Near-Surface Soil Carbon, Carbon/Nitrogen Ratio, and Tree Species Are Tightly Linked across Northeastern United States Watersheds

Donald S. Ross, Scott W. Bailey, Gregory B. Lawrence, James B. Shanley, Guinevere Fredriksen, Austin E. Jamison, and Patricia A. Brousseau

Abstract: Forest soils hold large stores of carbon, with the highest concentrations in the surface horizons. In these horizons, both the total C mass and the C/N ratio may respond more rapidly to changes in tree species than lower horizons. We measured C and C/N ratios in the Oa or A horizon from 12 watersheds at 8 established forested research sites in the northeastern United States. The dominant tree species included *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Picea rubens*, and *Tsuga canadensis*. In 710 plots, both soil C (50–530 g kg^{-1}) and the C/N ratio (11.6–45.3) had a wide range. In all but the Cone Pond watershed, both N concentration and the C/N ratio were strongly related to C content. For these 11 watersheds, the average C/N ratio $= 9.5 + 0.030 \times$ C g kg^{-1} ($R^2 = 0.97$, $P < 0.001$). Ratios at Cone Pond were much higher than would be predicted from this equation and charcoal was found in numerous samples, suggesting a source of recalcitrant C. Averaged by watershed, C concentration was also significantly related to C pools. The carbon concentration of the horizons sampled was negatively related to *A. saccharum* + *B. alleghaniensis* dominance and positively related to conifer + *F. grandifolia* dominance. The strong relationships between C, C/N ratio, and species suggest predictable patterns in C accumulation in near-surface soils. FOR. SCI. 57(6):460–469.

Keywords: carbon sequestration, carbon pools, Oa horizon, nitrogen

SOILS OF THE WORLD'S FORESTS have the capacity to retain and accumulate inputs of C, possibly offsetting a measurable fraction of anthropogenic emissions (Heimann and Reichstein 2008). The amount of C sequestered depends on a number of factors primarily related to management (Johnson and Curtis 2001, Jandl et al. 2007, Hedde et al. 2008), climate (Pastor and Post 1986, Davidson and Janssens 2006), and soil type (Hagedorn et al. 2001, Vejre et al. 2003, Kiser et al. 2009). Increased N deposition may enhance C sequestration in ecosystems that are N-limited (de Vries et al. 2009, Nave et al. 2009). Poorly drained soils and those high in clay content may also enhance C retention because of decreased decomposition rates in the former and greater physicochemical protection in the latter (Six et al. 2002). Carbon can be stabilized in mineral soil by physical protection in microaggregates, chemical protection through organomineral complexes with silt and clay particles, and biochemical protection by the formation of recalcitrant organic compounds (Six et al. 2002). Sollins et al. (2006, 2009) showed that denser organomineral particles were enriched in N (lower C/N ratio) and higher in microbial breakdown products than in the bulk organic matter (OM). The lighter fraction of OM in forest mineral soil, primarily particulate organic matter (POM), had the highest C/N ratio of any fraction (Swanston et al. 2002, Sollins et al. 2006), but this fraction appeared to decompose at a rate similar to that of heavier fractions on a per g of C basis (Swanston et al. 2002). Filley et al. (2008) studied OM changes in soil transitioning from grassland to woodland and found greater POM under woody species, possibly stabilized biochemically by having greater recalcitrance. In the northern forest, site conditions may promote the formation of thick, organic surface horizons (Oa) containing considerable amounts of free POM. For example, Ross et al. (2009) found an average Oa horizon thickness of 15 cm and C concentration of 441 g kg^{-1} (~76% OM) in 21 plots in the Buck Creek North watershed in the western Adirondacks. These near-surface forest soil horizons are more susceptible to disturbance than the mineral soil, and their role in C cycling needs to be better understood.

Tree species composition plays a role in C retention (Finzi et al. 1998, Lovett et al. 2004, Vesterdal et al. 2008) because the litter and roots of different species decompose at different rates (Berg and McClaugherty 2008). For example, litter from coniferous species will usually decay relatively slowly and over time create a relatively high C

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Acknowledgments: This work was supported by the Northern States Research Cooperative (US Award 02CA11242343110) and US Department of Agriculture Hatch funds (VT-PS-00912). Statistical consultation was provided by Alan Howard, IT Specialist, University of Vermont (UVM) Statistical Software Support and Consulting Services. Numerous undergraduate students assisted with the field and laboratory efforts, including Jerome Barner, Abby Boak, Graham Burkhart, Zachary Ewell, Shea Hagy, Rachel Hanish, Joe Ibrahim, Natalia Fajardo, Audrey Leduc, Adrienne Moretti, Isaac Paul, Lilah Ross, Chris Savastio, Stacy Thompson, Will Wheeler, Jason Wiener, and Kristin Williams. Sheila Tymon, an environmental science teacher at Peoples Academy in Morrisville, VT, assisted during one field season at Ranch Brook. Her support was provided by the UVM HELiX program summer of Science. Cooperators at the research sites included Beverley Wemple of UVM at Ranch Brook; Nancy Burt, Kathy Donna, and Hal Bell of the US Forest Service at Lye; Ralph Perron of the US Forest Service at Cone Pond; Jon Denner of the US Geological Survey (USGS) at Sleepers and Brush Brook; and Tom Suleski of the USGS at Buck Creek and Lye.

