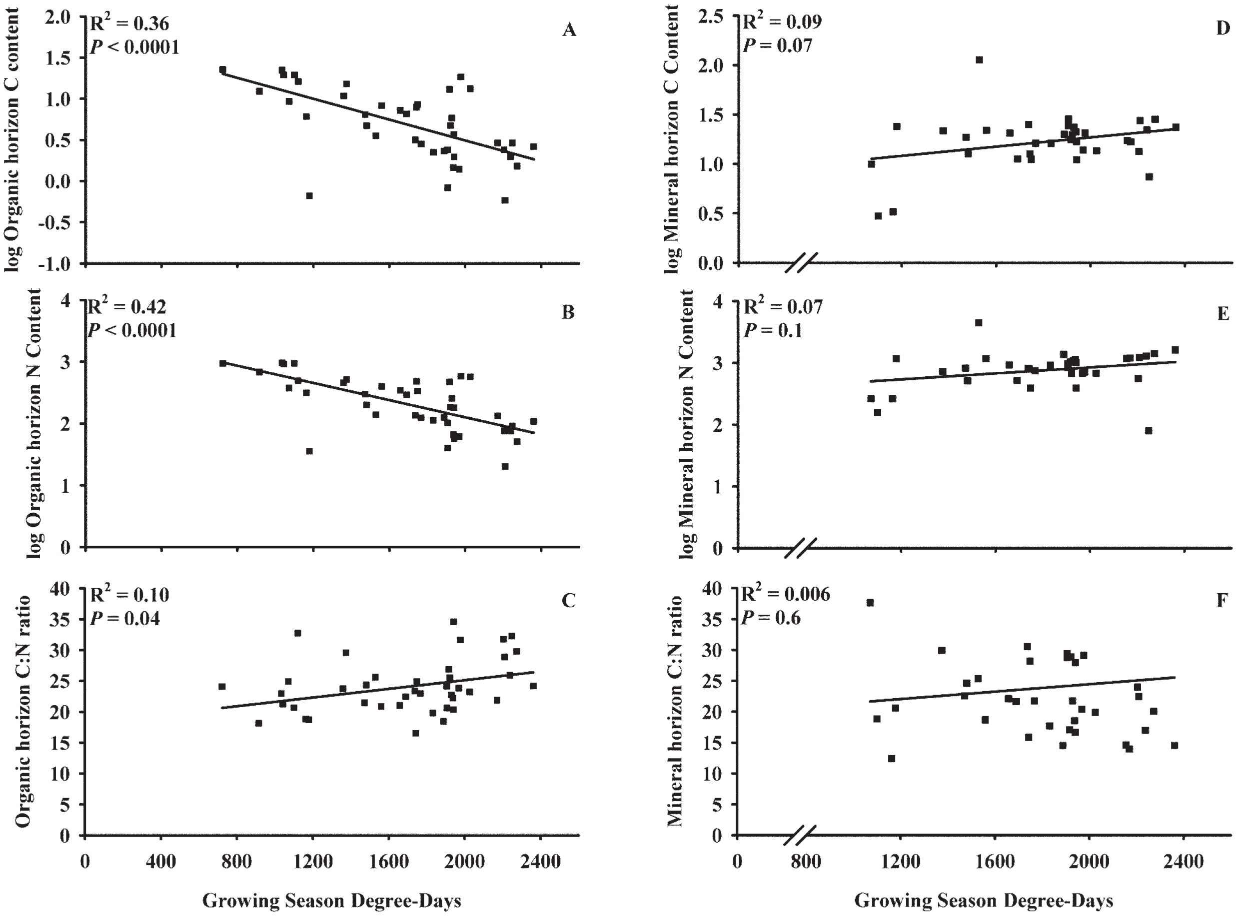

Fig. 3. The effect of growing season degree-days (GSDD) on organic horizon (A-C) and total mineral horizon (D-F) C and N storage and C/N ratio measurements for the pooled sites.

growing season had a significantly higher C/N ratio in the organic horizons (Fig. 3C), though no significant effects were observed with C/N ratios in either mineral horizons (Fig. 3F) or for the whole profile.

Organic horizon C (R^2 = 0.18, P = 0.005) and N (R^2 = 0.23, P = 0.001) amounts increased and the C/N ratio decreased (R^2 = 0.14, P = 0.02) with increasing MAP. Neither mineral-horizon nor the whole-profile C or N amounts were related to MAP. Organic horizon C and N amounts increased along the gradient of increasing N deposition, though the organic horizon C/N ratio was not significantly different across the gradient of N deposition (Fig. 4A–4C). There was an inverse relationship between N deposition and mineral horizon C (R^2 = 0.29, P = 0.0008) and N (R^2 = 0.20, P = 0.007; data not shown). Whole-profile C and N amounts, and C/N ratios were not significantly correlated with rates of N deposition.

