

DIVISION S-7—FOREST & RANGE SOILS

Landscape Determinants of Soil Carbon and Nitrogen Storage in Southern New England

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ABSTRACT

We present estimates of C and N storage from forest soils of northeastern Connecticut, USA. Fifty-six plots were sampled from the forest floor (FF) to 15 cm, and 21 of these plots were sampled to 60 cm. Carbon storage varied more in the FF ($2.32 \pm 1.06 \text{ kg C m}^{-2}$) than in the top 15 cm of mineral soil ($3.43 \pm 0.70 \text{ kg C m}^{-2}$). Nitrogen storage, however, varied less in the FF ($0.086 \pm 0.037 \text{ kg m}^{-2}$) than in the mineral soil ($0.224 \pm 0.068 \text{ kg m}^{-2}$). Carbon and N storage from the FF to 60 cm averaged 7.91 ± 1.74 and $0.56 \pm 0.13 \text{ kg m}^{-2}$, respectively. Variations in nutrient storage were explained using one and two-way ANOVAs, three-way multivariate regression trees (MRTs) and three site factors: forest stand composition, soil series, and topography. Carbon and N storage in the FF were best explained by stand composition. Carbon storage in the mineral soil was best explained by topography and N storage in the mineral soil was best explained by both stand composition and soil series. In general, hemlock (*Tsuga canadensis* Carr) stands and hill bottoms were associated with the most C and the soil series in the poorest drainage class and hardwood stands were associated with the most N. When these results were compared with other estimates from the region we observed that nutrient storage varied widely in the FF at local scales (<10 km), but varied more widely in the mineral soil at regional scales (>100 km). These data suggest that soil series and stand composition will provide good local and regional estimates of N storage. Similarly, stand composition will provide good local estimates of C storage. However, variables that explain variation in the mineral soil, such as topography and management history, will be needed to provide regional estimates of C storage.

SOILS HAVE BEEN suggested to be an important C sink due to the size (2400 Pg C to a 2-m depth) and the activity (approximately 50 yr turnover of approximately 75% A horizon C) of the soil C pool (Trumbore et al., 1996; Kirschbaum, 2000). Forest soils, in particular, are believed to account for roughly 70% of global biosphere to atmosphere CO₂ exchange (Waring and Schlesinger, 1985) and much of this exchange results from the decomposition of forest litter and root respiration (Vogt et al., 1982; Bowden et al., 1993; Bhupinderpal et al., 2003).

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It has long been suggested that rates of litter decomposition and root respiration vary under different forest species because of differences in litter quantity and quality among species (Zinke, 1962; Pare and Bergeron 1996; Templer et al., 2003). However, direct measurements of C and N pool sizes to specifically test this hypothesis are uncommon (Menyailo et al., 2002; Tremblay et al., 2002). One reason this type of sampling has been limited is because of the difficulty of accurately sampling heterogeneous forest soils (Kulmatiski et al., 2003).

A consequence of the lack of adequate sampling is that models of soil C and N cycling lack robust empirical data (Lexer et al., 1999; Burt et al., 2003). Baseline data are needed to better calibrate models of C and N cycling (Yost et al., 1993; Lexer and Honninger, 1998). In some cases it may be possible to collect these data in a factorial design that would parse the effect of each soil-forming factor (Cahallinor, 1967). In many cases, however, it will be impossible to sample all combinations of the soil-forming factors. For example, some forest tree species are not commonly found on steep slopes and other forest tree species are not commonly found on excessively drained soils.

As an alternative, baseline data can be collected in a way that can be readily used in spatially explicit nutrient budget models using GIS maps, in particular (Conant and Paustian, 2002; Coomes et al., 2002). Forest stand composition, soil series, and topography are common digitized layers in GIS models that provide a large amount of information on the soil-forming factors. Sampling designs that are stratified by these factors may not parse the individual effects of the soil-forming factors, but they will reflect the natural distribution of nutrient storage associated with these factors on the landscape (Garten and Ashwood, 2002).

Our objective was to provide estimates of C and N storage that were stratified by spatially explicit characteristics for which data are readily available: stand composition, soil series, and topography. We predicted that tree species with recalcitrant litter (Hemlock, Oak [*Quercus* spp.]) would demonstrate large C and N pools near the soil surface whereas forest stands with labile litter (Maple [*Acer* spp.], Ash [*Fraxinus*]) would demonstrate C and N pools that had moved deeper into the soil profile. We also predicted that soils with poor drainage

Abbreviations: FF, forest floor; GLM, general linear model; HH, hemlock/hardwood forest; Hm, hemlock forest; Hw, hardwood forest; MRT, multivariate regression tree; *n*, sample size; O, organic; PO, pine/other forest.

would realize slower decomposition and demonstrate larger soil nutrient pools than soils with better drainage. Finally, we predicted that litter and soil nutrients would move downhill over time producing an accumulation of soil nutrients at the bottoms of hillslopes.

MATERIALS AND METHODS

Site Description

The research was conducted in the 3173-ha Yale-Myers Forest in northeastern Connecticut, USA (42°N lat., 72°W long.). This forest was managed for agriculture, grazing, and intensive logging between 1730 and 1850. Agricultural activities were then abandoned and any remaining forests were heavily logged until about 1930. Some stands established during this time were later blown down during the hurricane of 1938. Stand ages estimated from increment cores taken at a height of 1.4 m, from the dominant tree in each plot were estimated at 85 ± 22 yr old but varied from 46, established after the hurricane of 1938, to 121 yr old, established after agricultural abandonment (Winer, 1955). Basal area in each plot averaged $31 \pm 8.4 \text{ m}^{-2} \text{ ha}^{-1}$.

Forest clearing and grazing at the site was likely to homogenize the pre-agricultural effects of forest stand composition on soil nutrient storage, but was less likely to homogenize the effects of topography or drainage class on nutrient storage. Therefore, we assumed that variations in soil C and N storage observed today reflects the past 100 yr of tree growth and the longer-term effects associated with soil series and topography.

