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The Imprint of Land-use History: Patterns of Carbon and Nitrogen in Downed Woody Debris at the Harvard Forest

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Abstract

Few data sets have characterized carbon (C) and nitrogen (N) pools in woody debris at sites where other aspects of C and N cycling are studied and histories of land use and disturbance are well documented. We quantified pools of mass, C, and N in fine and coarse woody debris (CWD) in two contrasting stands: a 73-year-old red pine plantation on abandoned agricultural land and a naturally regenerated deciduous forest that has experienced several disturbances in the past 150 years. Masses of downed woody debris amounted to 40.0 Mg ha^{-1} in the coniferous stand and 26.9 Mg ha^{-1} in the deciduous forest (20.4 and 13.8 Mg C ha^{-1}, respectively). Concentrations of N were higher and C:N ratios were lower in the deciduous forest compared to the coniferous. Pools of N amounted to 146 kg N ha^{-1} in the coniferous stand and 155 kg N ha^{-1} in the deciduous forest; both are larger than previously published pools of N in woody debris of temperate forests. Woody detritus buried in O horizons was minimal in these forests, contrary to previous findings in forests of New England. Differences in the patterns of mass, C, and N in size and decay classes of woody debris were related to stand histories. In the naturally regenerated deciduous forest, detritus was distributed across all size categories, and most CWD mass and N was present in the most advanced decay stages. In the coniferous plantation, nearly all of the CWD mass was present in the smallest size class (less than 25 cm diameter), and a recognizable cohort of decayed stems was evident from the stem-exclusion phase of this even-aged stand. These results indicate that heterogeneities in site histories should be explicitly included when biogeochemical process models are used to scale C and N stocks in woody debris to landscapes and regions.

Key words: coarse woody debris; land-use history; disturbance; biogeochemistry; forest floor; modeling; landscape; anthropogenic effects; management.

Introduction

A growing area of research in ecosystem science addresses the effects of past and present human activities on ecosystem structure and function. In temperate forests, the effects of both natural and anthropogenic disturbances spanning decades and centuries manifest themselves in the stocks and characteristics of woody debris (Spies and others 1988; Krankina and Harmon 1995; Duvall and Grigal 1999). Patterns of mass and nutrients in woody detritus have the potential to link landscape and biome-scale budgets of C (carbon) and N (nitrogen) in forests to land-use and disturbance history, forest management practices, and ecological responses to land-use and management history (Harmon and others 1986; Krankina and Harmon 1994; Brown

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and Schroeder 1999). Improved understanding of large-scale interactions of C and N in forested landscapes are, in turn, critical to gaining better understanding of controls on global C cycling (Townsend and others 1996; Nadelhoffer and others 1999).

Biogeochemical models that synthesize production, decomposition, and nutrient cycling processes are being used in an effort to develop a predictive understanding of ecosystem responses to the combined effects of rising carbon dioxide (CO_2), elevated deposition of N, and changes in land use or management practices (Townsend and others 1996; Schimel and others 1997; van Oene and others 1999). These models are necessarily parameterized, calibrated, or tested using observational data on pool sizes of C and N. Unfortunately, few data sets are available that characterize C and N pools in woody detritus at sites where two other important criteria are met: first, other aspects of C and N cycling are well characterized, allowing complete C and N budgets to be parameterized (Harmon and Sexton 1996); and second, specific aspects of the long histories of land use and disturbances are well documented.

Given the stochastic and disturbance-related nature of woody litter inputs, together with variabilities in rates of decay determined by species, size classes, and climate, pool sizes of woody detritus range widely even within a forest type. In temperate deciduous forests, in the absence of major recent disturbances, pools of downed woody biomass range over an order of magnitude from 5 to over 50 Mg/ha. In recent clear-cuts or after catastrophic windthrow, pool sizes can be much higher (Gore and Patterson 1986; Krankina and Harmon 1994). In temperate coniferous forests, masses of downed wood range even more widely because very high values are observed in some forest types. Masses range from 6 Mg/ha (Duvall and Grigal 1999) to as high as 490 Mg/ha in forests of the Pacific Northwest region of North America (Harmon and others 1986).

Previous work at the Harvard Forest (Massachusetts, USA) has produced detailed observations of numerous aspects of forest C and N cycling, although pool sizes of C and nutrients in woody debris have not been well quantified. Ecosystem stocks of C and N have been measured in living vegetation, forest floors, and mineral soils (Aber and others 1993; Magill and others 1997, 2000). Data from the Harvard Forest have played a key role in the development or parameterization of numerous models with a wide range of purposes: to link biomass production, N availability, and water use (Aber and Federer 1992); to link forest production and respiration to eddy-flux tower measurements of ecosystem C exchange (Aber and others 1996; Williams and others 1996); to study the effects of land-use history on ecosystem C and N storage (Aber and Driscoll 1997); to link the production of dissolved organics in soil to litter inputs and decomposition processes (Currie and Aber 1997); to interpret the redistributions of ^{15}N-enriched tracers in vegetation and soil pools while linking these to ecosystem C fluxes (Currie and others 1999); and to predict the effects of climate change on C and N cycling (Rastetter and others 1992; Aber and others 1995; Melillo and others 1995). In addition, some models of generalized processes across types of terrestrial ecosystems have used data from the Harvard Forest to parameterize temperate forest regions (Generalized Ecosystem Model, Rastetter and others 1992; Terrestrial Ecosystem Model, McGuire and others 1992).

Ecosystem budgets and synthetic models applied at the Harvard Forest have relied on woody detrital measurements from other temperate forests. Such extrapolation is problematic for woody detritus, because inputs at a particular site are highly stochastic, and pool sizes reflect the particulars of disturbance and land-use history (Roskoski 1980; Harmon and others 1986; Krankina and others 1999). Reliance on pool sizes of woody detritus from other sites limits the degree to which C and N cycling processes could be connected and understood at the ecosystem level, even though doing so is typically a major goal of budgeting and modeling investigations.

We studied current patterns in woody detritus in two forest stands at the Harvard Forest that had different and well-documented histories of land use and a wealth of existing information on other aspects of C and N cycling. Our primary objective was to quantify mass, C, and N pools in downed woody detritus in these forest stands, one a coniferous plantation and the other a naturally regenerated deciduous forest. A secondary objective was to include and quantify the amount of woody debris buried in the forest floor. Many studies of downed woody debris exclude material buried in the surface organic horizon of the soil (Brown 1974), but previous workers in New England had found significant storage pools of woody debris thus buried (McFee and Stone 1966; Lang and others 1981). We also expected buried logs to provide additional information about the long-term history of inputs of coarse woody debris as related to the history of land management.

Table 1. Characteristics of Forest Stands in 1988

	Pine Forest	Oak Forest
Stem density (no./ha)	1174	1937
Basal area (m^2/ha)	51.9	21.8
Tree biomass (g/m^2)	14656	11132
% biomass by species		
Red pine	98	0
Black and red oak	1	78
Red maple	>1	5
Black birch	1	8
Others	>1	9

From Aber and others (1993)

Methods

Site Description and History

The Harvard Forest (central Massachusetts, USA) is a site in the Long-Term Ecological Research (LTER) network sponsored by the US National Science Foundation. Elevations in the area studied here range from 365 to 390 m; monthly mean temperatures are −7°C in January and 19°C in July. Precipitation averages 110 cm/y and is distributed fairly evenly throughout the year (Van Cleve and Martin 1991). Here we consider the two forest stands included in the ongoing Chronic N study, in which N availability is being manipulated in large-scale forest plots (Aber and others 1993; Magill and others 1997). One stand is predominantly red pine (*Pinus resinosa* Ait.); the other is predominantly oak (*Quercus velutina* Lam., *Q rubra* L., *Betula lenta* L., *Acer rubrum* L.) (Table 1). Soils in both stands are coarse-loamy (in the oak stand, coarse-loamy over sandy-skeletal), mixed, frigid Typic Dystrochrepts. Soils are well drained and contain well-defined O horizons (mor type).