Multivariate Regression Tree Analysis of Carbon and Nitrogen Amounts for Pooled Sites

Considering all sites, MRT analysis indicated that the variability in organic horizon C and N storage was best explained by GSDD, while N deposition, aspect, and conifer importance, in different combinations, were of secondary importance (Table 3). Multivariate regression tree analysis explained similar variability in organic horizon C (65%) and N (69%) amounts. The greatest organic horizon C (17.4 kg m^{-2}) and N (805 g m^{-2}) contents were in the coldest plots (fewest GSDD), which were the highest elevation SF plots. The group of plots with the greatest number of GSDD and least amount of N deposition had the smallest organic horizon C (1.8 kg m^{-2}) and N (69 g m^{-2}) pools. This group included NH and PW plots. Groups of plots with the greatest and least C and N were significantly different, while groups with intermediate C or N content were not necessarily different (Fig. 5).

Multivariate regression tree analysis explained 62% of the SS in mineral horizon C and 64% of the SS in mineral horizon N contents. Growing season degree-days explained the greatest amount of SS in both mineral horizon C and N pools (Table 3). However, in contrast to trends in organic horizon C and N, mineral horizon C and N contents were positively correlated with GSDD (Fig. 3A–3D). Slope, conifer importance, and N deposition were secondary influences on mineral soil C amount (Fig. 6). Precipitation and % silt + clay were secondary influences on mineral horizon N content. The group with the greatest amount of mineral soil C (20.8 kg m^{-2}) included the least sloping plots with high conifer importance values and the longest, warmest growing seasons (NH and PW plots). The group of plots with the least amount of mineral soil C (2.0 kg m^{-2}) had the shortest growing seasons (Fig. 6). These were SF plots. The group with the greatest mineral soil N (1212 g m^{-2}) was subject to a longer growing season, less precipitation, and had finer-textured soil (NH and PW plots). Mineral soil N pools were smallest in the colder SF plots (86 g m^{-2}) with deep organic horizons and thin mineral horizons.