Manuscript received July 31, 2009, accepted October 5, 2010

forest floor. Rates within hardwood species also vary greatly with oaks generally decaying slower than beeches and maple species decaying faster than both (Gosz et al. 1973, Finzi et al. 1998, Lovett et al. 2004). However, it is not clear how different individual species and different combinations of species lead to overall differences in soil C sequestration. Another factor affecting C retention in forest soils is elevation because it affects climate. Soils at higher elevations tend to accumulate more C in the upper horizons because of relatively lower temperatures limiting decomposition rates. Most studies of tree species effects and soil profile distribution of C have been on lower elevation sites (e.g., Finzi et al. 1998, Vesterdal et al. 2008). The interaction between all of the above factors is complex, and more studies are needed on a wider range of soils.

The present study was undertaken because of the availability of a large data set from sites across the northeastern United States mountainous region. As part of a cross-site study of factors affecting nitrification rates (Ross et al. 2009), we have data from the Oa or A horizon (depending on C concentration) of plots throughout 10 small research watersheds. Combining these data with data from one additional small watershed and one larger watershed (960 ha), we investigated relationships between soil organic C, N, the C/N ratio and tree species composition. Results are confined to these near-surface horizons that probably reflect the current vegetation more so than the lower mineral horizons. This surface soil is also more susceptible to rapid change through environmental impacts such as physical disturbance (natural or human-induced), fire, and disease.

Methods

Study Sites and Sampling Protocol

Soil samples were taken from 12 established research watersheds that span the Catskill and Adirondack Mountains in New York, the Green Mountains in Vermont, and the White Mountains in New Hampshire (Table 1). The watersheds are all completely forested and at relatively high elevation for the northeastern United States (average elevation range between 564 and 1038 m) (Table 1). With the exception of Ranch Brook, the watersheds are small and contain primary or secondary stream networks. Land-use history is similar, in all but Cone Pond, with a legacy of logging approximately 80–120 years ago and no record of agricultural use (with the exception of Sleepers W9-C possibly having grazing in the 19th century); Cone Pond has no known direct human land use but was affected by a forest fire. Soils are primarily typical Spodosols and Inceptisols (Table 2) that have developed on glacial till overlying a variety of bedrock types. Ten of the 12 watersheds were sampled for a nitrification study, and more details on the sites and the sampling patterns can be found in Ross et al. (2009).

Using either established sampling points or new transects, 28–193 soil samples were taken from each watershed (Table 1). At four watersheds (two each at Buck Creek and Sleepers River), 2–7 samples were taken within 3 m of established grid points, and results were averaged to provide 21–27 plots in each watershed (Table 1). At the other watersheds, transects were usually oriented perpendicular to the slope, with most transects having 20–30 m between points and one sample taken at each point. At Ranch Brook, there were approximately 50 m between transect points, with 3 separate samples taken 1 m apart around each point. At HBEF W3, the distance between transect points varied with change in slope and landform.

Samples were taken from the uppermost horizon below the Oe that was at least 2 cm thick. Soil samples were taken from the sides of small pits and homogenized by hand, discarding easily separable roots and debris. Most sites did not have separate Oa and A horizons but, instead, one high C near-surface horizon. Horizons were designated as Oa if C was $>$200 g kg^{-1} and A if C was below this threshold (US Department of Agriculture Natural Resources Conservation Service 2006). The basal area of live trees with dbh $>$10 cm was measured within a 10-m radius of each transect or grid sampling point at most watersheds, with the exception of 9 m at Buck Creek and 5 m at Brush Brook (because there was only 10 m between transects).

Laboratory Analysis and Carbon Pool Calculations

Soils were either air-dried or dried at 55°C, sieved through 2-mm mesh, and ground to pass a 125-μm sieve. All samples were dried at 55°C before weighing for C, H, and N determination on an elemental analyzer (CE440;

Table 1. Watershed location, size, elevation, and sample numbers.

Watershed	Acronym	Location (mountains)	Town, state	Area (ha)	Average elevation (m)	No. of transect/ plot points	Total no. of samples
Brush Brook D	Br D	Green	Huntington, VT	15.4	841	80	80
Brush Brook G	Br G	Green	Huntington, VT	11.4	839	66	66
Buck Creek North	Bk N	Adirondack	Inlet, NY	33.7	649	21	57
Buck Creek South	Bk S	Adirondack	Inlet, NY	52	692	21	58
Cone Pond	CP	White	Thornton, NH	33	564	59	60
HBEF W3	HB W3	White	Woodstock, NH	41	642	28	28
HBEF W7	HB W7	White	Ellsworth, NH	76	772	113	114
Lye	Lye	Green	Sunderland, VT	121	759	130	130
Ranch Brook	RD	Green	Stowe, VT	960	801	74	221
Sleepers W9-A	Slp W9A	Green	Walden, VT	16	636	27	82
Sleepers W9-C	Slp W9C	Green	Walden, VT	7	566	27	73
Winnisook	Win	Catskill	Oliverea, NY	217	1038	64	64

Table 2. **Major soil series and series associations at each of the study watersheds and the soil classification of these series to the great group or family level and particle-size class.**

Watershed	Major soil series/complexes	Classification
Brush Brook	Houghtonville, Stratton-Glebe	Coarse-loamy to loamy-skeletal Haplorthods and Humicryods
Buck Creek	Tunbridge-Lyman, Rawsonville-Hogback	Coarse-loamy to loamy Haplorthods and Haplohumods
Cone Pond	Peru, Tunbridge, Lyman	Coarse-loamy to loamy Haplorthods
HBEF	Peru, Tunbridge, Lyman	Coarse-loamy to loamy Haplorthods
Lye	Mundal, Wilmington	Coarse-loamy Haplorthods, loamy Endoaquods
Ranch Brook	Marlow, Tunbridge-Lyman, Colton-Duxbury	Coarse-loamy, sandy-skeletal and sandy Haplorthods
Sleepers W9	Vershire-Dummerston, Cabot, Buckland	Coarse-loamy to loamy Udepts and Aquepts
Winnisook	Lackawanna, Arnot, Oquaga	Coarse-loamy to loamy-skeletal Udepts

Data are from Ross (2007) and US Department of Agriculture Natural Resources Conservation Service (2008) soils mapping.