The Prospect Hill tract, which includes the forests we studied here, is a 380-ha area in which the history of land use and disturbance is well known. The Prospect Hill tract was largely cleared for agriculture in the 19th century. Much of this tract was owned by one farmer in 1845, including the two forest stands we consider here (Raup 1966). In the latter decades of the 19th century, reversion to forest began to occur in patches as agricultural lands were abandoned. As a whole, the Prospect Hill tract was 25% forest in 1880 and grew to 85% forest in 1920 (Foster 1993). Reversion to forest generally proceeded first in areas that were more distant from roads, poorly drained, or marginal, including steeper slopes. Upland areas nearer to roads, such as the land containing the pine forest we studied here, generally reverted to forest later (Foster 1993). Today the tract is almost entirely forest.

The present mixed-oak stand is on land that was in pasture in 1840 (Foster 1992; Motzkin and others 1999) and bordered a woodlot that was in a low, poorly drained area. Because of its steeper slopes and proximity to the wet area, farmers abandoned this patch between 1840 and 1859, making it one of the earliest agricultural patches to be abandoned (Foster 1992). Following abandonment, much of the land in the Prospect Hill tract produced a naturally seeded crop of white pine (*Pinus strobus*) that was cut once stands reached merchantable size (Raup 1966). In the stand we study here, lower elevations bordering the woodlot were cut in 1885 and portions higher upslope were cut in 1900 (Foster 1992). Following the cutting of pine, hardwoods present in the understory grew to produce the naturally regenerated mixed-oak forest on this land today (Foster and others 1992).

The mixed-oak forest stand was subject to major disturbances in the early 20th century. First, this stand was heavily damaged (76%–90% of the canopy trees) by catastrophic windthrow during a hurricane that struck the area in 1938 (Motzkin and others 1999). Another major disturbance was the chestnut blight; American chestnut (*Castanea dentata*) was a significant species in this hardwood forest in the early 20th century. Because of the proximity of this area to a 19th-century lowland woodlot rich in hemlock (*Tsuga canadensis*), hemlock was a significant feature in the understory earlier in the 20th century and has grown steadily in importance in this tract of hardwood forest since the chestnut blight (Foster and others 1992). Although hemlock is not a major component of the vegetation on the permanent plots located on the upslope portions of this mixed-oak stand (Aber and others 1993) (Table 1), the larger-scale transects we use in the present study include areas with some hemlock.

The history of the land in the red pine forest contrasts with that of the mixed-oak forest in several important respects. Lying on a flatter, higher knoll and in close proximity to a 19th-century road, this patch of land was cultivated in the 19th century (Motzkin and others 1999). The land reverted to forest between 1900 and 1920, making it one of the last agricultural areas in the Prospect Hill tract to be abandoned (Foster 1992). The forest today is a red pine plantation that was planted in 1926. Located on a knoll, it is more likely to be exposed to strong winds than downslope forest stands. Across the

Prospect Hill tract, pines were in general more susceptible to damage from the 1938 hurricane than hardwoods. However, these red pine trees escaped notable windthrow damage from the 1938 hurricane, possibly because the trees were still young and small in stature in 1938 (Foster and Boose 1992; Motzkin and others 1999).

Volume and Decay Class Determinations along Transects

We used the line-intercept method along transects to measure volumes of woody detritus, which we later combined with densities and C and N concentrations to calculate mass, C pools, and N pools (Brown 1974; Gore and Patterson 1986; Harmon and Sexton 1996). Transects were designed to quantify woody debris under ambient (untreated) conditions; therefore, they did not cross experimental plots where N inputs are being manipulated as part of the ongoing Chronic N study. In each forest, we established three 100-m transects, the first oriented at random, and the others at bearings of 120 and 240 compass degrees relative to the first (Wells and Trofymow 1997). The purpose of orienting transects in this manner is to make it unlikely that the line-intercept method will undercount logs oriented in any systematic pattern, such as that created by large-scale windthrow. Specific starting points for each transect were also established randomly, but they were stratified areally so that each set of three roughly surrounded the clusters of permanent plots from the Chronic N study. Transects were broken or staggered in some cases to avoid crossing an access road or to remain within the pine plantation. Each set of three transects was contained in a homogeneous forest stand about 1–2 ha in area.

We used multiple size and decay classes to quantify pools of woody detritus. There were two reasons for this. First, since N concentration varies widely with size and decay class, this provided an important framework to scale C and N pools up to the ecosystem. Second, we expected the distribution of size and decay classes to reveal effects of land-use history and disturbance on pool sizes. The major size distinction we made was between coarse woody debris (CWD, at least 10 cm in diameter) and fine woody debris (FWD, less than 10 cm in diameter). We further separated FWD into four size classes based on diameter: 0.5 to less than 1.0 cm, 1.0 to less than 2.5 cm, 2.5 to less than 5.0 cm, and 5.0 to less than 10.0 cm. We separated CWD into three size classes: 10.0 to less than 25.0 cm diameter, 25.0 to less than 50 cm, and 50 cm or greater. On each 100-m transect, we used the entire length to quantify CWD (300 m total in each forest), while we used nested subtransects to tally smaller pieces of woody detritus. We used three random, 10-m subtransects to quantify FWD in size classes above 2.5 cm (90 m total in each forest). For size classes 0.5 to 2.5 cm, we used three random, 4-m sections (36 m total in each forest).

We classified detritus into decay classes in the field, with the number of decay classes varying by size class (Polit and Brown 1996). In the largest two size classes of FWD, we distinguished three categories: sound, intermediate, and rotten. In the size class 1.0 to less than 2.5 cm, we distinguished two categories, sound versus intermediate to rotten; for the finest size class (0.5 to less than 1.0 cm), we did not separate detritus into decay classes. For CWD, we used five decay classes, from relatively sound wood as decay class 1 to detritus with the most advanced decay as class 5. We distinguished decay classes in the field by the presence of bark and branches, the degree of sapwood degradation, the soundness of the heartwood, and the presence of moss and fungi (Sollins 1982; McCarthy and Bailey 1994; Krankina and Harmon 1995). We found that testing the soundness or softness of the wood with a wood chisel and rubber mallet provided one of the most consistent means of assessing decay class.

Each transect defined a vertical plane (Brown 1974). We quantified downed woody detritus, including stumps, and woody debris buried in the forest floor. Along the entire length of each 100-m transect, we excavated through the forest floor to the upper mineral soil horizon to measure and record branches, dead roots, logs, and fragments buried in the surface organic horizons (McFee and Stone 1966). We did not excavate into the mineral soil. We included branches above the forest floor if they were attached to a piece of downed material; likewise, we included logs off of the forest floor as downed material if they were resting on their own branches. We excluded live wood, standing dead wood (snags), and attached or suspended dead wood (pieces in which the weight was supported by other trees instead of the ground).

For each piece of downed woody debris, whether a fragment or an intact whole, we measured the maximum and minimum diameters (as opposed to recording only tallies within size classes) with large calipers where the piece crossed the transect plane, and we recorded the angle made with the horizontal for each piece as it lay in situ (Harmon and Sexton 1996). We identified the species of each piece where it was clear from bark or branching patterns; in most cases, we identified pieces simply as deciduous, coniferous, or unknown. Each piece was treated as having an oval cross section, with minimum and maximum diameters measured in the field, and with size class based on the maximum diameter. We estimated the percent missing (due to fragmentation or rotting) from an oval cross-sectional area where each piece crossed the transect, which we later took into account when calculating the volume of downed wood.

