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In Situ Decomposition of Northern Hardwood Tree Boles: Decay Rates and Nutrient Dynamics in Wood and Bark

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Abstract

The decomposition of coarse woody debris contributes to forest nutrient sustainability and carbon balances, yet few field studies have been undertaken to investigate these relationships in northern hardwood forests. We used a paired-sample approach to study the decomposition of sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Erhr.), and yellow birch (*Betula alleghaniensis* Britt.) boles at the Hubbard Brook Experimental Forest in New Hampshire. Mass loss over 16 yr followed a first-order exponential decay pattern with half-lives ranging from 4.9 to 9.4 yr in bark, and 7.3 to 10.9 yr in wood. Nitrogen and phosphorus concentrations increased significantly during decomposition, resulting in sharp decreases in C:N and C:P ratios. We did not, however, observe significant net increases in the amount of N or P stored in decomposing boles, as reported in some other studies. Calcium concentration decreased by up to 50% in bark, but more than doubled in wood of all species. The retention of Ca in decomposing wood helps maintain Ca pools in this base-poor ecosystem. Together, the exponential model for mass loss and a combined power-exponential model for changes in nutrient concentrations were able to simulate nutrient dynamics in decomposing boles after clear-cutting in an adjacent watershed.

(200 words; 200 Max.)

Introduction

Coarse woody debris (CWD) has long been recognized as an important ecological component of forest ecosystems (Harmon et al. 1986). During the decomposition of CWD, nutrients are returned to the soil (Klinka et al. 1995) and/or released to drainage waters (Hafner et al. 2005; Kuehne et al. 2008). For most nutrients CWD is a small pool compared to soils and living biomass (Creed et al. 2004; Laiho and Prescott 2004). Nevertheless, nutrient dynamics in CWD may be important to forest sustainability. In the case of N and P, CWD in temperate-zone forests can act as a net sink during early stages of decomposition, preventing losses from the ecosystem (Alban and Pastor 1993; Laiho and Prescott 1999). As a result, both C:N and C:P ratios typically decrease during CWD decomposition (Hermann and Prescott 2008). In base-poor stands that have experienced Ca depletion due to chronic acid deposition, the slow release of Ca from decaying wood helps to maintain favorable Ca:Al ratios in the rooting zone (Shortle et al. 2012).

Studying the rate of decomposition of CWD and the changes in CWD nutrient content in different forests is essential for modeling carbon and nutrient dynamics in a changing climate and for assessing impacts of stand-replacing disturbances such as pest outbreaks, ice and wind storms, and fire (Brais et al. 2006). Although there is a growing literature on CWD decomposition and nutrient dynamics, especially in conifer forests of the northwestern United States and in boreal forests of Canada (e.g., Means et al. 1992; Laiho and Prescott 2004; Brais et al. 2006; Hermann and Prescott 2008), there are still few studies from the northern hardwood forests of New England and the Great Lakes region (Arthur et al. 1993; Moroni and Ryan 2010).

Studying CWD decomposition is made difficult by the long time period over which it takes place. Most studies depend on a chronosequence approach in which decay class or wood

density is used as a proxy for the time of decomposition (Preston et al. 1998; Müller-Using and Bartsch 2009). In some cases, decomposition time is known based on records of disturbance (Arthur et al. 1993). A drawback of the chronosequence approach is that the initial mass of the CWD is not known, making accurate estimates of mass and nutrient losses difficult. *In situ* incubation studies address this problem, but require long study times. Also, if small CWD samples (e.g., 'cookies') are used, decomposition may proceed at a faster rate than occurs in larger CWD because of high surface area to volume ratios.

We studied mass loss and nutrient dynamics in decomposing bole segments of the three co-dominant tree species in a northern hardwood forest in the northeastern USA over 16 years. We used an *in situ* incubation procedure to: (i) determine the decay rates of wood and bark for the three principal tree species in the forest; (ii) assess the release or accumulation of nutrients in decomposing bark and wood tissues; and (iii) develop model relationships that can be used to estimate nutrient losses from decomposing CWD.

