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Nutrient Concentration of Down Woody Debris in Mixedwood Forests in Central Maine, USA

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Both nutrient concentrations and pre- and post-harvest pool sizes were determined across down woody debris decay classes of several hardwood and softwood species in a long-term, natural disturbance based, silvicultural experiment in central Maine. Concentrations of N, P, Ca, Mg, Cu, Fe, and Zn generally increased 2- to 5-fold with increasing decay class. Concentrations of Mn, Al and B did not differ among decay classes, while K decreased by 20–44% from decay class 1 to class 4. C:N-ratios declined with increasing decay class, while N:P-ratios increased from decay class 1 to 2 and then plateaued with further decay. Within decay classes, softwoods generally had lower nutrient concentrations and higher C:N-ratios than hardwoods; N:P-ratios did not differ between hardwoods and softwoods. Although gap harvesting increased the size of the overall down woody debris nutrient pools, mostly through a large pulse of decay class 1 material, harvesting generally reduced the nutrients held in advanced decay classes. Pre-harvest down woody debris pools for N, P, K and Ca were 11.0, 0.6, 2.1 and 21.1 kg ha^{-1}, respectively, while postharvest were 20.0, 1.3, 6.2 and 46.2 kg ha^{-1}, respectively. While the gap-based silvicultural systems sampled in this study doubled the size of the pre-harvest, downed woody debris nutrient pools, the post-harvest pools were estimated to be only 3.2–9.1% of aboveground nutrients.

Keywords Acadian Forest, hardwoods, softwoods, carbon-nitrogen ratios, decay classes, disturbance-based silviculture
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1 Introduction

Down woody debris (DWD) is an important component of forest ecosystems (Harmon et al. 1986, Krajick 2001). Generally, DWD plays two interrelated roles. First, it is a structural feature critical to a variety of organisms, particularly those whose life cycles are closely tied to decaying wood (deMaynadier and Hunter 1995, McComb and Lindenmayer 1999, Siitonen 2001, Jonsson et al. 2005). For example, research from northern Europe has clearly shown that reductions in DWD associated with intensive harvesting have led to significant declines in the richness and abundance of wood-decay fungi (Bader et al. 1995, Rydin et al. 1997) and beetles (Martikainen et al. 2000). In some undisturbed forests, DWD is important for the regeneration of various tree species, whose establishment and survival is enhanced on 'nurse logs' (Cornett et al. 2001, Svoboda et al. 2010). Second, DWD is a functional component of the forest, having important influences on soil biology, soil hydrology, geomorphology, and nutrient cycling (Harmon et al. 1986, Keenan et al. 1993, Duvall and Grigal 1999). Thus, silvicultural treatments that alter DWD volume, size, and/or spatial distribution, will unequivocally affect forest processes such as nutrient flow and respiration (Harmon et al. 1986, McComb and Lindenmayer 1999, Janowiak and Webster 2010).

Nevertheless, the importance of DWD, particularly regarding nutrient cycling, remains somewhat poorly understood, perhaps because it varies greatly by region and forest type. For example, Laiho and Prescott (1999) reported that DWD contributed less than 5% of the N and P released during cycling in conifer forests of southwestern Alberta. However, Arthur and Fahey (1990) cite several examples where a substantial component of a stand's nutrient capital is contained in DWD. In northeastern North America, there has been little research on the nutrient concentration of DWD except for work in mid to high-elevation, *Abies balsamea* ([L.] Mill) - *Picea rubens* (Sarg.) forests of the White Mountains of New Hampshire (Lambert et al. 1980, Foster and Lang 1982). This forest type differs markedly in structure and function from more common mixedwood types (i.e., containing conifer and softwood), which are becoming even more prevalent in northeastern North America as the result of extensive selective harvesting. Furthermore, with Arthur et al. (1993) as a notable exception, there is a general lack of information concerning nutrient concentration and dynamics of DWD in mixedwood stands. Instead, most research has been devoted to coniferous stand types, and to a lesser extent, pure hardwood types.

Thus, the objectives of our study were to: 1) characterize the nutrient concentration of DWD among decay classes and common tree species of northeastern North America; and 2) quantify the stand-level nutrient pool contained in the DWD of a mixedwood forests managed with expanding gap harvests. Results of this work provide insights into the importance of DWD with respect to nutrient dynamics for this forest type.

2. Methods

2.1 Study Area

This study was conducted within the Penobscot Experimental Forest (PEF) located near the town of Bradley, Maine (44°52´N, 68°38´W). This 1550 ha area lies on soil types derived from glacial till and ranging from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams and silt loams in flat areas between the ridges (Brissette 1996). The soils are principally Aquic or Typic Haplorthods or Podzols with slopes generally less than 8% (USDA Forest Service 1959).

Forest cover types are dominated by softwoods including *A. balsamea*, *P. rubens*, *P. glauca* ([Moench] Voss) *P. mariana* ([Mill.] B.S.P.), *Pinus strobus* (L.), *Tsuga canadensis* ([L.] Carr.), and *Thuja occidentalis* (L.). Common hardwoods in these types include *Acer rubrum* (L.), *Betula paperifera* (Marsh.), *B. populifolia* (Marsh.), *Populus tremuloides* (Michx.) and *P. grandidentata* (Michx.). Natural stand structures in this Acadian forest are typically uneven-aged and quite diverse with windstorms and insect outbreaks as the major disturbance events. Stand-replacing fires are thought to be extremely rare in the Acadian forest (Lorimer 1977, Seymour 1992, Seymour et al. 2002, Fraver et al. 2009).