Sample Collection, Preparation, and Analysis

Along each transect, we collected two samples at random from each combination of size and decay class. We cut entire cylinders, cross-sectional disks, or wedge-shaped (pie-piece–shaped) pieces. In every case, we took care to collect the correct proportions of heartwood, sapwood, and bark (where present). In some cases, where we encountered fewer than two pieces of detritus in a given size-decay category, we searched for additional, representative samples in the vicinity of the transect. Woody debris greater than 25 cm in diameter was rarely encountered in either forest, either along transects or in the vicinity, thus we were unable to find two samples within most size-decay classes. We also randomly collected samples of unattached bark encountered along transects.

We determined C and N concentration by dry combustion on a Carlo-Erba NC 2100 at the Appalachian Laboratory in Frostburg, Maryland. Samples for chemical analysis were dried to constant mass (70°C), ground to no. 20 mesh in a no. 4 Wiley mill, stirred well, subsampled (200 mg) for further grinding to a fine powder in a jar mill, and tested to pass through a no. 100 mesh sieve. These were again dried to 70°C and cooled in a laboratory desiccator until analysis by dry combustion. A 100-mesh grind (150 μm) is finer than sometimes recommended for soil fractions (compare Boone and others 1999). In wood, however, where N concentrations are as low as 0.1% and where analytical samples are as small as 10 mg, we found the 100-mesh grind to produce more reliable results, in agreement with Nelson and Sommers (1996). We ran triplicate analyses on samples chosen at random; differences between the highest and lowest values expressed as percentages of the triplicate means ranged from 0.4% to 0.8% for C, and from 0.5% to 6.6% for N.

We performed dry weight corrections (105°C) on all samples and report C and N results here on a dry weight, ash-included basis. Though soil organic pools are often described on an ash-free basis, woody detritus is typically reported on an ash-included basis because most studies of woody debris measure volume or mass, not C, and rely on studies like the present one to convert volume or mass into pools of C (for example, Gore and Patterson 1986). Multiplication of detrital mass (ash-included) by our C concentrations, or multiplication of detrital volume by our densities and C concentrations, are simple means by which others can use our data to estimate pools of carbon.

We took subsamples from each sample of woody debris, prior to grinding, for determination of bulk density. We weighed each piece to 0.001 g, sprayed it with wood sealant, then measured the displacement volume of water in a graduated cylinder.

We converted line-intersect tallies, diameter measurements, angles with the horizontal, and transect lengths to volumes of detritus in each forest and size-decay category using standard equations provided by Harmon and Sexton (1996). Next, we converted volumes to masses using mean densities that we determined within each forest and size-decay category. Finally, we multiplied mass pools by our mean concentrations of C and N in each forest and size-decay category to obtain pool sizes of C and N. Amounts of unattached bark were small, and we found no standard methods to scale this material up to ecosystem pools; we thus neglected unattached bark from our calculations of C and N pools.

For the finest three size classes of FWD (less than 5 cm diameter), we incorporated data from a concurrent study in these forest stands. The concurrent study took place on permanent plots, was limited to FWD size classes less than 5 cm diameter, and focused on changes in C and N pool sizes and recovery of ^{15}N tracers under N amendments (Currie and others 2002). Combining these results with the present results allowed us to increase sample size in the finest three size classes. At the same time, it allowed us to average the results for detrital mass determined with areal quadrat methods in the concurrent study with those determined by line-intercept methods in the present study, thus producing more robust estimates of C and N pool sizes in the finest three size classes. For densities of woody detritus, we combined results from 141 samples collected in the concurrent study with 145 samples collected along transects, for a total of 286 density measurements. For C and N concentrations in the finest three size classes, we combined results from the concurrent study collected only from ambient (untreated) plots.

Data were tested for normality and transformed where necessary. Logarithmic transformations produced normal distributions for N concentrations and wood density data, but failed for C concentrations and ratios of C:N. Box-Cox transformations (Box and Cox 1964; StataCorp. 1997) were used to obtain normal distributions for C concentrations and ratios of C:N (with $\lambda = -3.99$ and 0.401, respectively). Analyses of variance (ANOVA) were used to test for significant effects ($P < 0.05$) of forest stand, detrital size class, and decay class on detrital densities, C and N concentrations, and ratios of C:N.

Results

Detrital Chemistry and Density

Carbon concentrations exhibited a tight range in detrital samples, whereas C:N ratios and densities exhibited wide variabilities from piece to piece of detritus, even within some size and decay classes. The overall mean and standard deviation in C concentration was 50.9 ± 0.2% (oven-dried [105°C] mass, ash-included basis), and there was no significant difference between forests.

Our results showed increasing N concentrations and decreasing C:N ratios with stage of decay (Figure 1). This trend was significant (Table 2) in four of the seven size classes—all those from 1.0 cm to 25 cm. These were the only size classes in which we could test this relationship adequately. In the finest size class (0.5–1.0 cm), decay stages were not distinguished; in the largest two size classes (at least 25 cm), pieces in early stages of decay were not encountered in either forest stand.

Within the more sound decay classes, we expected C:N ratios to grow larger with increasing size class, but we noted no such trend in the results. We expected such a pattern for sound wood due to a larger ratio of wood to bark; bark has been observed previously to exhibit higher N concentrations than heartwood or sapwood (Harmon 1992). However, we encountered too few sound pieces in larger size classes to test this relationship. In the oak forest, no sound wood was encountered larger than 5 cm; in the pine forest, no sound wood was encountered larger than 25 cm in diameter. It is possible that our sample numbers were insufficient to resolve trends across size classes, given the highly heterogeneous nature of decaying woody debris. Size class was a significant categorical variable related to N concentrations (Table 2), highlighting the importance of stratifying the sampling and pool-size calculations by size class.

Overall, woody detritus in the pine forest had lower N concentrations and higher C:N ratios than that in the oak forest (Figure 1A). This did not appear to be an artifact of the distribution of decay

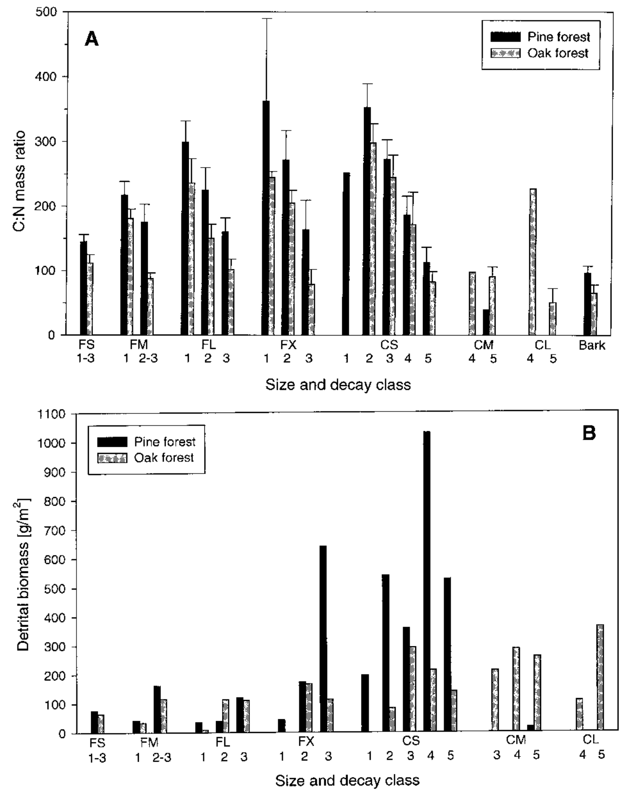

Figure 1. (**A**) C:N mass ratios and (**B**) biomass pool sizes (dry weight [105°C], ash-included basis) of woody detritus in size and decay classes. Abbreviations of size and decay classes are listed in Table 3. In (**A**), means ± 1 SE are shown; numbers of samples analyzed for chemistry within each forest type and category are listed in Tables 3 and 4. For any categories not shown, or where values in (**B**) are zero, woody debris was not present in that combination of size and decay classes.

classes present. While only the oak forest had pieces of highly decayed detritus in large size classes (Tables 3 and 4), C:N ratios were higher in pine forest detritus than in oak forest detritus in nearly every size and decay class.