Exeter Analytical, North Chelmsford, MA or NC Soil FlashEA 1112; CE Elantech, Lakewood, NJ). Standard and quality control soils were obtained from the North American Proficiency Testing program. On a few high C/N ratio subsamples of 2-mm sieved soil from Cone Pond, charcoal was separated by hand using tweezers and a binocular microscope, and the difference in sample weight was measured. Soil pH (1:2, v/v with distilled water) was measured on field-moist samples from the 10 watersheds in Ross et al. (2009) using standard techniques.

For all watersheds except HBEF W3, a disturbed bulk density (BD) measurement was obtained by packing field-moist subsamples into a volumetric spoon (in duplicate using 10 ml) and drying at 55°C. The resulting values compared favorably to BD calculated from soil OM using the equation of Huntington et al. (1989), assuming the standard conversion multiplier of C to OM of 1.724:

$$\text{Calculated BD (Mg m}^{-3}) = 0.99 \times \text{disturbed BD} - 0.04 \quad R^2 = 0.74 \quad P < 0.001.$$

The slope near 1.0, the low intercept, and the relatively good fit all demonstrate that the disturbed BD measurements were probably close to those found in the field. This disturbed bulk density measurement was not available for the HBEF W3 samples, and BD was calculated from the Huntington et al. (1989) equation, again assuming that OM is 1.724 × C. Carbon pools were calculated on a per m^2 basis using the horizon depth, BD, and C concentration. These estimates reflect only what is contained in the individual horizon sampled and not in the entire soil profile.

Statistical Analyses

Statistical analysis was performed using SAS 9.1 (SAS Institute, 2003). Regression analysis was performed using the general linear model and residuals were plotted to ensure normality and even distribution of variance. Because of innate variability and the fact that most soil samples were only single points within the vegetation plots (litterfall source area), comparisons between the soil and vegetation data were only performed on watershed averages.

Results

In the near-surface horizons sampled, we found a wide range of total C (49.6–529 g kg^{-1}) and N concentration (3.0–28.4 g kg^{-1}) with the C/N ratio varying between 11.6 and 45.3. Of the 710 plots, 162 had samples with C <200 g kg^{-1} and were classified as A horizons, whereas the remaining 542 were Oa horizons. We reiterate that the samples were taken from the first horizon below the Oe, and, thus, there was either only an A or an Oa from each plot even if both were present. Over this large range in C/N, there was a good relationship between C and N (Figure 1a), especially if samples from the Cone Pond watershed were not included (because of its fire history, discussed below). A valid linear fit between C and N was not possible because the distribution of the residuals across the range of data was uneven. The linearized version of the relationship shown in

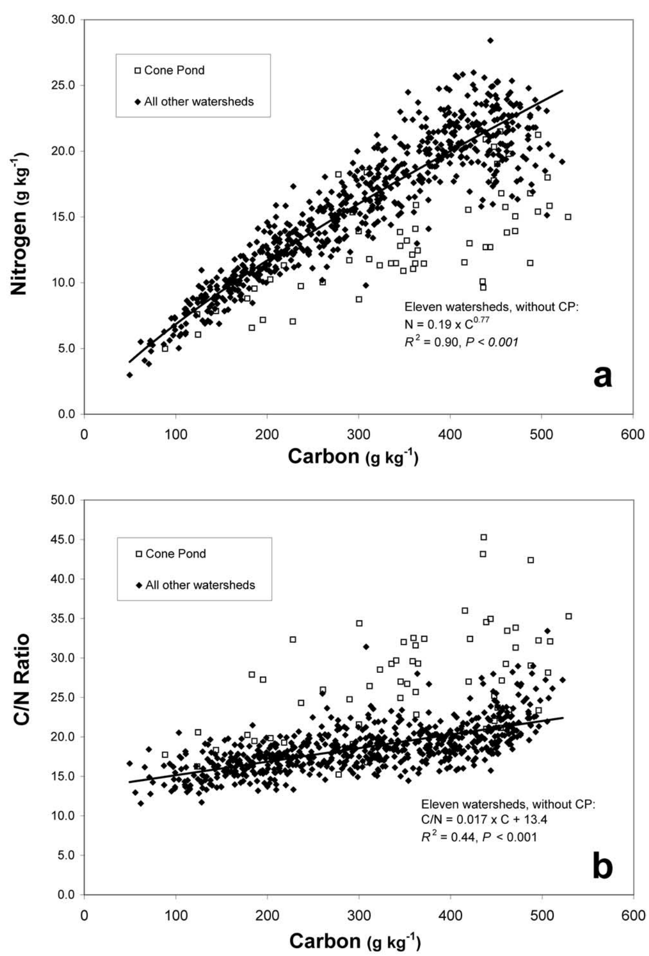

Figure 1. The relationship between carbon and nitrogen concentration (a) or C/N ratio (b) in Oa and A horizon samples from 710 plots in 12 northeastern United States watersheds. The regression line was calculated from 11 of these watersheds (solid squares).