2.2 Study Design

Within the PEF, this study was conducted in experimental plots of the Acadian Forest Ecosystem Research Program (AFERP) at the University of Maine. This long-term experiment is testing silvicultural treatment regimes using expanding harvest gaps, similar to the German "Femelschlag" silvicultural system, that emulate natural disturbance regimes of the Acadian Forests (Saunders and Wagner 2005, Arseneault et al. 2011). The experiment includes three treatments: 1) a 20% overstory removal on a 10-year cutting cycle, with 10% of stand basal area retained in mature trees (creating 0.2 ha gaps); 2) a 10% overstory removal on a 10-year cutting cycle, with 30% of stand basal area retained in mature trees (creating 0.1 ha gaps), and 3) an unharvested control. The three treatments were applied to plots that are approximately 10 ha in size (total of 90 ha under study) and replicated three times within a randomized complete-block design. The three blocks were replicated in time with the initial gap harvests being implemented during the winters of 1995, 1996, and 1997 for successive blocks.

The experiment includes 20 systematically placed, permanent 0.05 ha sample plots within each replicate. During the summer of 1995, 1996, and 1997 (prior to harvesting), the abundance and composition of DWD was measured on each sample plot. Post-harvest measurements of DWD were made in the summer of 1998, 1999, and 2000, so that all sample plots were re-measured three growing seasons after harvest. All DWD occurring inside each sample plot was inventoried. Measurements included diameter at large and small ends (measured with calipers), length, species (when possible) and decay class. Decay classes were defined following Fraver et al. (2002) where: class 1 – sound wood with intact bark, small to medium branches present and often suspended above the ground by branches; class 2 – sound to slightly rotten wood with intact to sloughing bark, only stubs of larger branches present, and log lies on duff, but still round in cross-section; class 3 – rotten wood with little attached bark, partially buried in duff, and log beginning to assume oval cross-section; and class 4 – rotten wood, almost no bark (except *Betula*), buried substantially in duff but still distinguishable from general duff layer, and decidedly oval in cross-section. Only pieces > 9.5 cm in diameter at the large end were included in the sample.

2.3 Nutrient Analysis

As described in Fraver et al. (2002), we collected approximately 20 cross-sectional disks, including bark if present, from logs of decay classes 1 and 2 for each of the four most abundant softwoods (*A. balsamea, P. rubens, T. occidentalis, T. canadensis*) and the three most abundant hardwoods (*A. rubrum, B. papyrifera, P. grandidentata*). A total of 272 disks were collected from randomly selected logs within undisturbed areas across the nine treatment plots. Concurrently, we collected approximately 50 samples each from softwood and hardwood logs in decay class 3 and 4. These samples consisted of mostly friable, broken wood fragments. All samples were placed in labeled, sealed plastic bags, returned to the laboratory, and refrigerated until being processed. To avoid contamination, samples were handled with Nitrile gloves, both in the field and in the laboratory.

From the 272 disks, we randomly chose six subsamples from each species by decay class combination for nutrient analysis (6 replicates × 7 species × 2 decay classes = 84 samples). In addition, we randomly selected 24 subsamples from each of the decay class 3 and 4, softwood and hardwood samples for nutrient analysis (24 replicates × 2 wood types × 2 decay classes = 96 samples). These 180 subsamples were analyzed for percent total C (% TC), percent total N (% TN), Ca, Mg, Mn, P, K, Al, B, Zn, Cu, and Fe content. All chemical analyses were performed by the Maine Agricultural and Forestry Experiment Station Analytical Laboratory. Percent total carbon and total nitrogen was determined using the LECO C/N 2000 analyzer (LECO Corporation, St. Joseph, Michigan). Concentrations of the remaining 10 elements were determined using an inductively-coupled plasma atomic emission spectrophotometer (ICP-AES; Thermo Jarrell Ash PlasmaComp 975, Franklin, Massachusetts) on dry-ashed samples.

2.4 Statistical Analysis

We used nonparametric analyses for the nutrient concentration data set because (1) most continuous variables were highly non-normally distributed and not easily transformed into normal distributions, (2) several concentrations were non-continuous, and (3) several nutrient concentrations included thresholds (e.g., laboratory tests for B concentration gave only an upper limit). Nonparametric ranking methods overcome these data limitations, allowing use of all data points by considering the data on the ordinal scale. Further, because they make no assumption of normality, these methods had substantially greater power than equivalent parametric tests for our data (Conover 1998).

Thus, all response variables were rank transformed, first across decay classes and then within each decay class. Two nonparametric tests were used. First, the Kruskal-Wallis test was used to test the null hypothesis that there were no differences in mean rank nutrient concentration among the eight wood types (H-S; i.e., hardwood vs. softwood) by decay class (DC) combinations. This approach required grouping the data for all species in decay classes 1 and 2 into hardwood (*A. rubrum*, *B. papyrifera*, and *P. grandidentata*) and softwood (*A. balsamea*, *P. rubens*, *T. canadensis*, and *T. occidentalis*) types. Second, the Friedman test was used to test the null hypothesis that there were no differences in mean rank nutrient concentration among the seven species. In this case, decay class was used as a blocking variable since it was not of primary interest. If the null hypothesis was rejected in either test, multiple comparison tests were calculated on the ranks to determine which pairs of populations differed. All tests were conducted at $\alpha = 0.05$. Multiple comparison tests used the Bonferroni adjustment.