In 1993 the Yale-Myers Forest was composed of 29% hemlock, 32% oak, 20% pine [*Pinus* spp.], and 20% hardwoods. These forest species do not typically occur in monocultural stands, so for this study six stand compositions were selected to represent the forest types found in non-wetland forests across southern New England. Stand compositions were defined by tree basal area as follows: hardwoods (Hw) <25% hemlock, <50% oak, and <25% pine; hemlock/hardwood (HH) 25 to 60% hemlock, and <50% oak; oak (Oak) >50% oak; pine (Pine) $\geq 75\%$ pine; pine/other (PO) 25 to 75% pine; and hemlock (Hm) $\geq 60\%$ hemlock.

Hardwood plots were dominated by sugar maple (*Acer saccharum* Marsh) (13% of total tree cover in all plots), black birch (*Betula lenta* L.) (7%), black cherry (*Prunus serotina* Ehrh.) (7%) and pignut hickory (*Carya glabra* Mill Sweet.) (4%) with red maple (*Acer rubrum* L.) (1%), paper birch (*Betula papyrifera* Marsh) (1%), shagbark hickory (*Carya ovata* Mill.) (1%), bitternut hickory (*Carya cordiformis* Wang.) (1%), and white ash (*Fraxinus americana* L.) (2%) common. Oak plots were dominated by red oak (*Quercus rubra* L.) (20%) with some white oak (*Q. alba* L.) (1%). Pine plots were dominated by white pine (*Pinus strobus* L.) (19%) with some red pine (*P. resinosa* Ait.) (1%). Pine/other plots contained pines with any other tree species. Hemlock plots were dominated by eastern hemlock (24%).

Parent material at Yale-Myers Forest is mostly glaciofluvial and glacial till. The glaciofluvial till is derived from schist and gneiss and is a water sorted mixture of sand and gravel. One of the four soil series sampled in this study, the Hinckley series developed on the glaciofluvial deposits. The Hinckley soils are sandy-skeletal, mixed, mesic Typic Udorthents (Roberts, 1981). The glacial till at the site is derived from schist, gneiss, and granite and is a poorly sorted mixture of silt, sand, and clay (<18%) with pebbles, cobbles, and boulders that underlay a thin layer of loess (Peper and Pease, 1975). The remaining three soil series sampled in this study, the Charlton, Paxton, and Woodbridge soil series, developed on glacial till. Charlton

soils are coarse-loamy, mixed, active, mesic Typic Dystrudepts. Paxton soils are coarse-loamy, mixed, active, mesic Oxyaquic Dystrudepts. Woodbridge soils are coarse-loamy, mixed, active, mesic Aquic Dystrudepts. The Hinckley soils are in the driest drainage class, excessively drained; followed by Charlton and Paxton soils, well drained; then by Woodbridge soils, moderately well drained.

Pinus spp. were common on the Hinckley soils and absent from Woodbridge soils. *Tsuga canadensis* was most common on the Woodbridge soils and absent from the Hinckley soils. All forest types were found on the Paxton and Charlton soils. These are the most common soils of upland forests in Connecticut, Rhode Island, and Massachusetts (Roberts, 1981).

Sampling Design

We sampled 56 plots at a scale (0.1-ha plots) that would be relevant to mapping units in soil series and forest cover maps (Pastor and Post, 1986). All plots were >100 m apart and <10 km apart. Plots were selected so that each of the six forest stand composition types were represented on the two dominant soil series (Table 1). Additional plots were selected to represent the relatively common Woodbridge and Hinckley soils even though all stand composition types did not exist on these soils. Plots selected according to forest cover type and soil series were also described by their topography. As a result, estimates of nutrient storage stratified by topographic classes were determined from a random sampling design that could not account for covariation in stand composition or soil series.

Topography was grouped into four classes: top of slope, midslope, bottom of slope, and variable slope. A midslope classification was ascribed to all locations on the landscape where the slope exceeded 15% over an area ≥ 0.1 ha. A top-of-slope classification was ascribed to all locations that were directly above a midslope and where the slope was <15%. A bottom-of-slope classification was ascribed to all locations that were directly below a midslope and where the slope was <15%. All remaining locations were classified as having a variable slope. To address variation in slope that occurred at scales smaller than 0.1 ha, microtopographic features (i.e., wind-throw pits) were noted. Wind-throw pits did not typically demonstrate exposed soil and their size and appearance indicated that they were a product of the hurricane of 1938 (Winer, 1955). Sampling points were classified as a wind-throw-pit or not a wind-throw-pit.

Soils were sampled during the summers of 1997 and 1998 using two techniques: composite coring ($n = 56$) and excavation mensuration ($n = 21$). The composite coring procedure involved sampling five subplots (center and cardinal points) in each plot. Forest floor samples were removed by sawing

Table 1. Sampling distribution for the composite core technique. The sampling distribution for Charlton (C), and Paxton (P) soils within topographic classes is shown in parentheses.

Classification levels	Hemlock/ Hardwood		Pine/ Oak			Hemlock
	Hardwood	Pine	Oak	other	Hemlock	
Sample size	10	9	6	9	8	14
Soil series						
Charlton	3	4	3	5	3	7
Paxton	4	3	3	4	2	3
Woodbridge	3	2	0	0	0	4
Hinckley	0	0	0	0	3	0
Topography						
Top of slope (2C, 6P)	1	2	1	3	2	0
Midslope (7C, 6P)	3	3	0	0	1	8
Bottom of slope (4C, 1P)	4	2	0	1	2	3
Variable slope (12C, 6P)	2	2	5	5	3	3

around a 15 by 15 cm square template. The volume of the FF was determined by measuring the depth from the surface of the FF to the mineral soil on each of the four sides of the square template. Coarse woody material >1 cm in diameter was removed from FF samples.

After the FF was removed, a small diameter (4.1 cm) galvanized steel tube was plunged 6 cm below the mineral soil surface and extracted. Cores were measured from the bottom up and cut at 3 cm because compaction during sample extraction was assumed potentially large in the top 3 cm (0–3 cm) and relatively small in the bottom 3 cm (3–6 cm). Subsamples from the same plot and depth were composited. Samples from the 6- to 15-cm depth were removed from directly below the 0- to 6-cm samples whenever possible. Where coarse fragments prevented sampling directly below the 0- to 6-cm sample, samples were removed from the nearest undisturbed soils and within 0.5 m of the original sampling point.