Figure 1a is

$$\ln \text{N (g kg}^{-1}) = -1.64 + 0.733 \times \ln \text{C (g kg}^{-1}) \quad R^2 = 0.90 \quad P < 0.001.$$

The strong relationship between C and N was expected, because nearly all forest soil N is a component of soil OM and associated with C. Relatively small variations in the amount of N per unit C create the range in C/N (Figure 1b).

Drainage did not appear to have an effect on soil C concentration or pool in this study. Of the 680 plots with soil moisture data (HBEF W3 and two other individual plots were missing this data), 153 had a wetness ratio of >1.25, which Ross (2007) found to indicate an excess of water. The wetness ratio is the soil moisture content (by weight) relative to that predicted at field capacity by C concentration. The average C concentration in these 153 horizons was 267 g kg^{-1}, significantly less (t test $P < 0.001$) than the 315 g kg^{-1} found in the remaining, drier horizons. The thickness of the Oa or A horizon was significantly greater in the wetter soils (8.3 versus 6.5 cm). However, there were no significant differences between the wetter and drier soils in either disturbed bulk density or the calculated C pool. Except in riparian areas and near groundwater seeps, these upland soils, especially the near-surface horizons, were well drained.

Charcoal at Cone Pond

Cone Pond had a large blowdown from a hurricane in 1815 and a fire circa 1820 (Buso et al. 1985), and charcoal was clearly present in a number of the soil samples collected, with none obvious in samples from the other watersheds. To investigate whether this charcoal was responsible for the outliers in the C/N ratio, we removed charcoal from seven samples representing the more extreme outliers from the regression line in Figure 1b. The contribution of readily identifiable and separable charcoal varied considerably: 0.70–105.3 g kg^{-1} with an average of 23.1 g kg^{-1}. If this charcoal was assumed to have no N and the amount of C subtracted from the numerator, it only lowered the remaining soil C/N ratio by an average of 5% (~25% in the sample with the highest concentration). Forest fires may leave black carbon or char that is not easily separable (Preston and Schmidt 2006), and one method for estimating its contribution is to examine the H/C ratio. Expressed on a molar basis, as opposed to the weight basis generally used for C/N, biomass usually has an H/C ratio between 1.3 and 1.7; charcoal has a ratio of approximately 0.6 and charred biomass is in between (Preston and Schmidt 2006). In samples from the Cone Pond watershed, we found a significant decrease in the H/C ratios with an increase in the C/N ratio:

$$\text{H/C (mol mol}^{-1}) = 1.74 - 0.115 \times \text{C/N (kg kg}^{-1}) \quad R^2 = 0.37 \quad P < 0.001 \quad n = 59.$$

For all other watersheds combined, there was still a significant negative linear relationship between C/N and H/C ratios, but with a much lower R^2 of 0.12 and a much lower slope of −0.015. Thus, we believe this is ample supporting evidence that black carbon was responsible for the large deviations in C versus N in the Cone Pond samples. However, because it was also the watershed with the highest conifer basal area (Table 3) and high C/N ratios are often associated with conifers, we cannot unequivocally assign the C versus N deviations to black carbon.

Carbon versus C/N Ratio

Because the slope of the regression between C and N was curvilinear (Figure 1a), the N concentration increased at a lower rate than the C concentration, thus increasing the C/N ratio (Figure 1b). Averaging C, N, and C/N by watershed created tight linear relationships between C versus N and C versus C/N, again, if Cone Pond was not included (Figure 2). Interestingly, the slopes of linear fits in Figures 1b and 2b are not the same, with the averaged data showing a steeper change in C/N ratio. Thus, the watershed averages predict a lower C/N ratio at low C and a higher C/N ratio at high C concentration. For example, 100 g kg^{-1} C predicts a C/N ratio of 12.6 using the averaged data equation but 15.2 using the linear equation derived from all the data; the predicted C/N ratios at 400 g kg^{-1} C are 21.7 and 20.3 for the averaged and full data equations, respectively. This may

Table 3. Basal area of live tree species (>10 cm dbh) averaged for the plots in each watershed.

	Sugar maple (*A. saccharum*)	Yellow birch (*B. alleghaniensis*)	American beech (*F. grandifolia*)	Paper birch (*B. papyrifera*)	Red maple (*A. rubrum*)	White ash (*F. americana*)	Red spruce (*P. rubens*)	Balsam fir (*A. balsamea*)	Eastern hemlock (*T. canadensis*)	Sum of conifer basal area	Total plot basal area
	(m^2 ha^{-1})										
Brush Brook D	5.45	15.67	4.43	1.43	0.08	0.02	0.48	1.69	0.00	2.17	29.97
Brush Brook G	8.23	13.34	1.06	4.51	0.12	0.00	0.45	0.23	0.00	0.68	28.65
Buck Creek N	0.62	2.73	8.05	0.07	7.90	0.00	5.34	0.94	4.69	10.98	30.90
Buck Creek S	6.32	2.31	16.29	0.00	0.00	0.00	0.44	0.00	0.01	1.11	25.66
Cone Pond	0.46	0.77	1.02	1.65	2.02	0.04	8.10	1.08	4.58	13.75	19.91
HBEF W3	6.91	3.80	6.52	1.59	0.90	0.28	4.87	1.35	0.60	6.82	26.84
HBEF W7	3.38	12.91	0.70	4.47	0.05	0.00	2.94	2.18	0.06	5.18	27.38
Lye	7.43	3.90	2.91	1.92	1.07	0.00	2.65	1.67	0.09	4.41	21.72
Ranch Brook	5.67	9.57	4.52	0.73	1.33	0.00	0.61	0.04	1.47	2.12	24.80
Sleepers W9-A	18.64	3.51	0.13	0.00	0.00	5.46	0.06	0.81	0.00	0.88	28.90
Sleepers W9-C	19.16	4.98	0.05	0.68	0.05	2.56	1.11	1.28	0.00	2.39	30.22
Winnisook	0.00	15.11	7.62	0.10	0.82	0.02	0.00	0.37	0.00	0.37	24.34

Minor species measured but not included here were American basswood (*Tilia americana*), striped maple (*Acer pensylvanicum*).