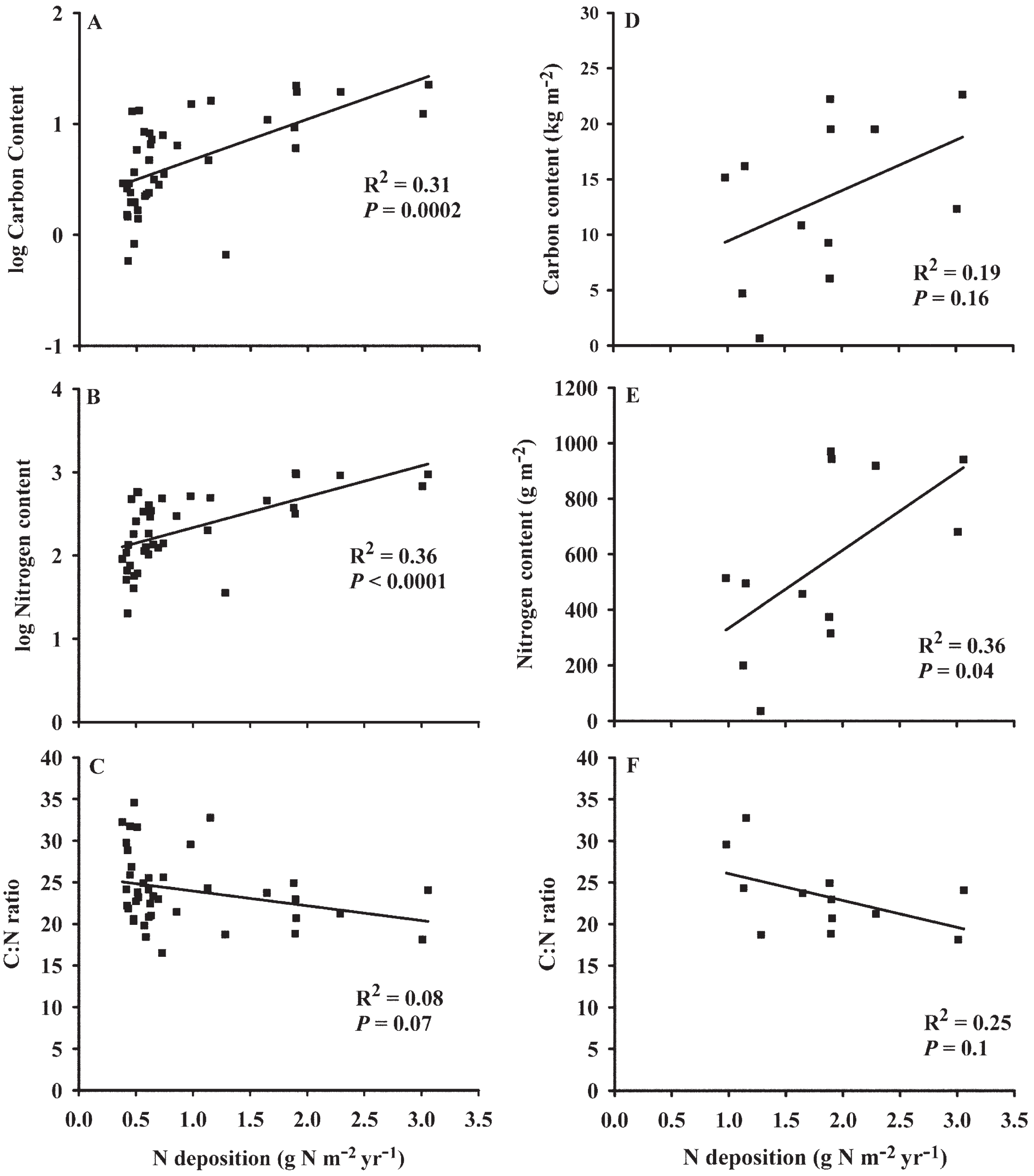

Fig. 4. The effect of inorganic atmospheric N deposition on organic horizon (Oe+Oa) C and N storage and C/N ratio for all sites sampled (A-C) and for 12 spruce-fir (SF) sites (D-F). Carbon and N content for the pooled data were log transformed.

Table 3. Variability in C and N storage explained (% sums of squares explained) by different predictor variables in multivariate regression tree (MRT) analyses of total organic, total mineral and whole-profile (organic + mineral) soil pools.

		Variable								
Soil stratum	Nutrient	GSDD†	MAP‡	N deposition	Aspect	% silt + clay	Conifer Importance	Rock volume	Slope	Total§
		% SS¶ explained								
Total organic	C	51	–	8	1	–	5	–	–	65
	N	58	–	9	–	–	2	–	–	69
Total mineral	C	55	–	3	–	–	3	–	3	64
	N	50	8	–	–	6	–	–	–	64
Whole-profile	C	13	–	–	–	18	8	8	1	48
	N	17	–	–	–	21	–	8	1	47

† Growing season degree-days.

‡ Mean annual precipitation.

§ Represents the total sums of squares explained for each tree.

¶ Sums of squares.