A quantitative excavation technique was used to determine C and N storage below 15 cm and was performed as described in Huntington et al. (1988) with the following modifications. A 50 by 50 cm frame was secured to the ground and the pit was excavated in FF, 0- to 3-, 3- to 6-, 6- to 15-, 15- to 30-, 30- to 45-, 45- to 60-, and >60-cm layers. Samples were sieved through a 2-cm wire mesh in the field, weighed, and returned to the lab for analyses.

Samples were stored at <10°C before sample preparation. Forest floor samples were dried to a constant weight at 70°C, homogenized in a Wiley or Cyclotech mill to <2 mm and analyzed for total C and N content via dry combustion in a CHN elemental analyzer (LECO CNH-600). Mineral soil samples were dried to a constant weight at 105°C, sieved to <2 mm and analyzed for C and N content via dry combustion using three 200-mg subsamples from each sample. Fine roots and rocks >2 mm were removed and weighed. Bulk density was determined for the fine soil (<2 mm) only. Inorganic carbonate-C was assumed absent due to the siliceous parent material and moderate acidity (pH 2–4). Hydrogen ion concentrations (pH) were determined for homogenized samples using a 10:1, water/sample slurry for FF samples and a 1:1, water/sample slurry for mineral soil samples.

Statistical Analyses

The variation in soil C and N storage associated with stand composition, soil series, and topography were each tested individually using data from composited core samples ($n = 56$) and a general linear model (GLM) using SAS for Windows v. 8 (SAS Institute, Cary, NC). A two-way model was also developed to model C and N storage using both forest stand composition and soil series. Two-way models were run on both the complete dataset ($n = 56$) and a subset of data for which all stand composition/soil series combinations were present ($n = 44$; Table 1). Multiple means comparisons were accomplished using a Duncan test. In all cases, significant differences were accepted at $P < 0.05$.

It was not possible to sample all potential classification combinations because many combinations did not exist on the landscape. As a result our sampling design was not factorial. Despite the potential for confounding interactions between incomplete classification levels, we felt each classification was likely to provide explanatory power for variations in C and N storage on the landscape. To address this problem we used multivariate regression trees (MRTs) to determine combinations of site classifications that produced unique nutrient storage estimates (De'ath and Fabricius, 2000). Regression trees are well suited for datasets with missing treatment combinations, missing values, and high-order interactions and also

provide decision criteria that are readily applied in GIS models (De'ath, 2002).

Regression trees divided data into groups using least squares splitting criterion that were based on environmental classifications (e.g., topography, soil series, and forest stand composition type). The first split in each tree divided the complete dataset into two groups according to the environmental classification that produced the greatest reduction in the sum of squares. The environmental classification that produced the greatest reduction was determined by comparing all the potential splits in the data. For example, splitting the dataset of C storage estimates into Hm and HH plots versus all other plots may explain 45% of the total sum of squares in the dataset, while splitting the dataset into top of slope versus all other slope positions may explain 10% of the total sum of squares in the dataset, and splitting the dataset into Charlton and Paxton soil series versus all other soil series may explain 30% of the total sum of squares in the dataset. In this case splitting the data according to forest composition type provides a superior reduction in the variation in the dataset and will be shown in the first split of the MRT.

Each split in an MRT was represented graphically as a branch in a tree. Each branch in the tree was labeled with the levels of the classification variable that were placed in that branch (e.g., Hm and HH versus all other forest composition types). The length of each branch represents the proportion of the total sum of squares explained by each split in the data. Regression trees used to model C and N storage were required to maintain at least three samples in each terminal node (leaf). A V-fold cross validation process, where $V = 10$, was used to identify the MRT with the smallest estimated error rate (De'ath and Fabricius, 2000). A bootstrap aggregation technique was then repeated 100 times and the resulting trees were combined by averaging to produce final MRTs with between four and nine terminal nodes. All MRTs were calculated using Salford systems CART 5.0 software for windows (Salford Systems, San Diego, CA).

RESULTS

Carbon and Nitrogen Pool Sizes by Depth

Average total C and N pool sizes [FF–15 cm] were 5.75 ± 1.27 and 0.31 ± 0.08 kg m⁻², respectively, using the coring technique (Table 2). From the FF to 60 cm, the C pool size was 7.91 ± 1.74 kg C m⁻² (range 4.0 to 11.3 kg C m⁻²); and the N pool size was 0.56 ± 0.13 kg N m⁻² (range 0.31 to 0.82 kg N m⁻²) using the excavation technique (Table 3). Therefore, samples taken with the coring technique, to –15 cm, captured 73 and 62% of the variation observed in C and N storage, respectively, of the –60-cm depth. Carbon and N pool sizes varied more, as a percentage of the mean, in the FF where the coefficients of variation were 45 and 43%, respectively, than in the mineral soil where the coefficients of variation were 20 and 31%, respectively. The standard deviation in C storage also decreased from the FF to the top 15 cm of mineral soil (from ± 1.06 to ± 0.70 kg C m⁻²), but the standard deviation in N storage increased from the FF to the top 15 cm of mineral soil (from ± 0.37 to ± 0.68 kg N m⁻²).

Forest stand composition

The effect of stand composition, soil series, and topography were first analyzed using one-way and two-way

Table 2. Mean C, N, C/N ratios, and pH (± 1 SE) by stand composition and depth at the Yale-Myers Forest, Connecticut, USA. Forest floor (FF) samples were obtained from a 15 by 15 cm area excavation. Mineral soil was obtained using the coring technique.