Methods

Site Description and Experimental Design

This study was performed at the Hubbard Brook Experimental Forest (HBEF) in central New Hampshire, USA (43° 56′ N, 71° 45′ W). Most of the HBEF is northern hardwood forest, dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Erhr.), and yellow birch (*Betula alleghaniensis* Britt.). Together, these three species accounted for 86% of the above-ground living tree biomass in a similarly situated stand at the HBEF when this study was initiated in 1991 (Siccama et al. 2007).

The mean annual temperature in the area where this research was conducted is 5.5 ^{o}C (std. dev. = 0.61 ^{o}C), with average daily temperatures ranging from -8.5 ^{o}C in January to 18.8 ^{o}C in July (Bailey et al. 2003). Average annual precipitation at the HBEF is 1395 mm and is spread throughout the year (Bailey et al. 2003). About 30% of the annual precipitation falls as snow.

This work was conducted in the area of the south-facing experimental watersheds 1-6 at the HBEF. This area has an average slope of about 25% and is underlain by base-poor bedrock and glacial till (Johnson et al. 1968). Soils are typically coarse-grained and podzolic in nature, with an organic forest floor averaging 7 cm in depth (Johnson et al. 1991). Away from seeps and streams, soils are very well-drained (Bailey et al. 2014). To the best of our knowledge there was never standing water at our sites.

In July 1990 and May 1991, 71 trees of the three dominant species were felled with a chain saw. The trees were approximately 50-70 years old. From each felled tree, two adjacent segments of the bole, each approximately 1.5-m long (range: 0.99 – 2.22 m), were isolated with a chain saw. After measuring the length and the diameter at each end, one of these segments was then placed on the forest floor under fully intact forest canopy. The incubated bole segments were placed on sloping ground, approximately perpendicular to contours, in two similar stands approximately 200 m apart. The other 'fresh' segment was taken to the lab for sampling. Each of the 71 samples incubated *in situ* was therefore paired with a fresh sample from the same tree.

After measuring the dimensions of the fresh bole-segments, disks about 8-10 cm thick were cut from one end of each segment. The bark was separated from the wood of each disk, and both were dried at 80^{o} C to constant weight. The density calculated for these disks and the measured bark/wood mass ratio for the fresh bole were used with the initial dimensions of the incubated bole to compute the initial masses of wood and bark for the paired sample left in the

field. Subsamples were collected from the fresh wood disks by drilling from the side to the center with a 2.5-cm drill bit. The dried bark samples and the wood shavings were ground in a Wiley mill. Subsamples from the same log were composited for chemical analysis.

We collected incubated boles from the field in April, 1993 (2Y); May, 1997 (6Y); May-July, 2001 (10Y); and July, 2007 (16Y). Three boles of each species (nine total) were collected in 1993, 1997 and 2001. In 2007, three beech, six maple and six birch boles were collected. After removing any surface litter the bole was gently rolled onto a sampling tarp, and any loose material was collected in a bag. The boles were then returned to the lab and laid out on kraft paper, along with the loose debris collected in the field. After measuring the dimensions of each log, we then removed the bark from the bole and gathered the bark fragments from the debris. All of the collected bark and wood were dried at 80 ^{o}C to constant weight, which was recorded. These masses were compared to the calculated initial masses to determine the mass loss during decomposition. Subsamples of the wood were collected by drilling to the center of the log with a 2.5-cm bit. Wood and bark samples were ground in a Wiley mill for chemical analysis. Two beech boles collected in 2001 (10Y) had so little bark remaining that it was not sampled and judged to be completely decomposed. The samples collected in 1997 (6Y) were inadvertently discarded after mass determination, so we have no chemical data for those samples. In total, 42 incubated boles have been collected from the field to date. Chemical measurements have been made on 64 bark samples (33 fresh, 31 decomposed) and 66 wood samples (33 fresh, 33 decomposed).