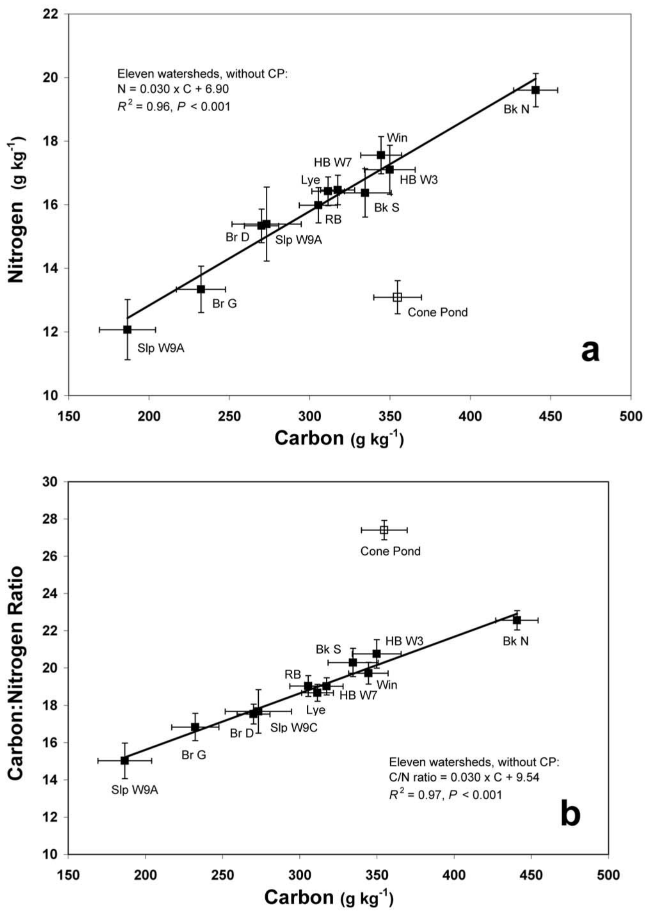

Figure 2. The relationship between carbon and nitrogen concentration (a) or C/N ratio (b) for the data in Figure 1 averaged by watershed. The regression line does not include Cone Pond. Error bars represent the SEM. See Table 1 for watershed acronyms.

result partially from the different number of points in each average but also from the distribution of C and C/N ratio within a watershed being different from the distribution of the overall data set. For example, Buck Creek North had a high range in C concentration (260–511 g kg^{-1}) and a relatively higher (than average) range in the C/N ratio (19.7–29.0). The combined individual plot data (Figure 1) are somewhat a series of overlapping watershed data.

Carbon Pools and C Relationship to Tree Species

Carbon pool size (Table 4; Figure 3) was approximated from the thickness of the individual horizon and a disturbed bulk density measurement. For all data, there was a weak but significant relationship ($R^2 = 0.15$, $P < 0.001$) between C pools and C concentration. For 10 watershed averages (Cone Pond was omitted from the regression for consistency and HBEF W3 was omitted because carbon was used to calculate bulk density), there was a clearer significant trend ($R^2 = 0.61$, $P = 0.005$) toward higher C pools with higher C concentration (Figure 3).

Vegetation data were collected around all sampling points and, because many of these points consisted of only one soil sample, we focused our analysis only on watershed averages (Table 4). One of three hardwood species dominated in nine of the watersheds—sugar maple, yellow birch, or American beech. Watershed HBEF W3 had a more even distribution of the three northern hardwoods and red spruce, whereas Cone Pond and Buck Creek North were largely red spruce and eastern hemlock (Table 3). These latter two also had the highest concentrations of C. The litter of sugar maple has been found to have a rapid turnover, resulting in high N mineralization (Finzi et al. 1998, Lovett et al. 2004) and Ross et al. (2009) found nitrification rates of yellow birch to be as high as those for sugar maple. For this reason, we combined the two species in our analysis and the sum of sugar maple and yellow birch basal area had a strong inverse relationship with watershed average C concentration (Figure 4a). The combination of the two species was a better predictor ($R^2 = 0.74$ for all watershed averages except Cone Pond) than sugar maple alone ($R^2 = 0.47$). The basal area of the remaining major hardwood species, American beech, had a positive rather than negative relationship with C. When combined with all conifer species, it provided a strong positive linear relationship with watershed average C (Figure 4b). These two relationships are similar in strength, but with opposing slopes, largely because the species included comprise most of the plot basal area.