Variable	Hardwood (n = 10)	Hemlock/hardwood (n = 9)	Pine (n = 6)	Oak (n = 9)	Pine/other (n = 8)	Hemlock (n = 14)
	FF					
Depth, cm	5.1c \pm 0.2 [†]	7.3a \pm 0.3	4.4c \pm 0.1	5.7abc \pm 0.1	5.6bc \pm 0.2	7.0ab \pm 0.1
C, kg m ⁻²	1.80c \pm 0.25	2.80ab \pm 0.04	1.59c \pm 0.25	1.84c \pm 0.21	2.10bc \pm 0.36	3.16a \pm 0.24
N, g m ⁻²	75.3ab \pm 12.9	104a \pm 15.5	60.2b \pm 8.0	77.3ab \pm 11.2	86.1ab \pm 11.0	106.0a \pm 7.0
C/N ratio ^{NS‡}	25.1 \pm 1.3	26.8 \pm 1.4	29.3 \pm 1.2	26.3 \pm 2.7	25.7a \pm 1.69	29.6 \pm 0.67
pH	4.88a \pm 0.15	4.27bc \pm 0.16	4.19bc \pm 0.12	4.54ab \pm 0.12	4.07cd \pm 0.19	3.76d \pm 0.07
	0–3 cm					
C ^{NS}	0.93 \pm 0.06	1.02 \pm 0.06	0.99 \pm 0.07	0.92 \pm 0.06	0.85 \pm 0.17	0.99 \pm 0.069
N ^{NS}	63.2 \pm 3.2	60.7 \pm 5.8	57.2 \pm 4.4	58.8 \pm 4.4	53.1 \pm 11.6	47.3 \pm 3.3
C/N ratio	14.7b \pm 0.3	17.8ab \pm 1.4	17.5ab \pm 0.9	16.1b \pm 1.4	19.1ab \pm 3.4	21.3a \pm 1.1
pH	4.39a \pm 0.15	3.92b \pm 0.13	3.79b \pm 0.10	3.80b \pm 0.10	3.75bc \pm 0.20	3.44c \pm 0.03
	3–6 cm					
C ^{NS}	0.83 \pm 0.08	0.71 \pm 0.05	0.71 \pm 0.04	0.79 \pm 0.04	0.84 \pm 0.09	0.69 \pm 0.04
N	61.5a \pm 6.6	48.3ab \pm 6.6	48.3ab \pm 3.61	55.4a \pm 4.4	46.0ab \pm 9.0	35.9b \pm 3.17
C/N ratio	13.8b \pm 0.6	15.6b \pm 1.0	15.0b \pm 0.9	14.7b \pm 0.84	20.3a \pm 2.5	19.8a \pm 1.2
pH	4.48a \pm 0.12	4.14b \pm 0.09	4.12b \pm 0.07	4.16b \pm 0.06	4.00bc \pm 0.12	3.77c \pm 0.03
	6–15 cm					
C ^{NS}	1.70 \pm 0.14	1.58 \pm 0.19	1.54 \pm 0.14	1.63 \pm 0.10	1.66 \pm 0.23	1.65 \pm 0.10
N ^{NS}	133.5 \pm 12.6	119 \pm 20.6	116 \pm 10.3	122 \pm 15.0	111 \pm 14.1	90.7 \pm 6.54
C/N ratio	13.1b \pm 0.7	15.2b \pm 2.1	13.4b \pm 0.5	15.5ab \pm 2.8	15.8ab \pm 1.5	19.1a \pm 1.2
pH	4.62a \pm 0.10	4.27b \pm 0.04	4.23bc \pm 0.03	4.34b \pm 0.05	4.22bc \pm 0.08	4.06c \pm 0.04

[†] Row values with different subscript letters indicate a significant difference at the 0.05 level with a Duncan means test.

[‡] NS = not significant.

GLMs. Results from MRTs are reported in a separate section below. Stand composition was associated with most measured descriptors of the FF (depth, C concentration, C pool size, N pool size, and pH) with the exception of N concentration and C/N ratios (Table 2). Specifically, C concentrations in the FF increased across the stand compositions ranging from hardwood (270 g kg⁻¹) to hemlock (410 g kg⁻¹) (Hw_a < Pine_a < PO_a < Oak_{ab} < HH_{ab} < Hm_b; stand compositions followed by similar letters are not significantly different) (F_{5,50} = 4.29, P < 0.01). When these concentrations were multiplied by

the bulk density of the FF, Hemlock stands demonstrated 199 and 176% of the C and N storage in the FF of pine stands (Fig. 1).

Stand composition also explained variation in N storage in the mineral soil (0–15 cm) (F_{5,50} = 3.13, P = 0.02), and total C storage (FF–15 cm; F_{5,50} = 2.76, P = 0.03), but not C storage in the mineral soil (F_{5,50} = 0.59, P = 0.7; Fig. 1). When analyses were restricted to the samples for which all potential stand composition types and soil series combinations existed the same results were observed. Stand composition again explained variation in

Table 3. Mean total soil C and N storage (± 1 SE) under different forest cover types at the Yale-Myers Forest, Connecticut, USA. Forest floor (FF) and mineral soil samples from 0- to 3-, 3- to 6-, 6- to 15-, 15- to 30-, 30- to 45-, and 45- to 60-cm depths were obtained using the excavation mensuration (pit) technique.

Variable	Stand composition						Average (n = 21)
	Hardwood (n = 5)	Hemlock/Hardwood (n = 3)	Pine (n = 2)	Oak (n = 3)	Pine/Other (n = 3)	Hemlock (n = 5)	
	FF						
C, kg m ⁻²	1.75 \pm 0.32	2.82 \pm 0.04	1.46 \pm 0.35	2.15 \pm 0.98	1.45 \pm 0.56	3.29 \pm 0.67	2.26 \pm 0.29
N, g m ⁻²	83.3 \pm 19.7	112 \pm 5.15	47.5 \pm 7.50	110 \pm 69.6	53.7 \pm 17.9	102 \pm 21.8	87.9 \pm 12.9
	0–3 cm						
C	1.02 \pm 0.11	1.06 \pm 0.23	0.72 \pm 0.08	0.77 \pm 0.11	0.70 \pm 0.32	0.80 \pm 0.10	0.86 \pm 0.06
N	80.8 \pm 11.72	59.8 \pm 14.03	43.4 \pm 3.19	43.8 \pm 12.24	36.5 \pm 7.28	41.2 \pm 10.55	53.2 \pm 5.64
	3–6 cm						
C	0.91 \pm 0.26	0.69 \pm 0.06	0.76 \pm 0.02	0.59 \pm 0.13	0.76 \pm 0.20	0.74 \pm 0.10	0.76 \pm 0.07
N	73.3 \pm 18.06	44.0 \pm 3.10	47.7 \pm 2.52	38.8 \pm 12.12	39.9 \pm 3.06	39.4 \pm 6.64	48.9 \pm 5.45
	6–15 cm						
C	1.47 \pm 0.27	1.47 \pm 0.17	1.16 \pm 0.27	1.45 \pm 0.36	1.38 \pm 0.34	1.06 \pm 0.15	1.33 \pm 0.10
N	130 \pm 19.8	102 \pm 14.4	75.7 \pm 9.63	91.6 \pm 28.4	78.0 \pm 8.50	71.7 \pm 13.6	94.0 \pm 8.27
	15–30 cm						
C	1.33 \pm 0.21	1.20 \pm 0.30	0.85 \pm 0.16	1.50 \pm 0.56	1.39 \pm 0.39	1.66 \pm 0.40	1.38 \pm 0.13
N	135 \pm 9.58	133 \pm 12.1	72.8 \pm 0.19	118 \pm 28.9	105 \pm 14.43	140 \pm 49.9	123 \pm 12.7
	30–45 cm						
C	0.71 \pm 0.13	1.02 \pm 0.18	0.70 \pm 0.56	1.03 \pm 0.56	0.90 \pm 0.30	0.71 \pm 0.10	0.79 \pm 0.08
N	102 \pm 10.9	115 \pm 22.5	79.3 \pm 0.56	96.1 \pm 0.56	83.7 \pm 14.3	69.9 \pm 13.1	86.6 \pm 8.00
	45–60 cm						
C	0.55 \pm 0.20	0.58 \pm 0.13	0.64 \pm 0.56	0.61 \pm 0.56	0.96 \pm 0.42	0.52 \pm 0.20	0.54 \pm 0.10
N	77.5 \pm 18.1	75.0 \pm 17.8	91.0 \pm 0.56	77 \pm 0.56	77.3 \pm 12.3	72.1 \pm 20.7	65.5 \pm 8.57