Because there are no exact nonparametric tests for interactions (Conover 1998), we conducted two-way analysis of variances (ANOVA) on the full, rank-transformed data for each nutrient (i.e., including all four decay classes) as an indirect way to isolate simple interactions in ranked data sets (W. Halteman, U. Maine, pers. comm.). All significant interactions between DC and H-S are reported.

Separate parametric ANOVAs were performed on the log-transformed C:N and N:P ratios (C:N = % total C / % total N; N:P = (% total N / % total P), using DC and H-S as independent factors.

Finally, we assessed the influence of silvicultural treatments in DWD nutrient pools by comparing pre-harvest pools to those one year post-harvest. Estimates of the total DWD nutrient pool were calculated from volume estimates reported by Fraver et al. (2002). We pooled DWD pre-harvest volume estimates since there were no differences among the replicates in either DWD volume or DWD diameter distributions (Fraver et al. 2002). Nutrient pools for all wood-type-by-decay-class combinations are reported for the pre-harvest conditions. Silvicultural treatment effects are summarized across blocks using both the pre- and post-harvest DWD volume estimates.

3 Results

3.1 Nutrient Concentration among Wood Types and Decay Classes

With the exceptions of Mn, Al, and B, nutrient concentration among hardwood and softwood decay classes were variable and different ($p < 0.0001$) from one another (Table 1). Nutrient concentration generally increased with increasing decay class; most nutrients increased between 2- and 5-fold. A notable exception to this trend was K, which decreased by 44% in hardwoods and 20% in softwoods from decay class 1 to decay class 4. Further, softwoods had lower nutrient concentration than hardwoods at comparable decay classes (Table 1). For example, Ca concentrations were on average 44% higher in hardwoods than in softwoods when averaged across decay classes.

Interactions between H-S and DC were detected for some nutrients. Several nutrients had this interaction: % total N ($F = 4.075$, $p = 0.0079$), P ($F = 3.266$, $p = 0.0227$), Cu ($F = 4.167$, $p = 0.0070$), and Zn ($F = 3.980$, $p = 0.0090$). For these nutrients, the interaction appeared isolated to decay class 3; softwoods tended to have similar nutrient concentrations as hardwoods, even though hardwoods tended to have higher nutrient concentrations in most of the other decay classes (Table 1). Fe showed a slightly different

Table 1. Median nutrient concentration of hardwood and softwood down woody debris in the four decay classes. Numbers in parenthesis indicate the interquartile range of the data. With the exception of percent total carbon (% TC) and percent total nitrogen (% TN), all units are in parts per million. Sample sizes were n = 18 for hardwood decay classes 1 and 2, and n = 24 for all others. Within each row, medians with the same letter represent decayed wood classes not significantly different from one another as determined using Bonferroni-adjusted multiple comparisons based on the nonparametric Kruskal-Wallis test.

Nutrient	Hardwoods Decay class				Softwoods Decay class				Kruskal-Wallis test	p-value
	1	2	3	4	1	2	3	4		
% TC	47.24^{a} (47.08–48.31)	47.07^{a} (46.72–48.84)	47.41^{a} (46.80–48.48)	48.59^{ab} (46.76–51.49)	48.58^{ab} (48.19–48.94)	48.64^{ab} (48.15–48.50)	48.58^{a} (47.76–49.26)	51.85^{b} (48.94–54.72)	41.16	<0.0001
% TN	0.15^{a} (0.09–0.20)	0.15^{a} (0.08–0.23)	0.23^{b} (0.20–0.39)	0.53^{c} (0.34–0.69)	0.09^{ad} (0.07–0.13)	0.08^{d} (0.07–0.09)	0.27^{b} (0.19–0.31)	0.37^{bc} (0.23–0.40)	114.52	<0.0001
P	92^{abc} (83–149)	69^{ab} (48–150)	157^{ac} (79–186)	253^{d} (159–314)	52^{be} (38–95)	29^{e} (22–54)	141^{cd} (102–203)	187^{cd} (98–271)	85.95	<0.0001
K	589^{a} (384–947)	315^{abc} (158–564)	493^{ae} (281–716)	330^{ad} (229–585)	254^{ac} (179–569)	131^{bc} (<99–292)	281^{bce} (185–411)	202^{bcd} (159–401)	37.84	<0.0001
Ca	3135^{abc} (1760–4810)	4290^{ab} (2330–6510)	5185^{ad} (3160–8545)	8815^{d} (5675–13,250)	2235^{bc} (1770–2635)	2115^{c} (1455–3330)	3260^{abc} (1845–4100)	3630^{ab} (2450–4765)	58.42	<0.0001
Mg	259^{ab} (192–367)	321^{a} (267–597)	346^{a} (268–718)	464^{a} (311–827)	152^{b} (123–235)	147^{b} (116–321)	252^{ab} (179–386)	347^{a} (246–519)	48.48	<0.0001
Mn	98^{a} (21–235)	142^{a} (28–321)	110^{a} (28–252)	75^{a} (20–195)	198^{a} (12–289)	77^{a} (17–156)	161^{a} (86–307)	133^{a} (35–407)	8.86	0.2629
Al	<12.4^{a} (<12.3–<12.4)	<12.4^{a} (<12.3–<12.4)	<12.4^{a} (<12.3–<12.5)	<12.6^{a} (<12.4–<14.9)	<12.4^{a} (<12.3–20.2)	<12.4^{a} (<12.3–<12.5)	<12.4^{a} (<12.4–<12.5)	<12.4^{a} (<12.3–31.3)	11.51	0.1178
B	<0.989^{ab} (<0.986–<0.994)	<0.989^{ab} (<0.987–<0.994)	<0.992^{ab} (<0.986–<0.997)	<0.995^{a} (<0.988–<1.170)	<0.989^{ab} (<0.984–<0.993)	<0.991^{ab} (<0.986–<0.993)	<0.992^{ab} (<0.986–<0.994)	<0.987^{b} (<0.984–<0.991)	13.70	0.0569
Cu	3.35^{ac} (1.54–8.04)	2.54^{ab} (0.99–5.74)	3.53^{a} (2.38–4.54)	6.96^{c} (4.52–9.36)	1.12^{b} (0.59–2.32)	0.79^{b} (0.32–1.78)	4.11^{ac} (2.33–5.75)	3.64^{ac} (1.87–7.21)	62.74	<0.0001
Fe	6.21^{a} (5.63–7.18)	6.39^{ab} (5.04–10.20)	14.20^{cef} (8.78–52.85)	50.45^{d} (29.60–77.30)	12.40^{bce} (8.06–15.30)	10.44^{abc} (6.21–16.10)	21.20^{def} (11.65–44.00)	31.90^{df} (16.35–79.15)	84.45	<0.0001
Zn	34.3^{ab} (10.2–67.7)	35.3^{ab} (12.1–77.0)	24.4^{ab} (10.5–53.6)	90.1^{b} (21.8–113.5)	6.3^{c} (4.1–18.6)	11.1^{c} (4.5–14.9)	21.3^{a} (16.4–31.3)	23.3^{ab} (19.8–33.1)	57.34	<0.0001