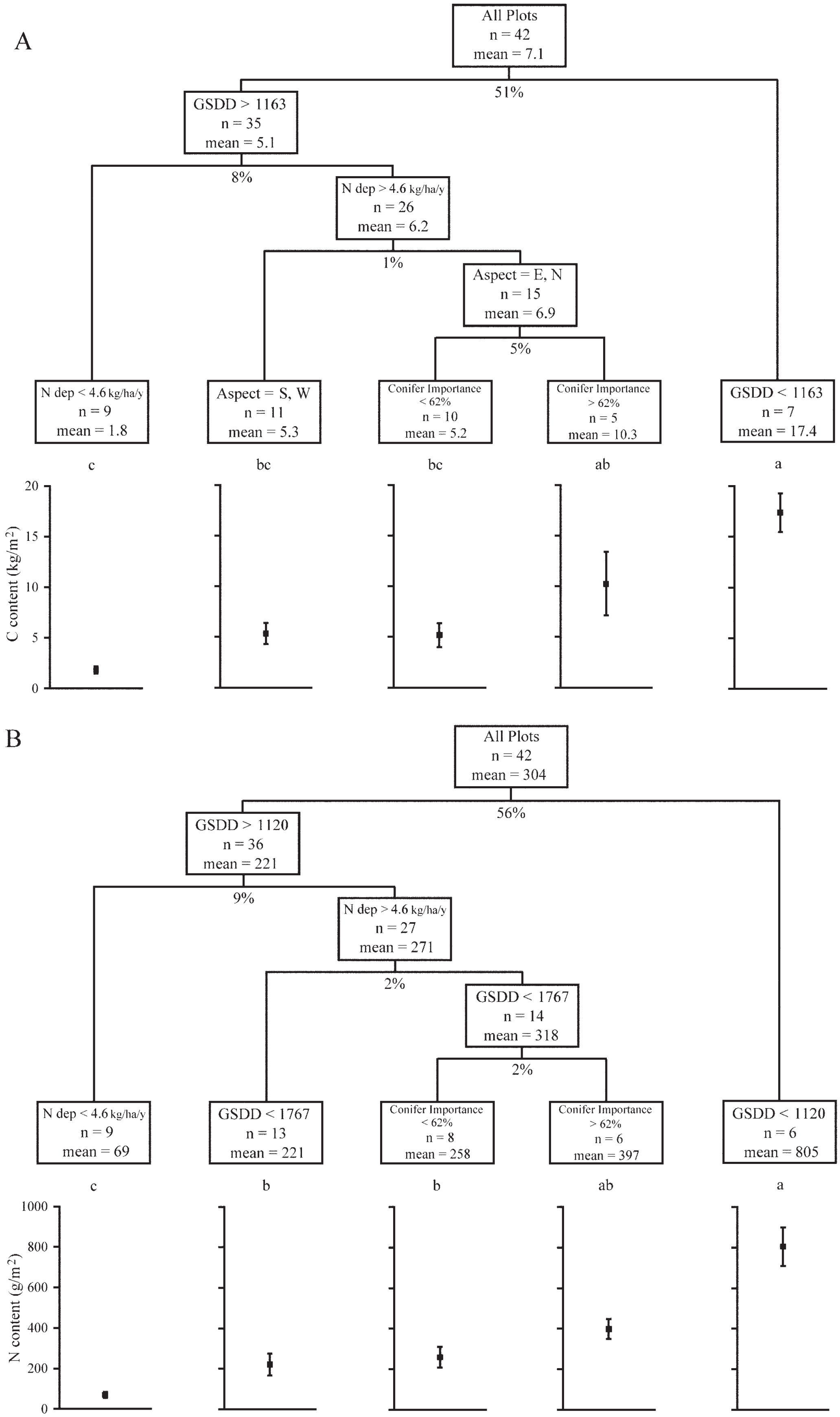

Fig. 5. Multivariate Regression Tree (MRT) for organic horizon (Oe + Oa) C (A) and N (B) storage. Individual boxes represent groups determined by the splitting criterion and are defined by the number of sites (*n*) and the mean C (kg m^{-2}) or N (g m^{-2}) storage value of those sites. The amount of variability explained by each split is represented as a percentage at each node. Graphs under each terminal group represent the mean ± 1 standard error of that group. Groups not connected by the same letter are significantly different.

Multivariate regression tree analysis of whole-profile C and N contents in 41 plots indicated that a different suite of predictor variables was related to the observed storage patterns. Growing season degree-days, % silt + clay, rock volume, and slope were the important influences (Table 3). Further, conifer importance was an additional influence on whole-profile C. These models explained considerably less SS for whole-profile C (48%) and N (47%) than those for organic horizons and mineral horizons treated separately (Table 3).