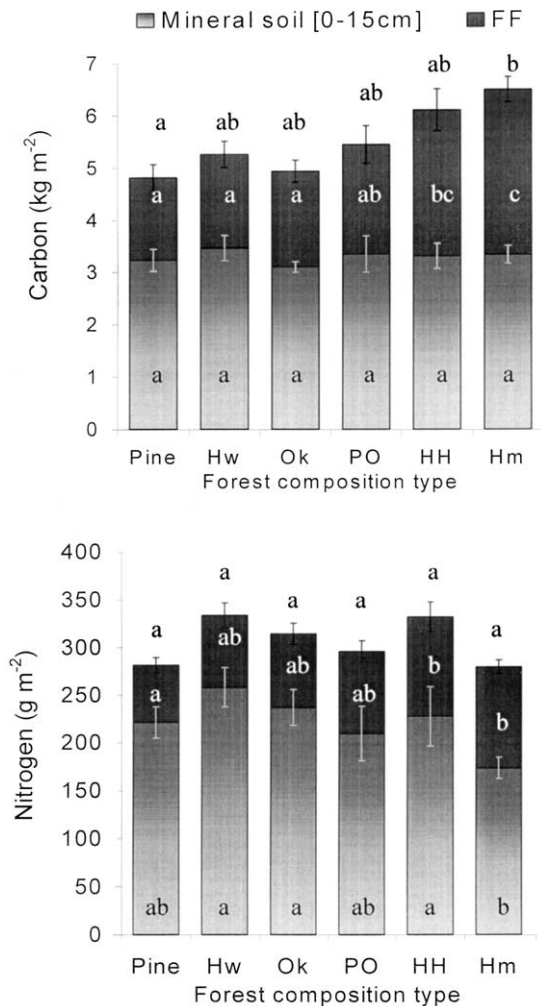


Fig. 1. Mean C and N storage (± 1 SE) in the forest floor (FF) and mineral soil (0–15 cm) stratified by six forest types (Pine = pine, Hw = hardwood, Ok = oak, PO = pine/other, HH = hemlock hardwood, Hm = hemlock) at the Yale-Myers Forest, Connecticut, USA. Bars in the same depth strata with different lower case letters are significantly different. Letters above the bars indicate differences in total storage (FF–15 cm).

N storage in the mineral soil (0–15 cm) ($F_{5,32} = 2.96$, $P = 0.03$), and total C storage (FF–15 cm; $F_{5,32} = 3.78$, $P < 0.01$), but not C storage in the mineral soil ($F_{5,32} = 0.29$, $P = 0.90$).

For the FF, C/N ratios did not differ between different stand composition types ($F_{5,50} = 1.94$, $P = 0.10$). However, C/N ratios found deeper in the soil profile did vary with stand composition (Table 2). Ratios of C/N in the mineral soil were lower in hardwood plots and higher in hemlock plots. This trend was significant in the 0- to 3-, 3- to 6-, and 6- to 15-cm depths ($F_{5,50} = 3.21$, 7.37, 2.97, $P = 0.010$, 0.0010, 0.020, respectively). Similarly, FF and mineral soil pH differed by a full unit between Hm (3.8) and Hw (4.9) plots. Differences in pH among forest stand composition types were greatest in the FF and significant in each depth strata to 15 cm (Table 3).

Soil Series

Mineral soil C storage (0–15 cm) was lower in Paxton soils than in Woodbridge or Hinckley soils ($F_{3,52} = 4.07$,

$P = 0.01$; Fig. 2). Similarly, total C storage (FF–15 cm) was lower in Paxton soils than in Hinckley soils ($F_{3,52} = 2.90$, $P = 0.040$; Fig. 2). Nitrogen pool sizes did not vary with soil series ($F_{3,52} = 1.67$, 1.36, $P = 0.20$, 0.30 for the FF and 0- to 15-cm strata, respectively). We also analyzed nutrient storage on the Charlton and Paxton soils alone because all stand composition types were represented on these two soil series. The Charlton soils were associated with more total C than the Paxton soils ($F_{1,32} = 6.21$, $P = 0.020$).

Topography

Soil C accumulated at the bottom of both large (0.1 ha) and small (1 m) hillslopes. Soil N accumulated at the bottom of small hillslopes. Carbon and N pool sizes in the FF were found to be larger in the wind-throw pits than outside wind-throw pits (3.0 vs. 2.2 kg C m⁻² and 111 vs. 80 g N m⁻²; $P = 0.01$ and $P < 0.001$ for C and N, respectively). Soil C (FF–15 cm) varied across the hillslope (>0.1 ha) and was greater at the bottom of the slope than the other topographic positions ($F_{3,52} = 4.15$, $P = 0.01$; Fig. 3).