Densities of individual samples of woody detritus ranged from 0.14 to 0.89 g/cm^3 (data not shown); means by size and decay class ranged from 0.24 to 0.62 g/cm^3 (Tables 3 and 4). Detritus in the pine stand exhibited significantly lower densities overall than detritus in the mixed-oak stand. Inspection of the data by size and decay class indicated that this result, as with the C:N ratios, was not an artifact of the distributions of size and decay classes present. Pine forest detritus had lower mean density than oak forest detritus in nearly every category. Woody detritus is typically viewed as decreasing in density as decay proceeds (Harmon and others 1986). We tested this view of wood decomposition within each

Table 2. Results of ANOVA Tests

Variable	Forest	Size Class	A. Model = Forest or Size Class		
Density	**	**			
C:N ratio	**	**			
			B. Model = Decay Category within each Size Class (in cm)		
	1.0 to <2.5	2.5 to <5.0	5.0 to <10.0	10.0 to <25.0	25.0 to <50.0	≥50.0
Density	**	**	n.s.	**	n.s.	n.s.
C:N ratio	**	**	**	**	n.s.	n.s.

***, significant at $P < 0.01$; n.s., not significant*

Table 3. Characteristics and Pool Sizes of Woody Debris in the Pine Forest

Size Class	Decay Class	Code	(*n*)	Density	% C	% N	C Pool (g C m^{-2})	N Pool (g N m^{-2})
0.5 to < 1.0 cm	All	FS 1–3	(10)	0.42 ± 0.026	51.6 ± 1.9	0.38 ± 0.11	39.0	0.286
1.0 to < 2.5 cm	Sound	FM 1	(10)	0.44 ± 0.015	51.5 ± 2.3	0.26 ± 0.09	21.6	0.109
	Intermediate & Rotten	FM 2–3	(11)	0.37 ± 0.031	52.0 ± 2.2	0.41 ± 0.27	83.7	0.657
2.5 to < 5.0 cm	Sound	FL 1	(8)	0.46 ± 0.036	50.0 ± 1.0	0.18 ± 0.06	17.8	0.065
	Intermediate	FL 2	(9)	0.35 ± 0.018	52.0 ± 4.1	0.26 ± 0.08	20.5	0.102
	Rotten	FL 3	(12)	0.30 ± 0.018	51.0 ± 3.5	0.43 ± 0.30	61.0	0.516
5.0 to < 10.0 cm	Sound	FX 1	(2)	0.37 ± 0.033	49.1 ± 0.1	0.15 ± 0.08	21.6	0.068
	Intermediate	FX 2	(5)	0.36 ± 0.061	50.6 ± 2.4	0.20 ± 0.07	87.5	0.354
	Rotten	FX 3	(5)	0.42 ± 0.075	50.9 ± 2.8	0.55 ± 0.51	326.3	3.504
10.0 to < 25.0 cm	1	CS 1	(1)	0.38	50.5	0.20	99.4	0.394
	2	CS 2	(5)	0.37 ± 0.050	50.0 ± 0.5	0.15 ± 0.03	269.7	0.799
	3	CS 3	(6)	0.25 ± 0.021	49.7 ± 0.9	0.20 ± 0.06	178.5	0.705
	4	CS 4	(6)	0.28 ± 0.030	51.2 ± 0.6	0.36 ± 0.28	527.6	3.678
	5	CS 5	(7)	0.24 ± 0.039	52.4 ± 1.1	0.59 ± 0.33	276.6	3.127
25.0 to < 50.0 cm	1–4	—	(0)	—	—	—	0	0
	5	CM 5	(1)	n.d.	54.0	1.36	9.6	0.242
≥50.0 cm	1–5	—	(0)	—	—	—	0	0
Sloughed Bark	—	Bark	(6)	0.33 ± 0.036	50.4 ± 1.9	0.55 ± 0.15	n.d.	n.d.

n.d., not determined; (n), number of samples for chemical analysis.
"Code" is shorthand for size/decay classes.
Concentrations of C and N and masses of detrital pools are listed on a dry mass (105°C) ash-included basis (means ± 1SE).

forest type and detrital size class. Densities decreased significantly within many combinations of forest and size class (Table 2). In nearly all other cases, trends of decreased densities with decay were present but were not statistically significant (Tables 3 and 4).

Pools of Detrital Mass, C, and N

Quantities of mass and C, which exhibited similar patterns to each other, revealed some similarities and some differences between forests. Similar between forests was the breakdown between coarse and fine woody debris; CWD pools held greater masses and C than FWD pools (Tables 3 and 4). Likewise, little CWD was encountered in the sound category in either forest (none in the oak forest). The pine forest held greater detrital mass overall and in FWD and CWD separately. FWD exhibited a greater relative difference between forests than did CWD (FWD was 83% higher in the pine forest); most of this difference between stands in the mass of FWD was due to a large pool of rotten wood in the 5–10-cm size class in the pine forest (Tables 3 and 4).

One of the most striking differences between these two forests was the contrasting biomass distributions among size and decay classes of CWD (Figure 1B). In the oak forest, detritus was distrib-

Table 4. Characteristics and Pool Sizes of Woody Debris in the Oak Forest

Size Class	Decay Class	Code	(*n*)	Density	% C	% N	C pool (g C m^{-2})	N pool (g N m^{-2})
0.5 to < 1.0 cm	All	FS 1–3	(13)	0.44 ± 0.025	50.6 ± 2.5	0.52 ± 0.20	31.9	0.328
1.0 to < 2.5 cm	Sound	FM 1	(12)	0.52 ± 0.029	50.3 ± 1.8	0.30 ± 0.09	16.5	0.099
	Intermediate & Rotten	FM 2–3	(12)	0.37 ± 0.027	50.6 ± 1.5	0.68 ± 0.36	58.7	0.786
2.5 to < 5.0 cm	Sound	FL 1	(8)	0.48 ± 0.024	49.5 ± 1.5	0.30 ± 0.25	4.4	0.027
	Intermediate	FL 2	(10)	0.44 ± 0.030	51.0 ± 1.5	0.42 ± 0.21	57.9	0.474
	Rotten	FL 3	(13)	0.30 ± 0.020	52.4 ± 2.5	0.61 ± 0.22	57.9	0.676
5.0 to < 10.0 cm	Sound	FX 1	(0)	0.49 ± 0.035	—	—	0	0
	Intermediate	FX 2	(6)	0.37 ± 0.038	49.8 ± 4.4	0.26 ± 0.06	83.5	0.427
	Rotten	FX 3	(7)	0.28 ± 0.038	50.9 ± 2.3	1.04 ± 0.65	57.9	1.187
10.0 to < 25.0 cm	1	CS 1	(0)	—	—	—	0	0
	2	CS 2	(5)	0.62 ± 0.017	48.1 ± 0.8	0.17 ± 0.03	40.0	0.139
	3	CS 3	(6)	0.44 ± 0.089	50.3 ± 3.1	0.24 ± 0.12	146.8	0.699
	4	CS 4	(3)	0.39 ± 0.084	51.4 ± 1.6	0.40 ± 0.30	110.8	0.859
	5	CS 5	(4)	0.25 ± 0.052	51.6 ± 2.3	0.72 ± 0.37	72.3	1.012
25.0 to < 50.0 cm	1–2	—	(0)	—	—	—	0	0
	3	CM 3	(0)	n.d.	n.d.	n.d.	110.3	1.127
	4	CM 4	(1)	0.39	51.9	0.53	148.7	1.519
	5	CM 5	(2)	0.33 ± 0.018	55.2 ± 0.22	0.62 ± 0.14	143.7	1.618
≥ 50.0 cm	1–3	—	(0)	—	—	—	0	0
	4	CL 4	(1)	0.50	48.9	0.22	53.3	0.234
	5	CL 5	(2)	0.27 ± 0.028	50.8 ± 1.3	1.19 ± 0.68	184.8	4.336
Sloughed Bark	—	Bark	(7)	0.44 ± 0.027	52.8 ± 6.9	0.96 ± 0.45	n.d.	n.d.