Discussion

The strong relationship between average C concentration and the C/N ratio, even with a low n of 11, is intriguing. Because C is on both axes, the statistical power of the relationship can be questioned. However, there is clearly a trend toward higher C/N with higher C shown in the power function of all C versus N data (Figure 1a) or the linear function (Figure 2a). A highly linear relationship between C and N, going through the origin, would be expected if the samples simply had different ratios of mineral and organic soil materials, without differences in the composition of the organic material. What our data show is that the composition of soil OM is not constant but has progressively less N with increasing C concentrations. To determine whether this relationship held true beyond our study area, we used data from a sampling of other recent studies on forest soils in North America (Van Cleve et al. 1993, Ohrui et al. 1999, Boggs et al. 2005), Europe (Smolander and Kitunen 2002, Laverman et al. 2000), and New Zealand (volcanic soils from Parfitt et al. 2005). These data included 52 samples described variously as the forest floor, O horizon, 0–5 cm, or LF horizon, not necessarily Oa or A horizons (as in our study). The relationship between C and the C/N ratio was not nearly as tight as in the present study, but the slope in the least-squares linear fit was remarkably similar to the 0.030 we found (Figure 2b):

$$C/N = 12.2 + 0.031 \times C\ (\text{mg kg}^{-1})$$

$$R^2 = 0.50 \quad P < 0.001.$$

The consistency of the relationship across diverse sites is evidence that the phenomenon of higher C/N ratios with higher C concentrations is global. The strength of the relationship found in our study may have been due to the large

Table 4. Carbon concentration and pool, nitrogen, C/N ratio, and pH in the Oa or A horizons averaged across the plots within each watershed.

Watershed	Carbon	Nitrogen	C/N ratio	Oa/A horizon depth	Oi/Oe horizon depth	Bulk density ($Mg\ m^{-3}$)	Carbon pool in Oa/A ($kg\ m^{-2}$)	pH
	. . . . .($g\ kg^{-1}$)			. . . . . .(cm)				
Brush D								
Mean	270.1	15.33	17.5	6.3	4.7	0.30	4.78	3.63
SE	10.7	0.53	0.3	0.5	0.3	0.01	0.44	0.04
Brush G								
Mean	232.3	13.34	16.8	4.3	4.7	0.35	3.01	3.99
SE	15.3	0.73	0.3	0.5	0.3	0.02	0.35	0.10
Buck North								
Mean	440.7	19.60	22.6	14.9	5.3	0.20	12.49	3.56
SE	13.7	0.52	0.6	2.6	0.3	0.01	2.15	0.03
Buck South								
Mean	334.5	16.37	20.3	5.2	3.6	0.28	4.62	3.72
SE	16.2	0.76	0.3	0.6	0.2	0.01	0.52	0.05
Cone Pond								
Mean	354.7	13.09	27.4	4.7	4.8	0.25	3.64	3.79
SE	14.8	0.52	0.9	0.5	0.4	0.01	0.41	0.05
HBEF W7								
Mean	317.4	16.46	19.0	6.5	4.7	0.26	4.73	3.94
SE	10.6	0.46	0.2	0.4	0.3	0.01	0.31	0.04
HBEF W3								
Mean	349.8	17.1	20.8	10.6	3.3	0.17	6.12	ND[1]
SE	15.8	0.77	0.7	2.2	0.3	0.01	1.28	
Lye								
Mean	311.5	16.42	18.7	9.1	5.0	0.27	6.80	3.71
SE	10.2	0.45	0.2	0.5	0.2	0.01	0.39	0.04
Ranch Brook								
Mean	305.5	16.0	19.0	9.3	4.2	0.31	7.35	ND
SE	11.9	0.6	0.3	0.6	0.2	0.01	0.49	
Sleepers W9-A								
Mean	186.7	12.07	15.0	6.2	3.2	0.34	3.39	5.18
SE	17.5	0.95	0.4	0.9	0.2	0.02	0.45	0.17
Sleepers W9-C								
Mean	273.2	15.39	17.7	2.8	3.7	0.30	2.00	4.97
SE	21.5	1.17	0.4	0.4	0.2	0.02	0.32	0.13
Winnisook								
Mean	344.5	17.56	19.7	5.7	4.3	0.30	5.22	3.44
SE	12.7	0.58	0.5	0.5	0.3	0.02	0.42	0.03

The bulk density was measured in disturbed samples in all but HBEF W3 (calculated from C using the equation of Huntington et al. 1989).
[1] ND, not determined.

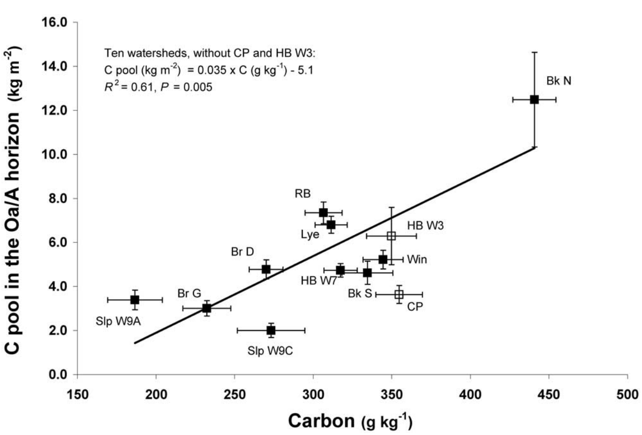

Figure 3. Carbon concentration versus carbon pool for all data averaged by watershed. The regression line does not include Cone Pond, to be consistent with the other figures, nor HB W3 because, in samples from this watershed, the bulk density used to calculate the carbon pool was calculated from C concentration. Error bars represent the SEM. See Table 1 for watershed acronyms.

number of samples going into the averages, to more uniform samples (i.e., the Oa or A), or to similarities among the watersheds (these latter two possibilities are discussed below).