Table 2. Median nutrient concentration of decay class 1 and 2, down woody debris as separated by species. With the exception of percent total carbon (% TC) and percent total nitrogen (% TN), all units are in parts per million. Although medians are listed for each decay class, low sample size in each species by decay class combination (n = 6) reduced power; therefore, decay classes were used as blocks. Within each row, median pairs with the same letter represent species not significantly different from one another as determined using Bonferroni-adjusted multiple comparisons based on the nonparametric Friedman test.

Nutrient	Species (Decay class 1/Decay class 2)							Friedman test	p-value
	Abies balsamea	*Picea rubens*	*Thuja occidentalis*	*Tsuga canadensis*	*Acer rubrum*	*Betula papyrifera*	*Populus grandidentata*		
% TC	48.54/48.12^{ab}	48.16/48.60^{ab}	48.88/48.52^{b}	48.38/49.07^{b}	47.20/47.63^{ac}	48.61/47.37^{abc}	47.14/46.97^{c}	27.81	0.0001
% TN	0.13/0.08^{a}	0.08/0.07^{a}	0.11/0.07^{a}	0.09/0.10^{a}	0.11/0.13^{ab}	0.19/0.21^{b}	0.12/0.11^{ab}	23.02	0.0008
P	86/32^{abc}	36/29^{a}	44/22^{ab}	88/62^{abc}	84/61^{abc}	120/128^{c}	93/75^{bc}	24.46	0.0004
K	461/289^{a}	193/109^{b}	234/<99^{b}	536/191^{ab}	545/260^{a}	387/202^{ab}	1059/503^{a}	25.62	0.0003
Ca	2355/2485^{ab}	1980/2070^{a}	4345/2956^{ab}	1925/1320^{a}	2335/4350^{ab}	3690/4465^{b}	3745/2790^{ab}	18.24	0.0057
Mg	312/327^{ac}	138/264^{ab}	135/102^{b}	148/135^{b}	209/394^{ac}	249/306^{ac}	395/320^{c}	32.46	<0.0001
Mn	216/129^{ad}	325/160^{ad}	4/10^{b}	128/77^{ac}	86/147^{ad}	238/313^{d}	17/23^{bc}	46.90	<0.0001
Al	27/<12.4^{a}	<12.4/<12.3^{a}	<12.4/<12.4^{a}	<12.4/<12.4^{a}	<12.4/<12.4^{a}	<12.3/<12.4^{a}	< 12.4/<12.4^{a}	12.03	0.0614
B	<0.990/<0.987^{a}	<0.985/<0.987^{a}	<0.988/<0.994^{a}	<0.988/<0.989^{a}	<0.988/<0.988^{a}	<0.987/<0.991^{a}	<0.990/<0.989^{a}	2.25	0.8951
Cu	1.98/2.73^{acd}	2.52/1.09^{ac}	0.47/0.22^{b}	0.71/0.79^{ab}	4.14/3.48^{cd}	11.32/4.93^{d}	1.14/0.74^{ab}	42.68	<0.0001
Fe	15.35/12.01^{a}	10.61/6.03^{ab}	12.95/12.35^{a}	8.20/8.71^{ab}	7.11/5.70^{ab}	5.55/9.09^{b}	6.06/5.74^{b}	18.97	0.0042
Zn	18.6/14.2^{a}	17.8/14.2^{a}	4.9/4.0^{b}	3.2/5.3^{bc}	9.9/10.8^{ac}	67.4/72.4^{d}	25.8/45.1^{ad}	49.79	<0.0001

pattern ($F = 3.970$, $p = 0.0091$); softwoods had higher concentrations than hardwoods for decay classes 1 and 2, but similar concentrations for decay classes 3 and 4 (Table 1).