n.d., not determined; (n), number of samples for chemical analysis.
"Code" is shorthand for size/decay classes.
Concentrations of C and N and masses of detrital pools are listed on a dry mass (105°C) ash-included basis (means ± 1SE).

uted across all size categories of CWD, and nearly all of the CWD mass was in the most advanced three of the five decay classes. Patterns of CWD mass in the pine stand stood in direct contrast to this in two ways. First, nearly all of the CWD mass in the pine stand was less than 25 cm in diameter. Second, the material was distributed across all five stages of decay, including the two most sound (least decayed) categories.

Pool sizes of N in woody detritus showed the combined effects of quantities of detrital mass and concentrations of N. The pine forest held the greater detrital mass, but the oak forest held detritus with greater N concentrations overall (Tables 3, 4, and 5). With N pools calculated within each combination of size and decay class and summed for each forest, the oak forest had a slightly higher overall pool of N in downed woody detritus. Breaking detritus down into FWD and CWD resulted in a split between forests. The pool of N in FWD was greater in the pine forest (due primarily to the large number of downed, rotten stems in the 5–10-cm size class in the pine) (Table 3). But the higher concentrations of N in highly decayed and somewhat larger pieces of CWD in the oak forest made the summed stock of N in CWD greater there.

The presence of stumps played a part in the differences in CWD between forest stands. (In virtually all cases, stumps appeared to have resulted from natural treefall rather than cutting.) Along the 300 m of cumulative, random transect length in each forest, transect lines fell across one stump in the pine forest and seven in the oak forest. The single stump that fell on our transects in the pine stand was an unidentifiable conifer, 12 cm in diameter. Most of those in the oak forest were not identifiable as to species, but two of the largest three were identifiable. The second largest we encountered (61 cm) was a hemlock (*Tsuga canadensis*) stump in decay class 4; the third largest (54 cm) appeared to be an oak spp. in decay class 5. The oak stump of 54 cm contributed more mass, C, and N to the overall pools than the hemlock stump of 61 cm. The hemlock stump was 85% void space, which we recorded in the field and which entered directly into our calculations of mass, C pools, and N pools.

Discussion

Ecosystem Pools and Processes

The mass of downed woody debris in our deciduous (mixed-oak) forest fell within the range typically reported in similar forests (Table 5). Detrital mass in our coniferous (red pine) forest was higher than typical values reported for coniferous forests of the eastern United States and higher than average values reported across red pine stands of the Great Lakes region (Duvall and Grigal 1999) (Table 5). Values of bulk density are key in the calculation of detrital masses and elemental pools, because density is used to convert field-measured wood volume to mass. Densities that we measured in sound wood agreed well with published values, whereas our values for rotten wood tended to be higher than typical published values across a range of species that includes the major species in our forests (Means and others 1985; Busse 1994; Duvall and Grigal 1999; Onega and Eickmeier 1991).

In both stands at the Harvard Forest, pools of N that we measured were larger than any others we found in the literature for temperate forests in eastern North America, though pool sizes of N have been infrequently determined (Table 5). Concentrations of N have been measured more commonly, though usually only in fresh wood or wood after a few years to 1 decade of decay. For coniferous forests across this and other regions, we found published concentrations of N in partly or highly decayed wood (excluding twigs) ranging from 0.05% to 0.61% (Busse 1994; Krankina and others 1999; Laiho and Prescott 1999; Edmonds 1987; Lang and others 1981; Barber and Van Lear 1984). These concentrations agreed with our findings for size-decay class averages in all cases except our N concentration of 1.36% in a category of well-decayed wood in the red pine forest (Table 3). For deciduous forests, other published values tended to agree reasonably with our results for partly decayed wood and to be somewhat lower than our results for well-decayed wood. Krankina and others (1999) reported N concentrations of 0.18% to 0.57% for birch (*Betula pendula*) in northwestern Russia. In a silver maple (*Acer saccharinum*) dominated forest in Illinois, USA, Polit and Brown (1996) found that N concentrations varied from 0.18% in large, sound, woody detritus and 1.36% in small, sound wood to 0.72% in rotten wood.

Higher N concentrations in well-decayed wood at

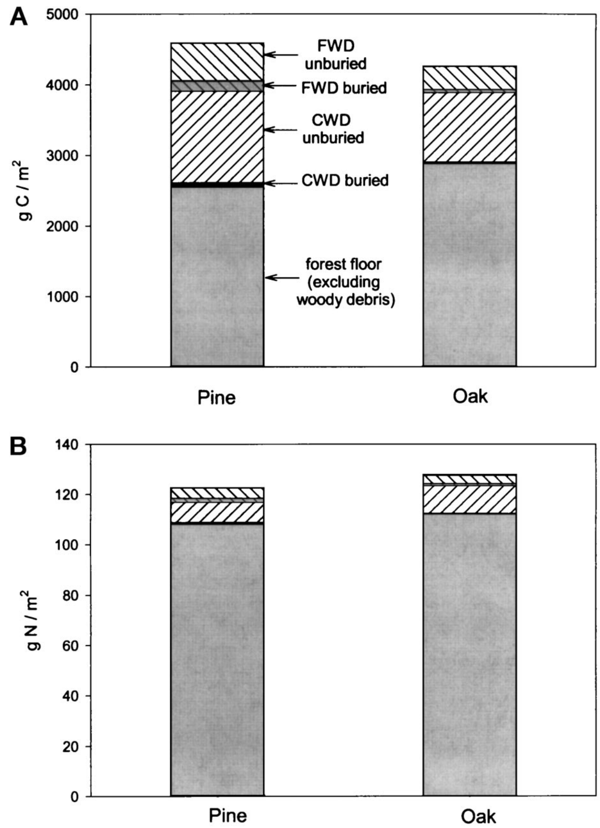

Figure 2. Contributions that pools of C (**A**) and N (**B**) in downed woody debris make to the overall forest floor pools in the pine forest and the oak forest. Data for C and N in forest floors excluding woody debris are from Magill and others (2000). FWD = fine woody debris less than 10 cm in diameter. CWD = coarse woody debris at least 10 cm in diameter. "Buried" refers to detritus deep in the forest floor that was not visible in the litter layer.

our site could be related to elevated rates of N deposition in this region. There is debate, however, concerning whether net immobilization of available N is likely to occur in woody debris as decay proceeds (Alban and Pastor 1993; Chueng and Brown 1995; Krankina and others 1999). In our forest stands, a long-term ^{15}N tracer study in FWD of reference and N-amended plots showed that elevated N inputs made minor differences in N concentrations and pool sizes. Patterns of ^{15}N recoveries in the tracer study also suggested differences in tree uptake of N were responsible, rather than N immobilization in downed woody detritus (Currie and others 2002).