These watersheds, with the exception of Cone Pond, contain second-growth forests with no documented evidence of fire. All are at relatively high elevation with steep terrain and were probably not in cultivation but were probably heavily logged. The current stands are similar in age (80–120 years) with little or no logging in the past circa 40 years. In a meta-analysis of experiments on north temperate forest soils, Nave et al. (2009) showed that greater N inputs led to a lower C/N ratio in the forest floor, whereas de Vries et al. (2009) recently showed a positive relationship between N deposition and C sequestration in European forests. Recent wet N deposition at our watersheds has varied between 4.3 and 6.3 $kg\ ha^{-1}\ year^{-1}$ (Ross et al. 2009) but with no pattern that helps explain the variation in C/N ratio. The same is true of climate variables such as precipitation and temperature. If it is assumed that the present-day status

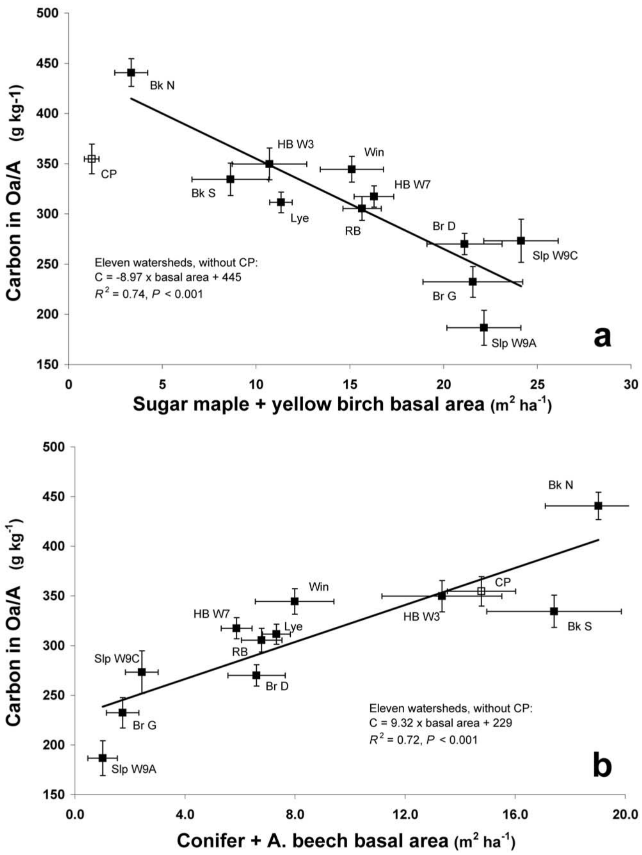

Figure 4. Predicted carbon concentration by the sum of the sugar maple and yellow birch basal area (a) or the sum of the American beech and conifer basal area (b). The regression lines do not include Cone Pond. Error bars represent the SEM. See Table 1 for watershed acronyms.

of the near-surface horizons was strongly influenced by the present second-growth forest over the past century, then it follows that the present differences between watersheds have been determined by some combination of vegetation and soil processes. Although the bedrock differs considerably between watersheds, soil textures are all fine sandy loam to silt loam with little clay content (Table 2). At all sites, soils were developed from glacial till and are either Inceptisols or Spodosols with the local topography and hydrology playing a role in profile development. The C concentration in the Oa or A horizon reflects not only inputs from litter and root turnover but also pedogenic processes that control the redistribution of C through the soil profile. The standard soil-forming factors of climate, time, and even topography are relatively similar among the watersheds. Parent material differs somewhat and the calcareous bedrock underlying Sleepers River may have prevented typical Spodosol formation (resulting in less developed Inceptisols) and increased the abundance of calciphilic tree species such as sugar maple and white ash. The watershed averages for sugar maple dominance (fraction of total basal area in each plot) were related to soil pH ($R^2 = 0.81$, $P < 0.001$). The strength of this relationship was highly influenced by the two Sleepers River watersheds that had very high sugar maple densities and relatively high pH values (Table 3). At the other watersheds, the reasons for the differences in tree species were not readily apparent. There was a wide range in exchangeable Ca and extractable Al in the soils sampled (Ross et al. 2009) but neither showed any clear trends with tree species composition. A complex interaction between local site factors and tree species probably exists.

In addition to similar land use histories, the tightness of our relationships may have been affected by our sampling protocol. We sampled the uppermost humified soil horizon, whether it was an A or an Oa. This approach may provide a more sensitive representation of the influence of tree species and pedogenic processes. Johnson et al. (2000) also sampled the Oa horizon in the Winnisook watershed and obtained results quite similar to our data (365.1 g kg^{-1} C, 17.5 g kg^{-1} N, and a C/N of 20.8; compare with our Winnisook data in Table 3). Many studies, including most of those cited above, sampled some combination of "forest floor" that may include Oi, Oe, and Oa material but may also omit A horizons. Sample processing also varies considerably between studies. If the entire forest floor is taken, it is more difficult to sieve and homogenize than the less fibrous Oa or A alone. Our sampling scheme and preparation method may have been optimum for detecting the differences we found.

Influence of Tree Species

The vegetation differences were strongly related to differences in C and N concentrations in the near-surface horizons (Figure 4). Tree species effects on soil C have been documented (e.g., Finzi et al. 1998, Vesterdal et al. 2008), but studies are difficult to compare because of the large number of different species and soil types. Carbon inputs are largely in the form of leaf litter and root turnover, with litterfall and decomposition rates being critical in determining the amount remaining in near-surface horizons. Decomposition rates of litter are a function of litter chemistry and climate (Aerts 1997, Berg and McClaugherty 2008). Litter chemistry varies with both species and local conditions, and lignin and N are important components (Melillo et al. 1982, Moore et al. 1999). Most studies show that turnover of sugar maple litter is relatively fast (e.g., Melillo et al. 1982, Lovett et al. 2004) and conifer litter is relatively slow (Berg and McClaugherty 2008). Less work has been performed on yellow birch and American beech but in one study Gosz et al. (1973) found litter decomposition rates over a 12-month period to be in the sequence of yellow birch > sugar maple > American beech. Using seedlings in a pot study, Sommerville et al. (2004) found that yellow birch leaves decomposed faster than those of sugar maple alone or when the two species were combined. Finzi et al. (1998) did not study yellow birch but found that soils under American beech had twice the forest floor mass as those under sugar maple, along with a higher C/N ratio (20.7 versus 15.0). Thus, there is some evidence supporting the grouping of the dominant species as we did in Figure 4. However, it needs to be reiterated that the relationships we found did not ascribe cause and effect, and it is likely that there is a two-way interaction between soils and species. Soil conditions can determine the species distribution which can, in turn, affect soil properties such as carbon retention.