3.2 Nutrient Concentration among Species

Differences among tree species in nutrient concentration were detected for all nutrients except Al and B (Table 2). Although hardwoods had higher nutrient concentrations in decay classes 1 and 2 on average than softwoods (Table 1), comparisons among the individual species did not always follow this trend (Table 2). Among softwoods, decayed *A. balsamea* had the highest nutrient concentrations for all elements except for P, Mn, and Ca, which were highest in *T. canadensis*, *P. rubens*, and *T. occidentalis*, respectively. *P. rubens* had the lowest concentrations of N, P, and K, while Mg, Mn, and Cu were lowest in *T. occidentalis* (Table 2).

Among hardwoods, *B. papyrifera* had the most nutrient rich DWD with significantly higher % total N, P, Ca, Mn, Cu and Zn concentrations than all other species. *P. grandidentata* had the highest K and Mg concentrations, and was intermediate in concentrations for most all other nutrients. *A. rubrum* was the least nutrient rich hardwood, but still had higher concentrations than softwoods for many of the nutrients (Table 2).

3.3 C:N and N:P among Wood Types and Decay Classes

Carbon-nitrogen ratios varied ($p < 0.001$) with DC and H-S (Table 3). Decay classes 1 and 2 did not differ ($p = 0.883$) from one another in either hardwood or softwood types (Fig. 1A). Likewise, decay classes 3 and 4 did not differ ($p = 0.990$) from one another in softwood types. This pattern, highlighted here but evident throughout the analysis, suggests a nonlinear trend across decay classes. Generally, nutrient concentrations change slowly from decay class 1 to 2, accelerate from decay class 2 to 3, and slow or level off from decay class 3 to 4.

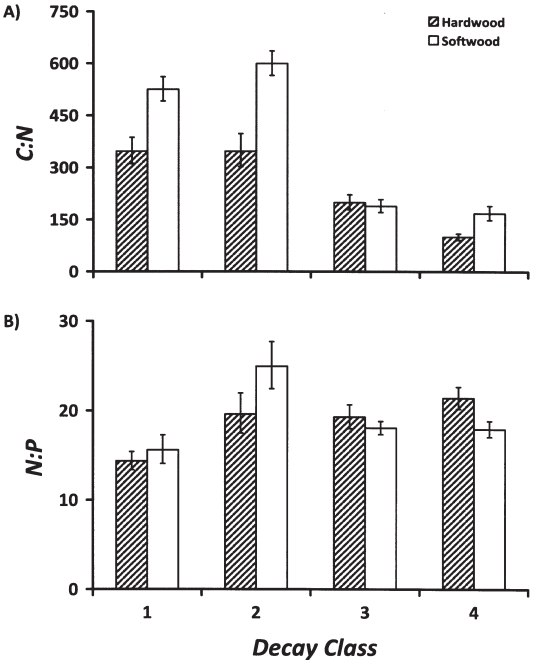

Fig. 1. Mean A) carbon-nitrogen (C:N) and B) nitrogen-phosphorus (N:P) ratios for each decay class for hardwood and softwood down woody debris. Bars indicate ± 1 standard error.

Table 3. Analysis of variance (ANOVA) for the effects of decay class (DC) and wood type (i.e., hardwood vs. softwood; H-S) on log-transformed, carbon-nitrogen ratios (C:N) and nitrogen-phosphorus ratios (N:P).

Source	df	C:N			N:P		
		MS	F	p-value	MS	F	p-value
DC	3	18.02	80.85	<0.001	1.168	8.31	<0.001
H-S	1	5.38	24.04	<0.001	0.004	0.03	0.866
DC × H-S	3	0.91	4.10	0.008	0.363	2.58	0.055
ERROR	172	0.22		0.141			

Hardwoods had a lower C:N than softwoods for all decay classes except decay class 3 (Fig. 1A). This pattern followed for % total N, P, Cu, and Zn, as noted above (Table 1). This pattern is responsible for significant interactions found for all these nutrients (Table 3).

Nitrogen-phosphorus ratios were affected by DC, but not by H-S (Table 3). N:P generally increased with decay class for both wood types and was slightly, albeit not significantly, higher in softwood for decay classes 1 and 2, but higher in hardwoods for decay classes 3 and 4 (Fig. 1B). This change in order between the wood types likely lead to the marginally significant interaction term between DC and H-S in the analysis ($p = 0.055$; Table 3).

3.4 Stand-Level Nutrient Pools

When presented on a per-ha basis, nutrient pools were substantially different among species groups (hardwood vs. softwood) and decay classes (Fig. 2). Pre-harvest DWD carbon content mirrored pre-harvest biomass estimates presented by Fraver at al. (2002). The other nutrients generally occurred at disproportionately higher amounts in the advanced decay classes, with the highest amount always found in decay class 3. For example, N pools were 3.7 ± 0.7 (mean $\pm$ SE), 6.7 ± 0.8, 14.1 ± 1.5, and 6.1 ± 0.8 kg/ha for decay classes 1–4, respectively. For many nutrients, decay class 4 generally had the lowest absolute nutrient content because that decay class was not as common within our sites.