Pools of C in woody detritus in the pine and oak forests added 80% and 48%, respectively, to pools of forest floor C that exclude woody debris (Figure 2). The contribution to N pools that exclude woody debris was smaller (accounting for 14% in each

Table 5. Comparison[a] of Pool Sizes[b] of Mass, C, and N in Downed Woody Debris

	< 10-cm diameter			> 10-cm diameter			Total Downed Woody Debris		
	Mass ($Mg\ ha^{-1}$)	C ($Mg\ ha^{-1}$)	N ($kg\ ha^{-1}$)	Mass ($Mg\ ha^{-1}$)	C ($Mg\ ha^{-1}$)	N ($kg\ ha^{-1}$)	Mass ($Mg\ ha^{-1}$)	C ($Mg\ ha^{-1}$)	N ($kg\ ha^{-1}$)
Harvard Forest red pine (this study)	13.3	6.8	56	26.7	13.6	90	40.0	20.4	146
Harvard Forest mixed oak (this study)	7.3	3.7	40	19.6	10.1	115	26.9	13.8	155
Subalpine fir, New Hampshire, USA (Lang and others 1981)[c]	4.7[d]	2.1	14	12.7[d]	6.1	56	17.4[d]	8.2	70
Red pine, unmanaged and young, mean across Minnesota, Wisconsin, Michigan, USA (Duvall and Grigal 1999)	—	—	—	—	—	—	23	—	—
Red pine, mature, means across MN, WI, MI, USA (Duvall and Grigal 1999)	—	—	—	—	—	—	6–10	—	—
Maple forest, Illinois, USA (Polit and Brown 1996)	—	—	—	—	—	—	6.6[d]	—	26.5
Oak-hickory, old growth, Indiana, USA (MacMillan 1988)[e]	—	—	—	—	—	—	18.0	—	45.4
Maple forest, Tennessee, USA (Onega and Eickmeier 1991)	9.39	—	—	7.95	—	—	17.3	—	—
Maple forest, old growth, Michigan, USA (Campbell and Gower 2000)	—	—	—	—	—	—	9	—	38
Hemlock forest, old growth, Michigan, USA (Campbell and Gower 2000)	—	—	—	—	—	—	22	—	95
Northern hardwoods, New Hampshire, USA (Roskoski 1980)	—	—	—	—	—	—	8–23	—	—
Northern hardwoods, 100 y to old-growth, New Hampshire, USA (Gore and Patterson 1986)	—	—	—	—	—	—	42–54	—	—
Beech-maple-hemlock, history of select cutting, New Hampshire, USA (Gore and Patterson 1986)	—	—	—	—	—	—	35	—	—
Maple-mixed hardwood, northeastern USA (Tritton 1980)[f]	—	—	—	—	—	—	4.7–38.4	—	—
Oak-basswood-maple, mature, Maryland, USA (McCarthy and Bailey 1994)[g]	7.6	—	—	25.4	—	—	33	—	—

[a] *Included here are temperate forests in eastern North America that had experienced no recent, major, natural, or anthropogenic disturbances, including logging.*
[b] *FWD (fine woody debris) and CWD (coarse woody debris) values are listed where they are comparable to the 10-cm diameter separation used in the current study. Pool sizes of C and N are listed only where C or N content were analytically determined.*
[c] *FWD measured as ≥ 1 cm and < 10 cm diameter. "Buried wood" in original reference is included here with CWD.*
[d] *Biomass reported on an ash-free basis.*
[e] *Woody debris > 5 cm diameter was quantified.*
[f] *Cited by Harmon and others (1986).*
[g] *FWD measured as ≥ 2.5 cm diameter and < 10 cm diameter.*

forest) because woody detritus has a higher C:N ratio than the bulk of forest floor mass. An overall, detrital mass-weighted C:N ratio for woody debris in our data was 140:1 for the pine forest and 89:1 for the oak forest. Other detritus in these forest floors, weighted by mass in stages of decay had C:N ratios of 24:1 in this pine stand and 26:1 in this oak stand (Magill and others 2000).

The small amounts of buried woody detritus that we found in both forests were expected in this pine stand, but they were not expected in the oak stand. Even though Lang and others (1981) estimated buried material to comprise 22% of the woody detritus in subalpine balsam fir forests in this region, we expected to find little buried material in our coniferous stand because it is the first stand to grow following reversion from agriculture. In contrast, given the age of the deciduous forest and its history of disturbance, we expected to find more buried material. McFee and Stone (1966) estimated that in forests of New England there was more detritus buried in the Oa horizon than was visible in the litter layer. Our results showed otherwise for the Harvard Forest.

The Imprint of Land-use and Disturbance History

Through the measurement of woody detrital pools along numerous chronosequences, investigators have development a paradigm of long-term CWD dynamics in unmanaged forests. When widespread mortality occurs in a mature forest, whether caused by fire, a pathogen, or other natural means, large inputs of CWD take place as snags and logs, while growth of a new stand is initiated (Oliver 1981; Boone and others 1988; Busse 1994). The total mass of CWD is expected to follow a U-shaped curve through time (Spies and others 1988); detritus from the previous stand decays slowly, while inputs of CWD from the new forest stand begin to increase after a lag time of several decades or longer (Harmon and others 1986). The paradigm of the U-shaped curve in CWD derives from temperate forests of the Pacific Northwest region of North America and from boreal forests of North America and Asia. A peak in downed CWD biomass or volume may be reached after 80 to 500 years, depending on the forest type, wood production, and climate (Spies and others 1988; Boone and others 1988; Sturtevant and others 1997; Clark and others 1998). The longest chronosequence study indicated that a steady state in CWD may not be reached for more than 900 years (Spies and others 1988), although this study took place in a type of forest (Douglas fir, *Pseudotsuga menziesii*) with characteristically long temporal dynamics.

Chronosequence studies in temperate forests of eastern North America have typically spanned stand ages of 100 years or less, and have typically been conducted in forests that were managed or that reinitiated following logging (Gore and Patterson 1986; Roskoski 1980; Duvall and Grigal 1999; McCarthy and Bailey 1994). Such stands typically have lower quantities of CWD and less predictable patterns of CWD dynamics than naturally initiated stands (Krankina and Harmon 1994; Wells and Trofymow 1997). The two forest stands we studied, though subject to management or disturbance in the last 150 years, could both be considered presently unmanaged and not recently disturbed. Our red pine stand, though an even-aged plantation, would fall in the category of unmanaged by the criteria of Duvall and Grigal (1999), who considered any stands lacking disturbance, logging, or thinning for more than 30 years to be unmanaged. Our mixed-oak stand is likewise unmanaged (lacking logging or thinning for approximately 100 years), while recovering from widespread damage caused by a natural disturbance, the 1938 hurricane.

The patterns of woody detrital mass within size and decay classes at a site can usually be linked to histories of forest disturbance and management. Following a recent major disturbance in a natural stand, large-size classes of debris in early decay classes are present (Busse 1994; Wells and Trofymow 1997). Later, during aggradation and vigorous growth in an unmanaged stand, large rotten pieces of detritus may be present from the previous stand but only smaller-size classes are input at first from the aggrading stand, including stems input from stem exclusion or from forest succession (Oliver 1981; Pastor and Post 1986). In our even-aged pine stand, the large cohort of rotten stems in the 5–10-cm size class represents the early part, and detritus in the 10–25-cm classes the later part of the stem exclusion phase, which persists to about 85 years in this forest type (Duvall and Grigal 1999). The virtual lack of woody detritus greater than 25 cm in diameter in our pine stand is consistent with the fact that a long agricultural period erased all traces of logs from prior forest stands. There are numerous living trees and some snags present that are larger than 25 cm in diameter, but evidently there has been no recent disturbance severe enough to cause extensive mortality or windthrow among those trees and snags. Our oak forest, in contrast, following 150 years of regrowth after reversion from agriculture, had undergone some logging and severe disturbance caused by both windthrow and pathogen-induced mortality. As a result, significant quantities of mass were present in woody detritus across a greater range of size categories.