Carbon Pools

Our study only sampled the Oa or A horizon, and it is possible or even probable that these samples did not reflect the entire soil profile. Trends in the size of C pools in lower mineral horizons have been found to be opposite to those in the surface, reducing differences in the whole soil profile under various tree species (Vesterdal et al. 2008). Differences in soil properties, such as texture (Hobbie et al. 2007) and fertility (Ladegaard-Pedersen et al. 2005), appear to have a greater influence on whole profile C retention than tree species. Organomineral particle associations in the mineral soil have an impact on C stabilization, and retention in the denser fractions appears to be controlled by the soil mineralogy (Sollins et al. 2009). Many studies have also shown that, even though there are high concentrations of C in the surface horizons, most of the total C pool resides in the mineral soil (e.g., Huntington et al., 1988, Pregitzer and Euskirchen 2004). In our relatively high elevation soils, classified as frigid with the exception of Winnisook (Ross 2007), these Oa or A horizons were a substantial C pool with the average ranging between 20 $Mg\ ha^{-1}$ at Sleepers River W9-C to 125 $Mg\ ha^{-1}$ at Buck Creek North (data from Table 1 converted from $kg\ m^{-2}$ to $Mg\ ha^{-1}$). When combined with the overlying Oe and Oi horizons, the near-surface pool would be even larger. We have no data on C in the upper forest floor from our study, but in four complete profiles from similar soils at similar elevations in Vermont, the Oe and Oi horizons comprised between 30 and 45% of the near-surface (i.e., Oa or A horizon and higher) C pool (US Department of Agriculture Natural Resources Conservation Service 2008). In these same profiles, the near-surface C pool comprised between 17 and 47% of the total soil profile C to a depth of 100 cm. In shallower soils and soils at even higher elevations, this percentage will increase. The near-surface horizons are more prone to loss of C through disturbances such as erosion and fire but, in these soils found at somewhat high elevations for the northeastern United States, they form an even greater percentage of the ecosystem C pool.

Implications

If one assumes that the starting point of our soils, after deglaciation circa 12,000 years ago, was low C mineral parent material, then it follows that the C has accumulated preferentially over N (as in Figure 1a). Interestingly, our linear fit of average C versus N (Figure 2a), if extrapolated, would predict 7 $g\ kg^{-1}$ N at $C = 0$ and a constant increase in both from that point. Likewise, Figure 2a predicts a C/N ratio of 9.7 at $C = 0$ and approximately 27 if the sample had 600 $g\ kg^{-1}$ C (or ~100% OM). It is therefore obvious that the data cannot be extrapolated very far in either direction. The slope of both Figure 2a and b is 0.030 and so for every increase of 100 $g\ kg^{-1}$ C there was either a constant increase of 3 $g\ kg^{-1}$ N or 3 in the C/N ratio. This equates to a simple mixing of additional C, from some starting point, at a constant C/N ratio of approximately 33. For example, using our lowest C/N ratio value of 15.0 (Sleepers River W9-A) as the starting point, increasing the C concentration from 187 to 440 $g\ kg^{-1}$ (our highest C average, Buck Creek North) with the added C having a C/N ratio of 33 will result in a C/N ratio of approximately what we found of 22.6. These near-surface horizons accumulate decomposition products of litter and root inputs, often of widely differing C/N ratios. Senescing leaf and needle litter have high C/N ratios (a range of 66–83 was found in eight northern coniferous and deciduous species by Moore et al. 2005), whereas fine roots of sugar maple have been found to have C/N ratios as low as 23 (King et al. 2005) and red spruce nonwoody roots as high as 76 (Wargo et al. 2003). The contribution of roots to stable organic matter may be high (Rasse et al. 2005, Crow et al. 2009) and the range in C/N ratios that we found is probably explained by the differing chemistries of the differing inputs, both above- and belowground.

It remains to be seen whether the relationship we found is valid in different watersheds and whether it can be used to predict changes that will occur within a watershed after changes in tree species composition. Historical records in Vermont, 1762–1820 (Cogbill et al. 2002), show a lower percentage of maple (15.3% for both sugar maple and red maple, *Acer rubrum*, combined) and a higher percentage of American beech (36.0%) than present-day surveys (28% sugar maple and 4% American beech) (US Forest Service 2008). This change suggests a lower C stock in the surface soil horizons today than presettlement. With global climate change, sugar maple is predicted to decrease in the region and oak species increase (Iverson and Prasad 2002), possibly increasing C stocks, but any such effect may be masked by changes in temperature and possibly precipitation associated with a changing climate. The near-surface horizons in soils from mountainous regions of the northeastern United States appear to hold a large, potentially labile, pool of C. Although a better understanding of factors controlling C pools in these soils is still needed, we have clearly shown a nonlinear trend between C and N retention and a strong linear relationship between C retention and tree species composition.

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