For all of the nutrients, softwood DWD contained the largest proportion of nutrient pools per ha (Fig. 2), probably because it occurred much more frequently within our plots. However, on a relative basis, hardwood DWD contained more of the nutrient capital than softwood DWD. For example, hardwood DWD contained 33% of the total K in DWD, even though it only made up 21% of the biomass. This same pattern occurred for Ca and Mg. Pools for the remaining nutrients roughly mirror biomass estimates (Fig. 2).

Gap harvesting affected nutrient content in DWD by creating a pulse of decay class 1 DWD and fragmenting decay classes 3–4 DWD (Fig. 3, Fraver et al. 2002). In all cases, the total nutrient pools in decay class 1 DWD increased, often quite dramatically. For example, N content for decay class 1 increased by 302%, 323%, and 714% for the control, 10% removal, and 20% removal treatments, respectively (Fig. 3). On the other hand, decay classes 3–4 consistently had lower nutrient pools after harvesting. In this case, N pools in decay class 4 decreased by 62%, 26%, and 28% for the control, 10% removal, and 20% removal treatments, respectively (Fig. 3). It should be noted that harvesting effects on DWD are partially confounded with the effects of the 1998 ice storm that damaged forests throughout New England (see controls in Fig. 3; Swisher 2001, Fraver et al. 2002).

4 Discussion

4.1 Nutrient Concentrations among Decay Classes

Nutrient concentrations of most elements significantly increased with advancing decay for both hardwoods and softwoods. This pattern has been frequently observed (Foster and Lang 1982, Arthur and Fahey 1990, Alban and Pastor 1993, Ganjegunte et al. 2004, Mladenoff et al. 2010), although the observation has not always been statistically significant or consistent across species (Krankina et al. 1999, Laiho and Prescott 2004). Although several explanations for these increases have been proposed, including concentration of nutrients due to mass loss, inputs by throughfall and litterfall, and root colonization (Foster and Lang 1982, Arthur and Fahey 1990), the most plausible explanation is the presence of nutrient-rich basidiomycetes within the log itself (Harmon et al. 1994). For Mn, Al, B and K, however, static to decreasing nutrient concentrations were observed with increasing decay class. Potassium is known to be highly mobile in DWD (Arthur and Fahey 1990, Krankina et al. 1999) and leaching likely reduces its concentration over time (Brown et al. 1996). Patterns for Mn, B and Al are not as easily explained, but have been observed as equally erratic in other studies, with concentrations depending greatly on species (e.g., Krankina et al. 1999).

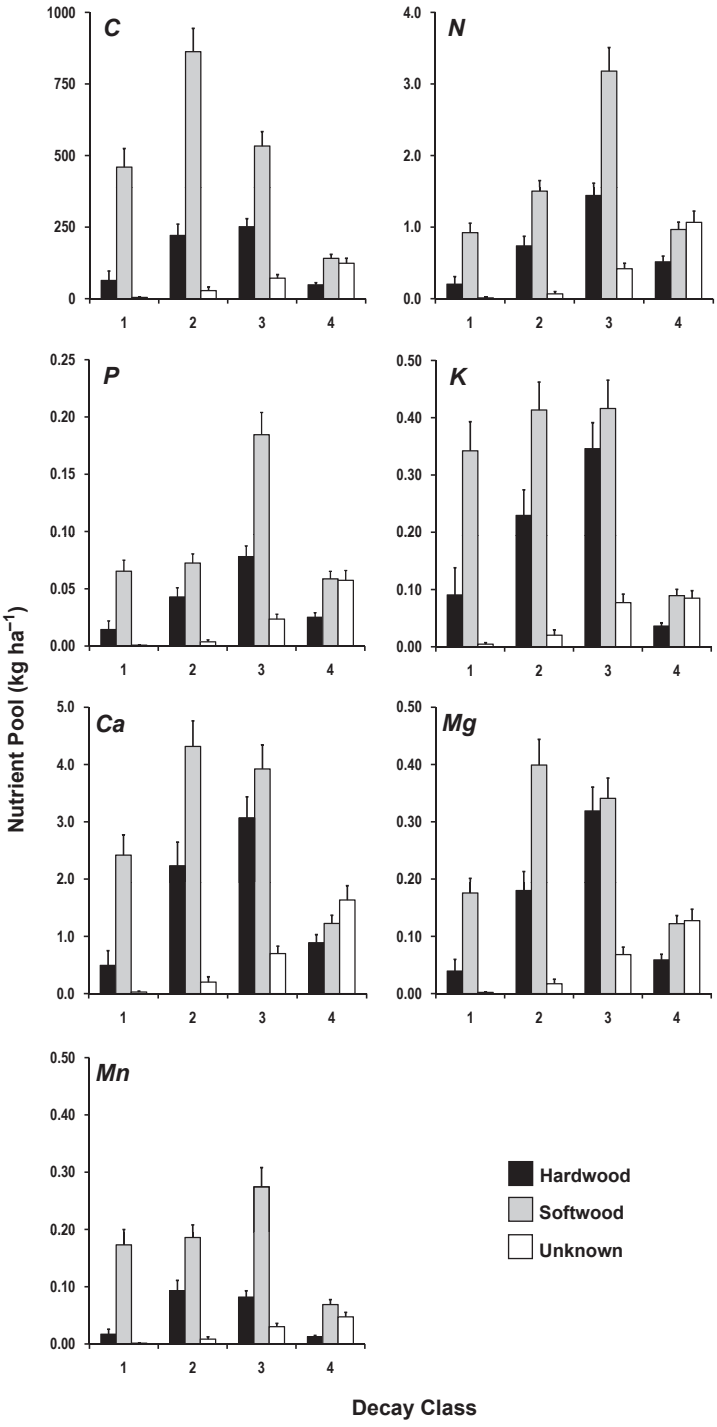

Fig. 2. Mean stand-level nutrient pool of down woody debris, as separated by wood type (hardwood vs. softwood) and decay class, before harvest in 1995. Bars indicate +1 standard error. Means and standard errors are calculated from volume estimates pooled across all replicates (Fraver et al. 2002).