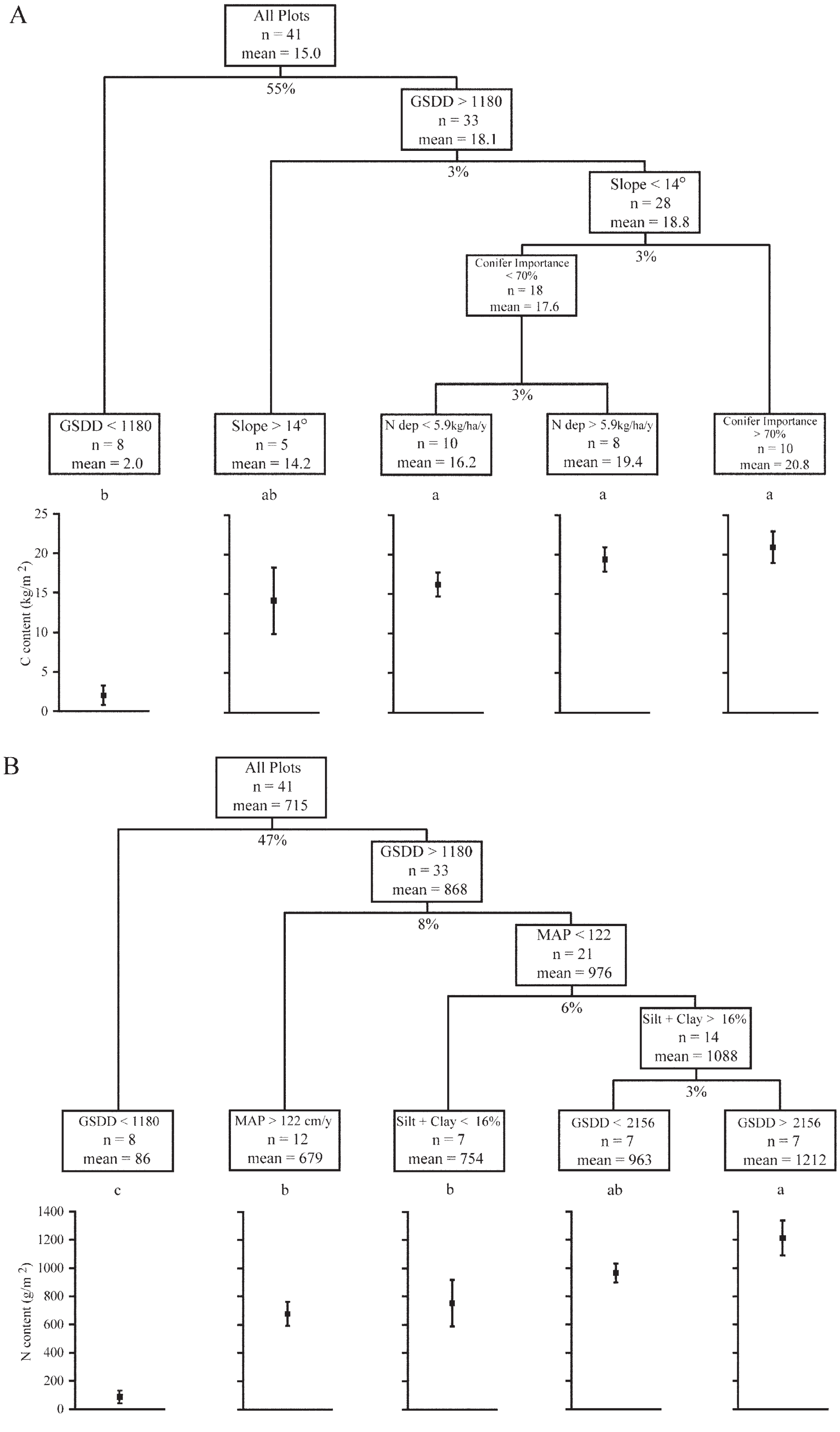

Fig. 6. Multivariate Regression Tree (MRT) for mineral horizon (A) C and (B) N storage. Individual boxes represent groups determined by the splitting criterion and are defined by the number of sites (n) and the mean C (kg m^{-2}) or N (g m^{-2}) storage value of those sites. The amount of variability explained by each split is represented as a percentage at each node. Graphs under each terminal group represent the mean ± 1 standard error of that group. Groups not connected by the same letter are significantly different.

The group with the greatest whole-profile C content (28.6 kg m^{-2}) was a combination of plots from all three forest types with a greater number of GSDD, finer-textured mineral soil (% silt + clay) and where conifer importance was relatively high. The group of plots with the greatest whole-profile N content (1453 g m^{-2}) was represented by NH and PW plots with longer growing seasons, less rock volume, and finer-texture mineral soil. Groups consisting of SF plots with steep slopes and a shorter, cooler growing season had the least whole-profile C (16.3 kg m^{-2}) and N (730 g m^{-2}).

DISCUSSION

Regional Comparisons of Soil Carbon and Nitrogen Amounts

Carbon and N amounts in the Adirondack forest soils sampled here were generally higher than previously reported estimates for similar northeastern U.S. forests (Table 4). For comparable depths stratified by forest type, our estimate of whole-profile C content in NH plots (157 Mg ha^{-1}, to a depth of 20 cm) was 26 to 76% higher than other reported measurements in similar northeastern U.S. forest soils (Table 4). Mineral horizon C content in NH sites (99 Mg ha^{-1}) was also greater than estimates of average maple-beech-birch forest mineral soil C storage (61 Mg ha^{-1}) in the USA (Johnson and Kern, 2003). Likewise, our estimate of average whole-profile N storage, 7000 kg ha^{-1} (to a depth of 20 cm), was higher than other reported values for similar NH forests (Table 4).

Estimates of whole-profile C and N (to a depth of 20 cm) in SF plots were similar to values reported for Whiteface Mt, NY (Friedland

Table 4. Soil C (Mg ha^{-1}) and N (kg ha^{-1}) storage in organic horizon (Oe + Oa), mineral horizon (0–20 cm) and whole-profile (organic horizon + mineral soil) pools of northern hardwood (NH), spruce-fir (SF) and pine-dominated (PW) forests from nine sites in the northeastern U.S. (i.e., HF = Huntington Forest; HB = Hubbard Brook; HV = Harvard Forest; CT = Connecticut; BB = Bear Brook; HVPH = Harvard Forest; Prospect Hill tract; HM = Howland, Maine; VT = Vermont; and AD = Adirondack).