The traditional conceptual model of a U-shaped curve in woody detrital biomass applies to a different degree in these two forests. In the red pine forest, this conceptual model applies poorly, because this stand is undergoing its first regrowth since reversion from agriculture, and no logs are present from any previous forest stand. In the oak forest, the conceptual generalization of a U-shaped curve applies somewhat better. This forest stand is not even-aged, although it has experienced major disturbances in the last 60 to 80 years, and downed woody detritus appears to be present from the previous forest stand as well as the current stand. The chronosequence curves in CWD mass drawn by both Roskoski (1980) and Gore and Patterson (1986) for northern hardwood forests in New Hampshire would place our mixed-oak stand, at 60 years of age, beyond the temporal minimum in the traditional U-shaped curve of woody detrital mass. The absence of sound wood in CWD of our oak forest indicates that there has been no recent severe windthrow or widespread mortality, or that inputs of CWD occur here as snags, with toppled snags being transferred to downed woody debris as already partially decayed (Harmon 1982). Snags are present in this forest, although we did not quantify the detrital biomass in snags in the current study. In mixed-hardwood forests 22 to 89 years of age in the Central Appalachians, McCarthy and Bailey (1994) determined that 28% to 20% (declining with age) of standing tree stems were dead snags.

Implications for Budgets, Modeling, and Scaling to Landscapes

As outlined above, forest C and N pools and fluxes from the Harvard Forest are widely used in budget calculations and in modeling investigations. In considering how results from the present study might be used to assess the contributions of woody detritus to C and N budgets in the region, several questions arise. First, are the results here expected to be regionally representative of forests in New England? Second, are there limitations in extrapolating these results directly to the landscape scale, and if so, what are the recommended methods for using these results to scale up to landscapes and to the region?

The oak stand we studied is likely to be representative of a significant portion of the landscape in central New England in terms of the species present, the general timing since agricultural abandonment, and the mix of disturbances that have occurred since reforestation (Foster 1992, 1993; Foster and others 1998). Following agricultural abandonment, forested land in the Prospect Hill tract was in a mosaic of even-aged stands. Superimposed upon this patchy landscape, however, was the patchy nature of disturbance from the 1938 hurricane and the responses in tree species growth (including hemlock) following the chestnut blight. Over time, the forested landscape is becoming more diverse in structure, including age structure (Foster 1993). Much of the commercial agricultural land of central Massachusetts was abandoned between 1850 and 1920 (Foster 1992). The 1938 hurricane was both a local and a regional disturbance. It caused extensive windthrow damage in about 50% of forests in Petersham township, Massachusetts (Foster 1993), as well as extensive damage further north, in New Hampshire (Reiners and Lang 1979).

The red pine stand at the Harvard Forest is somewhat less representative of coniferous forests regionally. Petersham is slightly outside the continuous native range of red pine, which begins at the northern boundary of Massachusetts and extends west to Minnesota (Burns and Honkala 1990). In the Great Lakes states, stands of this species are widely managed for timber (Duvall and Grigal 1999). Many sites in New England with an agricultural history support white pine (*Pinus strobus*), as did the mixed-oak stand at the Harvard Forest when it first reverted to forest in the 19th century (Raup 1966). To the extent that the CWD-producing properties of this stand are similar to those of an even-aged stand of other pines in the first stage of regrowth following agriculture, this stand can be considered regionally representative of such patches of landscape. Pine stands are common on the coastal plain, but they are less common in the mountainous regions of New England, which are more likely to have spruce-fir as coniferous forest above 450 m elevation (Reiners and Lang 1979).

An additional consideration in extrapolating C and N pools in woody detritus to larger scales is that pools of woody detritus are dynamic. The timing of our sampling, relative to past forest management and disturbance, played an important role in determining the pool sizes we measured. The pool sizes we measured in our pine stand are larger than those typically reported for eastern coniferous forests (although this phenomenon could have arisen through random chance, due to the placement of our transects). The pattern we observed across size classes suggests that our high measurement of biomass reflects the timing of development in this even-aged stand. Thus, these pool sizes should not be directly extrapolated across other pine stands of varying ages (Duvall and Grigal 1999). The same limitation is true of our results for the oak forest. We expect that our overall value of the C:N ratio in downed woody detritus is likely to be higher when the forest has progressed further in stand development so that more woody detritus is present from the current stand, at a higher C:N ratio than the well-decayed wood from the previous forest stand. Likewise, we expect that the occurrence or lack of occurrence of small disturbances over the past 1 to 2 decades has shaped the pool sizes that we measured. This problem in extrapolating to larger-scale C and N budgets could be partly overcome if standing dead snags were quantified in the field at the same time as downed woody detritus.

Our results suggest that the steady-state paradigm sometimes applied to pools of fine litter, or its products of decay and stabilization (for example, humus), should not be extended to pools of woody litter. Inputs of fine litter, including foliar litter, experience different annual variabilities than those of woody litter. Inputs of fine litter are often conceived as reaching an attractor state, a dynamic state in which year-to-year variability (in the absence of major disturbance) can be considered small compared to long-term means. This allows rates of production and decay to be meaningfully averaged, and pool sizes of detrital mass to be viewed as eventually reaching steady-state or attractor values. Inputs of woody detritus, in contrast, are more highly variable, decay rates are slower, and pool sizes are more clearly linked to particular combinations of disturbance and forest history over decades and centuries. Although there may be a long-term mean in woody litter inputs, annual and decadal variability about this mean is typically high; hence, there is no reliable steady annual value of woody litter inputs, even in old-growth stands (MacMillan 1988; Spies and others 1988). Results from studies like ours should not be interpreted as long-term averages or steady-state pools of woody debris.

To gain estimates of C and N pool sizes in woody detritus at larger scales, two different approaches could be used. Landscape-scale field studies of pool sizes could be conducted, using an experimental design developed to be robust at the larger scale either through random sampling (see for example, Brown and Schroeder 1999) or sampling of areas stratified by forest types, ages, or management histories (Duvall and Grigal 1999). The second approach would use process models parameterized at intensive-study sites, like ours, to extrapolate across landscapes. In this approach, it is critical that the controlling factors in producing landscape heterogeneity be captured in the models used to effect the scaling (King 1991; Currie and Aber 1997). Based on our results, models that scale C and N pools and fluxes from sites to landscapes should endeavor to capture the relationships between disturbance history, land-use history, vegetation history, and modeled values of C and N pool sizes in woody debris. For example, temporal curves derived from chronosequences can be incorporated into models of C and N pool sizes at larger scales (Krankina and others 1999). Results from studies like ours, directly illustrating the imprint of site history, should be useful in developing and testing such models for temperate forests in eastern North America.

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REFERENCES

Aber JD, Driscoll CT. 1997. Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochem Cycles 11:639–48.

Aber JD, Federer CA. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia 92:463–74.

Aber JD, Magill A, Boone R, Melillo JM, Steudler P, Bowden R. 1993. Plant and soil responses to three years of chronic nitrogen additions at the Harvard Forest, Massachusetts. Ecol Appl 3:156–66.

Aber JD, Ollinger SV, Federer CA, Reich PB, Goulden ML, Kicklighter DW, Melillo JW, Lathrop RGJ. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern US. Clim Res 5:207–22.

Aber JD, Reich PB, Goulden ML. 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. Oecologia 106:257–65.

Alban DH, Pastor J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can J For Res 23: 1744–9.

Barber BL, Van Lear DH. 1984. Weight loss and nutrient dynamics in decomposing woody loblolly pine logging slash. Soil Sci Soc Am J 48:906–10.

Boone RD, Grigal DF, Sollins P, Ahrens RJ, Armstrong DE. 1999. Soil sampling, preparation, archiving, and quality control. In: Robertson GP, Coleman DC, Bledsoc CS, Sollins P, editors. Standard soil methods for long-term ecological research. New York: Oxford University Press. p 3–28.