Multivariate Regression Trees

In addition to one-way and two-way GLMs, three-way MRTs were used to explain variation in total C and N storage (FF–15 cm; Fig. 4). Forest stand composition and topography explained the majority of variation in C storage by splitting the dataset in five of six nodes in the MRT (Fig. 4a). In this tree, C estimates were first split by forest stand composition type. Data from Hw, Oak, and Pine stands were placed into one group and data from HH, PO, and Hm stands were placed into a separate group. This split produced two groups of data, each more homogenous than the original group, one with a mean of 5.2 kg C m⁻² and the other with a mean of 6.2 kg C m⁻². This single split in the data accounted for 17% of the sum of squares in the original dataset. Each of these two groups was then split again according to topographic class. In the Hw, Oak, Pine group samples from hilltops (Top) and variable slopes (Var) were placed in a terminal node with 17 samples and a mean of 4.9 kg C m⁻². To summarize, this terminal node provides a prediction of 4.9 kg C m⁻² for samples removed from Hw, Oak, or Pine stands on hilltops or variable slopes.

Continuing from left to right in the MRT, the next terminal node predicts a value of 5.3 kg C m⁻² for Hw, Oak, and Pine stands on Middle or Bottom of slope positions and on Woodbridge, Paxton, or Hinckley soils, however these same plots found on Charlton soils were predicted to store 6.3 kg C m⁻². Moving further right in the tree, the next terminal node is defined by HH, Hm, and PO plots found on the Top of slope positions and predicts C storage of 4.6 kg C m⁻² under these conditions. The terminal node below this node is defined by HH plots in midslope positions and is predicted to store 4.9 kg C m⁻². It is important to note that this storage estimate is not unique from the storage estimate for the terminal node that is furthest left in the MRT, however

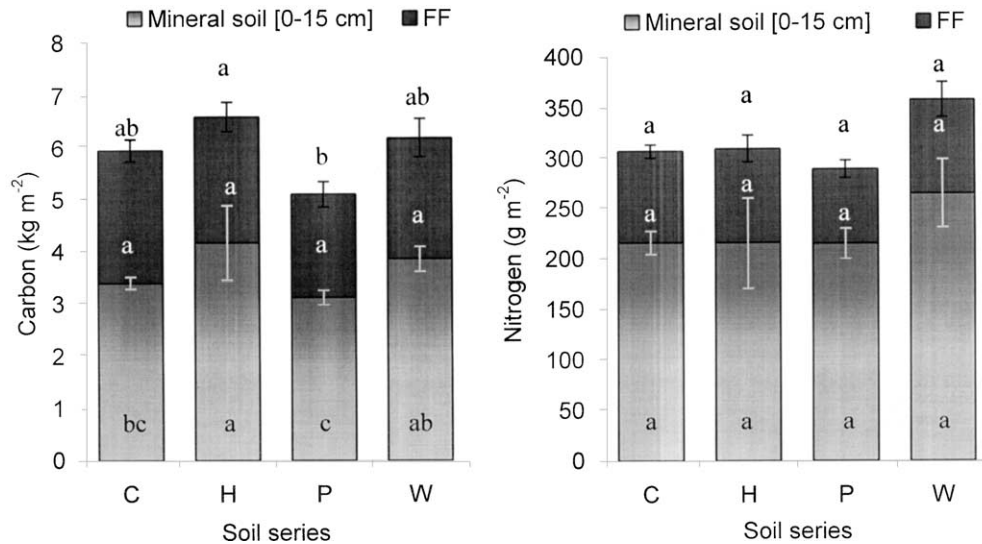


Fig. 2. Mean C and N storage (± 1 SE) in the forest floor (FF) and mineral soil (0–15 cm) stratified by soil series (C = Charlton; $n = 25$, H = Hinckley; $n = 3$, P = Paxton; $n = 19$, W = Woodbridge; $n = 9$) at the Yale-Myers Forest, Connecticut, USA. Bars in the same depth strata with different lower case letters are significantly different. Letters above the bars indicate differences in total storage (FF–15 cm).

this estimate is predicted to occur under a completely unique set of conditions.

The next terminal node, immediately to the right of the previously described node, was defined by Hm and PO plots on midslope positions and was predicted to store 6.4 kg C m⁻². The final two nodes, at the right end of the MRT are defined by HH, Hm, and PO forest composition types on Bottom of slope or Variable slope positions. Hemlock and PO plots on bottom of slope and variable slope positions were predicted to store 6.5 kg C m⁻². Hemlock/hardwood plots in the same slope positions were predicted to store 7.8 kg C m⁻².

Using the same procedure for total N storage (FF–15 cm; g m⁻²) we found that stand composition again provided a primary split in the data, but that subsequently dividing these data by soil series provided even greater explanatory power (Fig. 4b, Table 4). In this MRT HH, Hw, and Oak forest stand composition types were sepa-

rated from Hm, Pine, and PO composition types in the primary split producing two pools of data with means of 340 and 280 g N m⁻², respectively. The N estimates associated with HH, Hw, and Oak composition types were then split according to soil series with plots on the Woodbridge soil series estimated to store 430 g N m⁻². These first two splits in the data explained 13 and 17% of the variation in the original data pool, respectively. Two additional splits in the data according to topography and soil series found more N associated with hill-slopes and hill bottoms and the Charlton soil series. These final two splits in the data explained 2 and 7% of the variation in the original dataset, respectively. In this model, soil series were used in two separate nodes (splits). The first split by soil series explained 17% of the variation in the original dataset and the second split by soil series explained an additional 7% of the variation in the dataset. In the full model, therefore, soil series