Location	Forest Type	Organic horizon C	Mineral horizon C	Whole-profile C	Organic horizon N	Mineral horizon N	Whole-profile N	Source
		Mg ha^{-1}	Mg ha^{-1}	Mg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	
HF	NH	22	103	125	1100	4100	5200	Mitchell et al., 1992
HB	NH	30†	59	89	1300†	2800	4100	Huntington et al., 1988
WF	SF	71	117	188	2600	5100	7700	Friedland and Miller, 1992
HV	PW	23	–	–	940	–	–	Aber et al., 1993
CT	NH	24	65‡	89	1300	4200‡	5500	Finzi et al., 1998
BB	NH, RS	75	56‡	131	2400	2300‡	4700	Parker et al., 2001
HVPH	PW	25	49‡	74	900	2400‡	3300	Compton and Boone, 2001
HM	SF	73	51§	124	1100	1500§	1100	Fernandez, 1992
VT	NH	20	58	77	–	–	–	Johnson et al., 2009¶
AD	NH	58	99	157	2600	4500	7000	This Study
AD	PW	24	120	140	980	5600	6500	This Study
AD	SF	133	52	185	5700	2200	7900	This Study

† FF = Oi + Oe + Oa.

‡ 0–15 cm mineral soil.

§ 0–28 cm mineral soil.

¶ For well-drained soils, soil C was calculated as 0.5 × SOM.

and Miller, 1992; Table 4). Although there were differences in organic and mineral horizon storage between the two investigations, it is notable that our values of whole-profile C and N differed by <3% from those of Friedland and Miller (1992). Further, our estimates of organic horizon C and N storage in PW sites (24 Mg C ha^{-1}, 980 kg N ha^{-1}) differed by <10% from pine stands in the Harvard Forest (Aber et al., 1993; Compton and Boone, 2000; Table 4). Since some of the PW plots in this investigation (our observations) had an agricultural history, it is likely that this was also an important influence on soil C and N in these forests, though we did not use prior land use as a variable in this study.

Overall, the Adirondack forest soils sampled in this investigation, especially the NH soils, had larger soil C and N pools than similar forest soils in the northeastern USA. Moreover, since there were no significant differences in whole-profile C and N among the three forest types, the overall averages (24 kg C m^{-2} and 1.1 kg N m^{-2}) for the sites sampled in this study likely serve as a reasonable estimate of the C and N stored in well-drained forest soils across the Adirondack region, even though the distribution of plots among the three forest types is not representative of their relative abundance across the Adirondacks.

Relative Influence of Soil-forming Factors on Carbon and Nitrogen Contents, Pooled Sites

Although linear regression analysis indicated a significant influence of MAP on organic horizon C and N storage, MRT analysis revealed that GSDD and N deposition, and not MAP, were the important influences on C and N storages. As an influence on soil C or N content, greater precipitation typically stimulates productivity more than decomposition, thus soil organic matter content generally increases along gradients of increasing precipitation (e.g., Jenny, 1980). However, in the plots sampled here, MAP was directly correlated with elevation (Spearman's $\rho = 0.90$, $P < 0.0001$) and productivity decreases with increasing elevation in the Adirondacks (e.g., Joshi et al., 2003). If MAP is having any effect on soil C and N, it may be that wetter soils tend to be colder because the specific heat of water is much higher than that of the soil particles, thus resulting in colder temperatures which reduce decomposition rates.

The observed relationships among organic horizon C and N and the environmental variables in the set of pooled plots (Fig. 5) were consistent with established ecological principles. Decomposition would be slowed in plots with cooler temperatures, colder (north and east) aspects, and more conifer litter, which has higher lignin content (e.g., Melillo et al., 1982) and should decompose more slowly than hardwood litter (Taylor el al., 1989; Aber et al., 1990). Further, N deposition was directly related to organic horizon C and N. This is consistent with the interpretation of data from recent investigations which have suggested that N deposition is stimulating forest productivity (deVries et al., 2006; Kulmatiski et al., 2007; Magnani et al., 2007) and thus is contributing to greater forest soil C and N storage. However, the correlation between N deposition and GSDD (Spearman's $\rho = -0.95$, $P < 0.0001$) in this study makes any effect of N deposition difficult to separate from that of GSDD. When the rates of N deposition and the amounts of soil N were compared, it was clear that the influence of atmospheric N deposition on the soil N pool was minimal (see below).

For the set of pooled mineral-horizon data, GSDD was again the primary influence on C and N amounts (Table 3, Fig. 6). However, in this case, warmer sites had more C. These trends were likely attributable to the fact that annual net primary productivity (ANPP) in the Adirondack region is considerably higher at lower elevation sites (e.g., Joshi et al., 2003) where temperatures are warmer. Greater N deposition was also associated with greater C storage as well, though its contribution to SS explained was relatively minor (Fig. 6). Considering mineral horizon N, there was also a strong influence of GSDD and a tendency for N to accumulate in finer-textured mineral horizons. Interestingly, N deposition did not have a measurable effect on mineral soil N in the pooled data set. Based on the factors known to influence C and N accumulation in forest soils (e.g., Guo et al., 2006), and given the strong elevation gradient in this data set, we suggest that the relative importance of natural influences indicated by the MRT analyses (Fig. 6) is ecologically plausible.