Boone RD, Sollins P, Cromack KJ. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. Ecology 69:714–22.

Box GEP, Cox DR. 1964. An analysis of transformations. J R Stat Soc Ser B 26:211–43.

Brown JK. 1974. Handbook for inventorying downed woody material. USDA Forest Service general technical report INT-16, 1974. Ogden (UT): Intermountain Forest & Range Experiment Station. 24p.

Brown SL, Schroeder PE. 1999. Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. Ecol Appl 9:968–80.

Burns RM, Honkala BH. 1990. Silvics of North America: 1. Conifers. Agriculture Handbook 654. Washington (DC): Department of Agriculture, Forest Service. 675 p.

Busse MD. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci Soc Am J 58: 221–7.

Campbell JL, Gower ST. 2000. Detritus production and soil N transformations in old-growth eastern hemlock and sugar maple stands. Ecosystems 3:185–92.

Chueng N, Brown S. 1995. Decomposition of silver maple (Acer saccharinum L.) woody debris in a central Illinois bottomland forest. Wetlands 15:232–89.

Clark DF, Kneeshaw DD, Burton PJ, Antos JA. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can J For Res 28:284–90.

Currie WS, Aber JD. 1997. Modeling leaching as a decomposition process in humid, montane forests. Ecology 78:1844–60.

Currie WS, Nadelhoffer KJ, Aber JD. 1999. Soil detrital processes controlling the movement of ^{15}N tracers to forest vegetation. Ecol Appl 9:87–102.

Currie WS, Nadelhoffer KJ, Colman B. 2002. Long-term movement of ^{15}N tracers into fine woody debris under chronically elevated N inputs. Plant Soil. 238:313–323.

Duvall MD, Grigal DF. 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, U.S.A. Can J For Res 29:1926–34.

Edmonds RL. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, USA. Can J For Res 17:499–509.

Foster DR. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. J Ecol 80:753–72.

Foster DR. 1993. Land-use history and forest transformations in central New England. In: McDonnell MJ, Pickett ST, editors. Humans as components of ecosystems. New York: Springer-Verlag. p 91–110.

Foster DR, Boose ER. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. J Ecol 80:79–98.

Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510.

Foster DR, Zebryk T, Schoonmaker P, Lezberg A. 1992. Post-settlement history of human land-use and vegetation dynamics of a Tsuga canadensis (hemlock) woodlot in central New England. J Ecol 80:773–86.

Gore JA, Patterson WA 3rd. 1986. Mass of downed wood in north hardwood forests in New Hampshire: potential effects in forest management. Can J For Res 16:355–9.

Harmon ME. 1982. Decomposition of standing dead trees in the Southern Appalachian Mountains. Oecologia 52:214–15.

Harmon ME. 1992. Long-term experiments on log decomposition at the H.J. Andrews Experimental Forest. General technical report PNW-GTR-280. Portland (OR): US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 28 p.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, and others. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302.

Harmon ME, Sexton J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. Seattle (WA): US LTER Network Office, University of Washington. 73 p.

King AW. 1991. Translating models across scales in the landscape. In: Turner MG, Gardner RH, editors. Quantitative methods in landscape ecology. Ecological Studies, vol 82. New York: Springer-Verlag. p 479–517.

Krankina ON, Harmon ME. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Pollu 82:227–38.

Krankina ON, Harmon ME. 1994. The impact of intensive forest management on carbon stores in forest ecosystems. World Res Rev 6:161–77.

Krankina ON, Harmon MF, Griazkin AV. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can J For Res 29:20–32.

Laiho R, Prescott CE. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorous cycles in three Rocky Mountain coniferous forests. Can J For Res 29:1592–603.

Lang GE, Cronan CS, Reiners WA. 1981. Organic matter and major elements of the forest floors and soils in subalpine balsam fir forests. Can J For Res 11:388–99.

MacMillan PC. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can J For Res 18:1353–62.

McCarthy BC, Bailey RR. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Can J For Res 24:1317–29.

McFee WW, Stone EL. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Sci Soc Am Proc 30:513–16.

McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, Moore B III, Vorosmarty CJ. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochem Cycles 6:101–24.

Magill AH, Aber JD, Berntson GM, McDowell WH, Nadelhoffer KJ, Melillo JM, Steudler P. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. Ecosystems 3:238–53.

Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecol Appl 7:402–15.

Means JE, Cromack KJ, MacMillan PC. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can J For Res 15:1092–8.

Melillo JM, Kicklighter DW, McGuire AD, Peterjohn WT, Newkirk KM. 1995. Global change and its effects on soil organic carbon stocks. In: Zepp RG, and Sonntag C, editors. Role of nonliving organic matter in the Earth's carbon cycle. Dahlem Workshop Reports. Chichester (England): Wiley. p 175–89.

Motzkin G, Wilson P, Foster DR, Arthur A. 1999. Vegetation patterns in heterogeneous landscapes: the importance of land use history and environment. J Veget Sci 10:903–20.

Nadelhoffer KJ, Emmett FA, Gundersen P, Kjonaas OJ, Koopmans CJ, Schleppi P, Tietema A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398:145–8.

Nelson DW, Sommers LE. 1996. Total carbon, organic carbon, and organic matter. In: Sparks DL, editor. Methods of soil analysis. pt 3. Chemical methods. Madison (WI): Soil Science Society of America. p. 961–1010.

Oliver CD. 1981. Forest development in North America following major disturbances. For Ecol Manage 3:153–68.

Onega TL, Eickmeier WG. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull Torrey Botan Club 118(1):52–7.

Pastor J, Post WM. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2:3–27.

Polit JI, Brown S. 1996. Mass and nutrient content of dead wood in a central Illinois floodplain forest. Wetlands 16:488–94.

Rastetter EB, McKane RB, Shaver GR, Melillo JM. 1992. Changes in C-storage by terrestrial ecosystems—how C-N interactions restrict responses to CO_2 and temperature. Water Air Soil Pollut 64:327–44.

Raup HM. 1966. The view from John Sanderson's farm: a perspective for the use of the land. For Hist 10:2–11.

Reiners WA, Lang GE. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. Ecology 60:403–17.

Roskoski JP. 1980. Nitrogen fixation in hardwood forests of the northeastern United States. Plant Soil 54:33–44.

Schimel DS, VEMAP participants, Braswell BH. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol Monogr 67:251–71.

Sollins P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can J For Res 12:18–28.

Spies TA, Franklin JF, Thomas TB. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689–702.

StataCorp. 1997. Stata statistical software. Release 5.0. College Station (TX): Stata Corporation.

Sturtevant BR, Bissonette JA, Long JN, Roberts DW. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol Appl 7:707–12.

Townsend AR, Braswell BH, Holland EA, Penner JE. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. Ecol. Appl 6:806–14.

Tritton LM. 1980. Dead wood in north hardwood forest ecosystem [dissertation]. New Haven (CT): Yale University.

Van Cleve K, Martin S, editors. 1991. Long-term ecological research in the United States. 6th rev. ed. Seattle (WA): Long-Term Ecological Research Network Office, University of Washington. 178 p.

van Oene H, Berendse F, de Kovel CGF. 1999. Model analysis of the effects of historic CO_2 levels and nitrogen inputs on vegetation succession. Ecol Appl 9:920–35.

Wells RW, Trofymow JA. 1997. Coarse woody debris in chronosequences of forests on southern Vancouver Island. Information report BC-X-375. Victoria (BC): Pacific Forestry Centre, Canadian Forest Service.

Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, Melillo JM, Munger JW, Fan S-M, Nadelhoffer KJ. 1996. Modelling the soil–plant–atmosphere continuum in a Quercus-Acer stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. Plant Cell Environ 19:911–27.