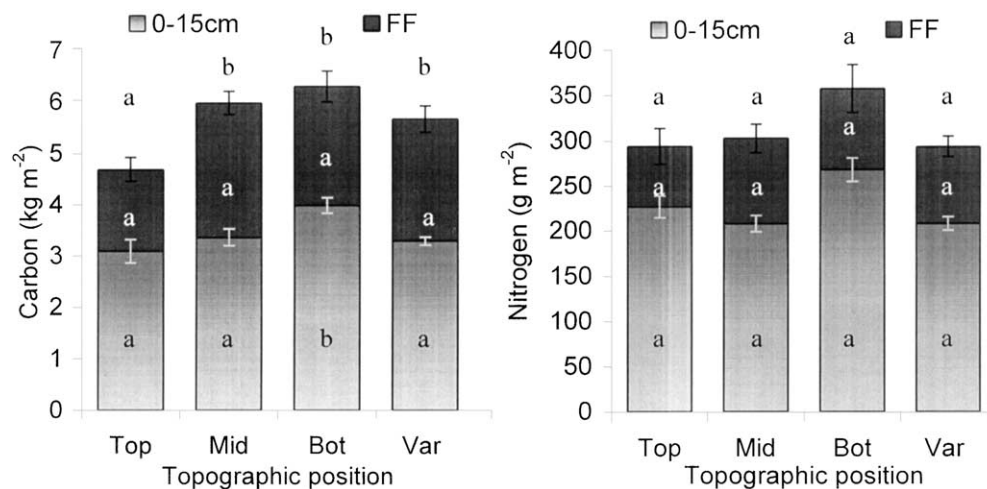


Fig. 3. Mean C and N storage (± 1 SE) in four soil depths stratified by topographic classes at the Yale-Myers Forest, Connecticut, USA. Four topographic classes were ascribed to areas that were >0.1 ha in size. Carbon storage varied by topographic class in the 0- to 3-, 3- to 6-, 6- to 15-, and FF- to 15-cm depths. In the figure Top = top of slope ($n = 8$), Mid = middle of slope ($n = 15$), Bot = bottom of slope ($n = 12$), Var = variable slope ($n = 21$).

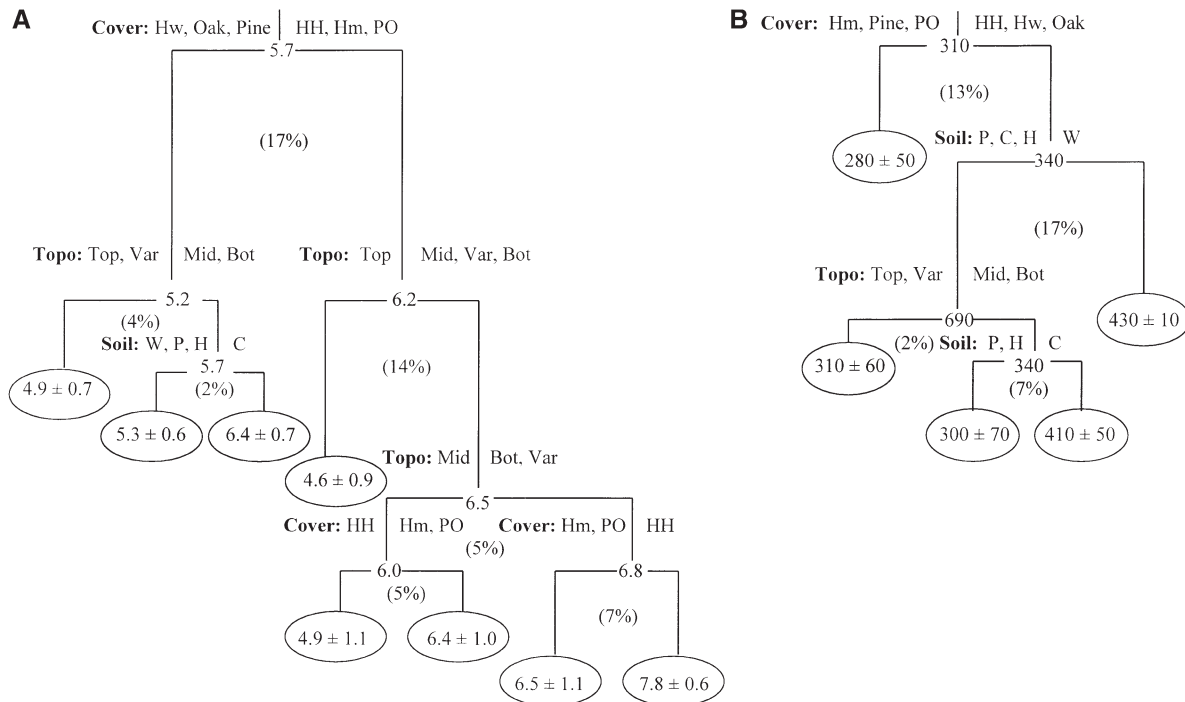


Fig. 4. Regression tree analyses for forest floor and mineral soil to 15 cm (FF-15 cm) at the Yale-Myers Forest, Connecticut, USA for (a) C storage (kg m^{-2}) and (b) N storage (g m^{-2}). Explanatory variables used were stand composition (Cover), topography (Topo), and soil series (Soil). Each branch is labeled with the level of the explanatory variable that defines that branch, where Hw = hardwood, Hm = hemlock, HH = hemlock and hardwood, Pine = pine, PO = pine and other forest species, Oak = oak, top = top of slope, mid = midslope, bot = bottom of slope, var = variable slope, C = Charlton soil series, H = Hinckley soil series, P = Paxton soil series, and W = Woodbridge soil series. For example, the first split in Fig. 4a places all data defined by a Hw, Oak, or Pine forest composition type in the subset of data on the left of the split. The value in each oval represents the mean storage estimate (± 1 SE) for the treatment combinations shown in the preceding branches of the tree. Similarly, the value in each 'T' in the tree represents the mean storage estimate for the levels of the classification listed in the previous branch. For example, plots with Hw, Oak, and Pine forest composition types stored 5.2 kg m^{-2} . The length of each branch is proportional to the ratio of the sum of squares explained by that split and is shown as a percentage in parentheses in the body of each branch.

explained 24% (23%, without rounding errors) of the variation in the original dataset.

Multivariate regression trees were also used to explain variation in C and N storage in the FF and mineral soil (Table 4). Forest stand composition explained more variation in C and N storage in the widely variable FF pools than either soil series or topography. Topographic classes, however, explained the less variable mineral soil C pool. Both soil series and forest stand composition were associated with mineral soil N pools.

DISCUSSION

Local Variation in Carbon and Nitrogen Storage

Carbon storage varied more in the FF than in the mineral soil (Tables 2 and 3). As a result, C storage was

Table 4. Variance in C and N storage explained by multivariate regression trees (MRT) using forest stand composition type, soil series, and topography as explanatory variables. The percentage of the sum of squares explained (% SS explained) by each variable for each depth strata and nutrient is reported.