The relative influences of the same set of predictor variables on whole-profile C and N were different from those for organic and mineral horizons when considered separately. These models also explained less of the total SS in the whole-profile C and N contents compared with organic and mineral horizons when assessed separately (Table 3). This finding was consistent with that of Kulmatiski et al. (2004) and Johnson et al. (2009) for C and N storage in similar New England forest soils. In the Adirondack plots, this outcome was due to the fact that as organic horizon C and N amounts increase with decreasing GSDD, the mineral soil pools decrease (e.g., Fig. 3). Accordingly, we suggest that analyzing organic and mineral horizons separately yields more meaningful results.

Differences in Soil Carbon and Nitrogen Contents among Forest Types

Organic horizon C pools have been found to vary with changes in species composition (Finzi et al., 1998). Kulmatiski et al. (2004) showed that in Connecticut, forest cover type was a good predictor of both organic horizon and mineral horizon N storage. In the Adirondacks, NH, SF, and PW forests are distinct ecosystems and the differences in biotic, edaphic, and climatic influences might be expected to produce different patterns of soil C and N storage. In this study, the SF plots had the greatest organic horizon C and N contents, and the largest fraction of the whole-profile C and N (approximately 70%) in the organic horizons. Conversely, over 80% of the whole-profile C and N stored in NH and PW soils were in the mineral horizons. As a result, whole-profile C and N amounts were not significantly different among the three forest types (Fig. 2). Moreover, whole-profile C/N ratios were also not different between the forest types.

It is interesting to note that increased N deposition was strongly associated with increased C and N amounts in organic horizons in SF plots (Fig. 4D–4F). Further, an MRT analysis of organic horizons in SF forests indicated that N deposition explained a substantial amount of the SS in C (54%), and N (79%) storage (data not shown). Given the strong gradients of atmospheric N deposition that exist across the Adirondack Mountains (Miller, 1993; Ito et al., 2002; McNeil et al., 2007) and the high deposition rates in the SF plots (which are among the highest rates of N deposition in North America), we might have expected that plots receiving greater rates of N deposition would have larger soil N, and possibly larger soil C pools and a lower C/N ratio, as a result. This was suggested by Aber et al. (2003) and is consistent with the findings of McNulty et al. (1991) who showed that organic horizon N concentration was positively correlated with N deposition in New England spruce-fir forests.

When N deposition was removed from the SF MRT analysis as a predictor variable, GSDD had a similar influence and accounted for 51 and 59% of the SS in organic horizon C and N storage, respectively. Moreover, a quantitative comparison of N deposition and N pools in SF soils suggested that the influence of atmospheric N deposition was limited. If we assume that (i) the current rates of N deposition throughout the Adirondacks have existed for the past 50 yr, and (ii) all of the N was retained in the soil (both generous assumptions), the mean rate of atmospherically derived N input only accounted for approximately 16% of mean organic horizon N content in SF plots. Omitting a single plot where N deposition was greater than organic horizon N storage, 50 yr of N deposition accounted for, at most, 30% of the organic horizon N pool (Fig. 7).

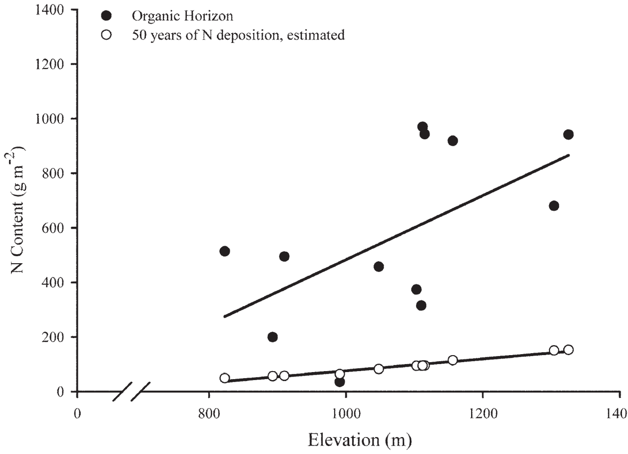

Fig. 7. A comparison between the effect of elevation on organic horizon N content (closed circles) and estimates of 50 yr of N deposition (open circles) for 12 spruce-fir (SF) plots. Lines are included for visual reference and represent linear regression fits to either the organic horizon N data or the N deposition estimates.

Compared with the whole-profile N content, 50 yr of atmospherically derived N averaged about 11% of the amount of whole-profile N stored in SF soils which is approximately the same as the whole-profile N variability. Accordingly, any effect of N deposition in SF soils would be difficult to detect. Also, using the same reasoning for the lower elevation NH and PW sites, the effects of atmospherically derived N on whole-profile N pools would be even less likely as the estimated 50-yr inputs of atmospherically derived N accounted for only ~2% of current amounts in these forest soils (Fig. 8).