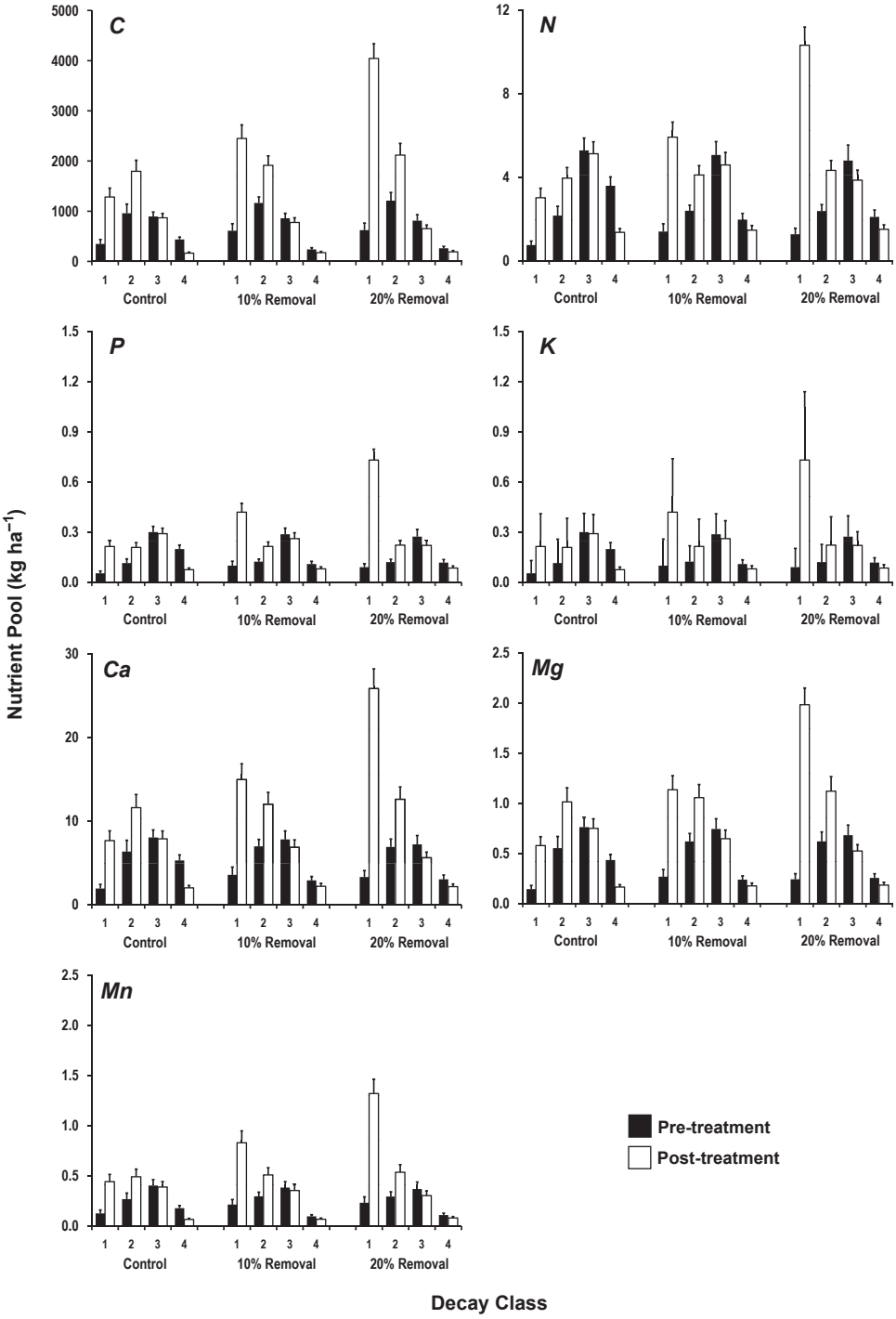

Fig. 3. Mean stand-level nutrient pool of down woody debris, as separated by decay class, before and after harvest. Bars indicate +1 standard error. Means and standard errors are calculated from only those plots within the three replicates for that particular treatment.

C:N sharply declined with DC, while N:P increased gradually with increasing DC. The C:N pattern demonstrated in this study is consistent with that found in other studies (e.g., Foster and Lang 1982, Arthur and Fahey 1990, Polit and Brown 1996) and has been proposed to be a function of translocation by fungal hyphae, N-fixation, and root colonization, among other sources (Harmon et al. 1986, Arthur and Fahey 1990, Harmon et al. 1994). N:P values in this study increased from ~15:1 in decay class 1 to ~20:1 in decay class 4. Other studies have also reported N:P to stabilize at 20 in advanced decay classes (Foster and Lang 1982, Arthur and Fahey 1990), although some authors have reported an increasing relationship (e.g., Mladenoff et al. 2010) and others a declining relationship (e.g., Krankina et al. 1999).