Depth strata	Forest floor		0–15 cm		FF-15 cm	
	C	N	C	N	C	N
% SS explained						
Stand composition	40	31	5	19	29	13
Soil series	5	4	10	21	2	23
Topography	17	23	18	0	23	2
Total	62	58	33	40	54	39

best predicted by a variable that explained variation in the FF: forest stand composition. Forest stand composition alone explained 29% of the variation in total C storage and when combined with topography and soil series, explained 54% of the variation in soil C storage to 15 cm (Table 4). Unlike C, N storage varied throughout the soil profile and was more difficult to model. One-way GLMs suggested that forest stand composition alone was associated with N storage, but when N storage was modeled with both soil series and forest stand composition in either a two-way GLM or a MRT, it became clear that an interaction between these two variables confounded the one-way analysis and that soil series was a powerful predictor of N storage (Table 4, Fig. 4).

A closer examination of the MRT for N storage provided an explanation for this confounding interaction (Fig. 4b). When a secondary node explains more variation in the data than a primary node, it suggests that the factor in the secondary node is strongly associated with a subset of data. In this case, N storage in HH, Hw, and Oak forest stand types varied widely and consistently with soil series, but N storage in Hm, Pine, and PO forest stand composition types did not vary with soil series. This result is consistent with our observation that pine stands were not found on the Woodbridge soil series. This split also revealed that Hm stands stored

very little N regardless of soil series. The results from this statistical tree demonstrate the ability of MRTs to produce meaningful predictions despite missing treatment combinations in the dataset.

Much of the variation in soil C and N storage associated with stand composition resulted from the unique litter found under hemlock stands. More specifically, the FF under Hm stands was more acidic, demonstrated higher C/N ratios, and stored 150 to 200% more C and N than pine or Hw stands (Table 2). Low pH is known to inhibit bacterial and some invertebrate (e.g., annelid) activity and may explain the increased nutrient storage in the FF and decreased storage in the mineral soil associated with Hm stands (Fig. 1). These data are particularly timely with respect to the woolly adelgid (*Adelges tsugae* Annand.) infestation, which threatens the growth of Hm across northeastern USA (Jenkins et al., 1999).

These results partially supported our prediction that forest stands with recalcitrant litter, such as Hm, stored larger nutrient pools at the surface and smaller nutrient pools deeper in the mineral soils than forest stands with more labile litter, such as in the Hw stands. There was little evidence from the one-way GLMs to support our prediction that soils with poor drainage would store more C or N. In fact, the Hinckley soils, which were in the driest drainage class and dominated by pine trees, demonstrated the greatest C storage (Fig. 2). Similarly, the Paxton soils, which are Oxyaquic Dystrudepts, stored less C and comparable amounts of N as their drier counterparts the Charlton soils, which are Typic Dystrudepts. Again, the MRT for N storage provided a potential explanation for these unexpected results. After isolating data from HH, Hw, and Oak stands in the first node of the tree, it was clear that the Woodbridge soil series (W), which is in the wettest drainage class, was associated with the greatest N storage, 430 g N m⁻² (Fig. 4b).

Regional Variation in Carbon and Nitrogen Storage

In this study, we observed that the strong association between forest stand composition and nutrient storage in the FF explains some variations in C and N storage. Results from this study and others would suggest that differential production and decomposition of leaf litter,

by various forest tree species, plays a dominant role in determining the patterns of nutrient storage on the landscape (Cahallinor, 1967; Zinke, 1962; Finzi et al., 1998; Menyailo, 2002). However, regionally, nutrient storage varied more in the mineral soil than in the FF (Table 5). For example, C storage varied by 3.8 kg C m⁻² in the top 15 cm of mineral soil but only by 1.4 kg C m⁻² in the FF among eight similar sites in New England, USA. Therefore, it is likely that site factors that explain variation in the mineral soil will best explain regional variation in nutrient storage.

Forest stand composition has not been observed to be well associated with variations in mineral soil C storage (Fig. 1; Finzi et al., 1998), but many other site conditions from management history (Compton and Boone, 2000) to soil texture (Tremblay et al., 2002) to climatic differences (Simmons et al., 1996) may explain variation in mineral soil nutrient storage across the region. Of these variables, soil series, topography, and management history are the most likely to be important for regional scale predictions of C storage, while forest stand composition and soil series should be effective predictive variables for N storage.

Each of the site variables used in this study was associated with 20 to 40% differences in nutrient storage means. That is to say that Hm stands, Woodbridge soils, and hill bottoms accumulated 20 to 40% more C or N than pine stands, Charlton soils, or hill tops, respectively. However, agricultural practices of the last century, the introduction of exotic pests such as the woolly adelgid, and/or local climatic differences may exert at least as strong an effect on soil C and N pool sizes as forest stand composition or soil series. Modeling nutrient storage in this region will require extensive, rather than intensive, direct sampling at a regional scale.

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Table 5. Soil C and N storage in the forest floor (FF) and mineral soil (0–15 cm) from eight sites in New England (i.e., northwest Connecticut = CT, NW; northeast Connecticut = CT, NE; New Hampshire = NH; Massachusetts = MA; and Rhode Island = RI). Soils in all sites were represented by moderately well to well drained, loamy to coarse loamy Dystrachrepts with the exception of the Haplorthods in NH. Oak trees were common in all but the NH sites.

Location	CT, NW1†	CT, NW2‡	MA1‡	MA2‡	MA3‡	NH§	CT, NE	RI¶
FF C, kg m ⁻² #	2.6	2.1	2.9	2.5	1.7	3.1	12.3	3.0
Soil C, kg m ⁻²	7.2	6.2	5.1	5.8	5.0	5.0	3.4	4.5
FF N, g m ⁻²	137	129	93	78	60	133	86	86
Soil N, g m ⁻²	490	354	198	255	268	263	224	189

† Finzi et al., 1998.

‡ Compton and Boone, 2000.

§ Huntington et al., 1988.

¶ Hooker and Compton, 2003.

Estimates of soil C and N storage determined in NH were adjusted by the ratios of C and N in the 0- to 15- and 15- to 30-cm strata in this study (Table 3) so that 68% of the C reported for the 10- to 20-cm depth strata in NH was assumed to have occurred between 10 and 15 cm. Similarly, estimates of soil C and N storage determined in RI were adjusted by the ratio of C and N in the 0- to 45- and 0- to 60-cm depth strata in this study so that 90% of the C reported for the 0- to 20-cm depth strata in RI was assumed to have occurred between 0 and 15 cm.

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