While MAP, N deposition, and GSDD were correlated variables that can influence soil C and N pools, it seems clear that the well-established relationships among cooler temperatures, increased conifer importance and the resultant decreased microbial decomposition rates were the most important factors in controlling soil C and N pools in the SF plots. This does not preclude the possibility of future effects of N deposition in these forests. However, we suggest that atmospheric N is still a small enough component of the soil N pool that its effect, if any, on spatial patterns of soil N storage was considerably less than that of temperature.

One aspect of the SF soils that may have been affected by atmospheric N deposition was the C/N ratio. Zarin et al. (1998) compared the whole-profile C/N ratios for upper montane conifer forests in polluted and unpolluted areas and found that forests receiving little or no atmospheric N inputs had C/N ratios > 30:1, whereas conifer forests subjected to sources of airborne N had C/N ratios closer to 20:1. Our estimates of 50 yr of N deposition suggest that N deposition could have lowered the C/N ratio in the SF soils from 28.4:1 to 23:1. Whether or not this has actually happened, and whether this could have had an effect on C pools, is a matter of conjecture at present.

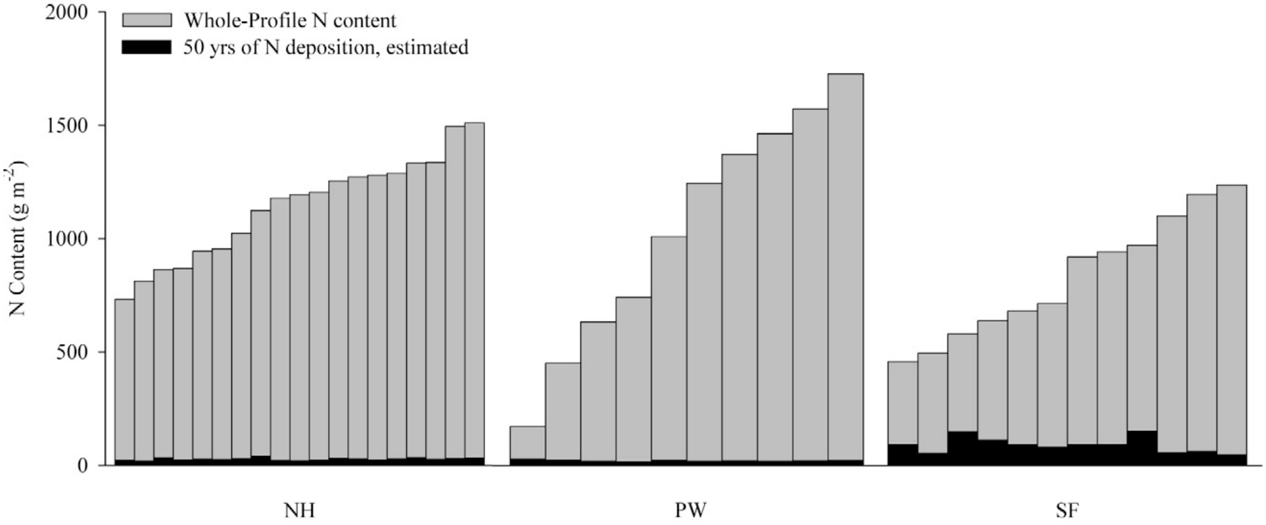

Fig. 8. Whole-profile N storage and the estimated contribution of 50 yr of N deposition for each plot in northern hardwood (NH), pine (PW), and spruce-fir (SF) plots.

CONCLUSIONS

This investigation of 42 Adirondack Mountain forest soils indicated that the soil C and N contents of these soils were greater than in similar forests of the northeastern USA. We also showed that whole-profile C and N contents and the C/N ratio were not different among NH, SF, and PW stands, thus we were unable to accept our original hypotheses. However, we observed that the greatest organic horizon C and N amounts were in high-elevation SF plots and that mineral soil C and N storage were greatest in the lower elevation northern hardwood and pine plots. Growing season degree-days had the greatest influence on the amounts of C and N in both organic and mineral horizons, while a range of other site factors contributed modestly at best to the SS explained in MRT analyses. Various combinations of those ancillary factors (soil texture, aspect, rock volume, and N deposition) were less important than GSDD and consistent with their expected roles. Atmospheric N deposition rates vary widely across this set of plots from regional background values (ca. 0.5 g N $m^{-2}yr^{-1}$) to some of the highest reported rates in North America (> 3 g N $m^{-2}yr^{-1}$). Despite the correlation with soil C and N contents, especially in the high-elevation SF plots, the quantity of anthropogenic N added over the past half-century or so was, at most, responsible for only a small portion of the current forest soil N pools and the differences in soil N content along the N deposition gradients.

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