4.2 Nutrient Concentrations among Wood Types

Hardwood DWD, on average, had significantly higher nutrient concentrations than softwood DWD. Harmon et al. (1986) outlines two major reasons for this commonly cited pattern. First, hardwoods generally have more living parenchyma and other tissues on a per unit volume basis within wood and bark tissues (Haygreen and Boyer 1996), leading to higher initial nutrient concentrations in both standing trees and recently down material (Arthur and Fahey 1990, Arthur et al. 1993, Mladenoff et al. 2010). Second, the anatomical features of hardwoods, including radially oriented rays and large diameter vessels, facilitate fungal colonization much more rapidly than softwoods (Harmon et al. 1986). Further, the composition of wood-decay fungal communities found on hardwoods differs from that on softwoods; in fact many fungi are fairly host-genus specific (Renvall 1995, Boddy 2001). Given that fungal species mineralize wood at different rates (Boddy 2001), it is reasonable to assume that differences in fungal community composition contribute to differences in decay rates between hardwoods and softwoods. These factors all contribute to species-specific differences in nutrient immobilization and mobilization (Harmon et al. 1986, Brais et al. 2006).

In terms of specific species, *Betula papyrifera* had the highest overall nutrient concentrationss regardless of decay class. While this result could be partially a function of the difficulty of assigning a proper decay class for this species (the bark is recalcitrant relative to the wood itself), the trend has been reported previously for a mixedwood, boreal stand (Krankina et al. 1999). This pattern may be attributed to lower levels of leaching over time as *Betula* bark can persist intact well into decay class 4 (Fraver et al. 2002, Krankina et al. 1999).

4.3 Stand-Level Nutrient Pools

The size of the DWD nutrient pools were lower in our study than those reported in other studies of nutrient pools in similar forest types of North America. Arthur et al. (1993) reported that nutrient content of dead boles that had been cut, felled and left in place in New Hampshire, USA, was 134.6, 11.0, 70.8 and 193.2 kg ha^{-1} for N, P, K and Ca, respectively; and was 92.6, 3.5, 5.3 and 26.7 kg ha^{-1} for N, P, K and Ca, respectively, 23 years later. In the present study, pre-harvest values for N, P, K and Ca pools were 11.0, 0.6, 2.1 and 21.1 kg ha^{-1}, respectively, and postharvest were 20.0, 1.3, 6.2 and 46.2 kg ha^{-1}, respectively. Arthur et al. (1993), not surprisingly, reported much higher DWD biomass than observed in this study, 116.5 and 12.7 Mg ha^{-1} after cutting and 23 years later, respectively; biomass in DWD for this study was only 5.8 and 11.0–17.1 Mg ha^{-1} pre- and post-harvest (depending on AFERP treatment), respectively (Fraver et al. 2002). On the other hand, Mladenoff et al. (2010) reported that N, P, K and Ca pools for hardwood-dominated, unharvested, mixedwood stands within a large forest management study in Wisconsin, USA, were 22.6, 1.3, 4.8 and 27.6 kg ha^{-1}, very similar to the pools reported in this study.

As a proportion of the total aboveground nutrient pool, DWD is thought to only hold $<10\%$ of carbon, nitrogen and most other nutrients in mature forest types similar to those studied here (Laiho and Prescott 2004, Fahey et al. 2005, Bradford et al. 2009, Evans and Kelty 2010). Our estimates of aboveground living biomass for AFERP sites are 150.8–199.9 Mg ha^{-1} pre-harvest and

122.2–197.4 Mg ha^{-1} post-harvest (unpublished data). Assuming that standing snags, fine woody debris and forest floor nutrient pools together are 2–5 times the size of the DWD pools (Fahey et al. 2005, Bradford et al. 2009), DWD comprises 2.1–4.3% of pre-harvest and 3.2–9.1% of post-harvest aboveground carbon. We suspect that other DWD nutrient relationships would mirror DWD biomass relationships in these forests, although there may be minor deviations in those proportions for some nutrients (e.g., Ca) in older stands due to accumulation in more decayed wood.

4.4 Harvesting Impacts on Nutrient Pools

If belowground biomass and soil nutrients are included in stand-level totals, DWD nutrient pools represent a relatively minor contribution to total nutrient pools in these forests (Arthur and Fahey 1990, Brown et al. 1996, Harmon et al. 1986); however, some authors suggest that nutrients released from DWD may supply a disproportionate share of nutrients accumulated in living biomass (Krankina et al. 1999). Likewise, although DWD nutrient pools increased significantly after harvesting, it is unlikely that the low-intensity, gap-based harvesting techniques used in AFERP would influence nutrient dynamics over the long-term through its effects on DWD volumes. It is more likely that harvesting would alter nutrient dynamics through soil disturbance (Evans and Kelty 2010), particularly if harvesting leads to increased erosion from the site. Laiho and Prescott (2004) suggests that there is little scientific basis for DWD retention guidelines based on nutritional importance alone. Given the relatively small DWD nutrient pools found in this study and the general lack of large diameter (>35 cm) material reported by Fraver et al. 2002, we feel that retention guidelines for DWD in these mixedwood forest types should primarily focus on their role as habitat for keystone forest floor predators (e.g., red-backed salamaders) and other wildlife.

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