Chemical Analyses

Total carbon, hydrogen and nitrogen were measured on oven-dried subsamples using a Carlo Erba EA1108 elemental analyzer. Other elemental concentrations were measured on HNO_3

digests of the samples. A crucible containing approximately two grams of oven-dried sample was placed in a muffle furnace (500 ^{o}C) overnight. The ash was then dissolved into 8 mL of 6 M HNO_3, filtered through a Whatman #40 paper filter, and brought to a volume of 50 mL using deionized water. The concentrations of Ca, Mg, K, P, and Mn were measured using inductively coupled plasma optical emission spectrometry (ICP-OES). All values were blank-corrected. Recovery of these elements from a standard reference material (apple leaves: SRM 1515, National Institute of Standards and Technology, Washington, DC, USA) ranged from 92% (Mn) to 99% (P).

Statistical Analyses

Log decay was modeled as a first-order decay process (Arthur et al. 1993):

$$\frac{M_t}{M_0} = e^{-k_d \cdot t} \quad [1]$$

where M_t is the mass remaining at time t (yr); M_0 is the initial mass; and k_d is the first-order decay constant (yr^{-1}). The value of k_d was estimated by non-linear regression using the 'nlinfit' routine in Matlab (Mathworks Inc., Natick, MA, USA).

Brais et al. (2006) used a combined power-exponential equation to describe the change in the concentrations of nutrients during decomposition of CWD. We used a slightly modified form of their equation:

$$Y_t = a \cdot (t+1)^b \cdot e^{k_n \cdot t} \quad [2]$$

where Y_t is the concentration of the nutrient (N, P, K, Ca, Mg, Zn) at time t (yr). Parameters a, b, and k_n were estimated by non-linear regression using the 'nlinfit' routine in Matlab. Using t+1 in the power term has the desirable property that $Y_t = a$ when $t = 0$. Thus, parameter a can be interpreted as the concentration of the nutrient in fresh wood or bark.

To take advantage of the experimental design, we used paired t-tests to test the significance of differences in chemical concentrations between fresh and decomposed wood and bark at each sampling (2Y, 10Y, 16Y). One-sample t-tests were used to test the hypothesis that the fraction of a nutrient remaining was significantly different from 1.0 on each of the sampling dates. All statistical tests were carried out with a significance level of 0.05 using Minitab 16 (Minitab, Inc., State College, PA, USA).

Results

Decay Rates

Mass loss in individual bole samples was highly variable, especially at 6 and 10 years (Fig. 1). The average mass loss (wood + bark) for all species was 15% after 2 years, 36% after 6 years, 58% after 10 years, and 73% after 16 years. The maximum mass loss at 16 years was 91%. Beech boles had the shortest half-life (7.2 yr), whereas yellow birch had the longest (10.7 yr; Table 1). The 95% confidence intervals for the first-order decay constants for beech and yellow birch boles did not overlap, suggesting a significant difference in decay rates (Table 1). Decomposition rates of bark were much more rapid than wood in sugar maple and beech, and similar to wood in yellow birch. In sugar maple, there was no overlap in the 95% confidence intervals for wood and bard decay constants. There was no relationship between the initial diameter of the bole and the mass loss after 16 years of *in situ* decomposition (Fig. 1), despite considerable variation in both initial mass and diameter (mass range: 10.6 – 66.4 kg).

Nutrient Concentrations and Ratios

The concentration of N generally increased in wood and bark during decomposition (Tables 2, 3). Significant increases were observed by 16Y in bark and wood of sugar maple and

yellow birch. Increases in beech were not significant (bark) or marginally significant ($P < 0.10$: wood). Phosphorus concentrations also increased significantly in sugar maple wood and bark and yellow birch wood, with a marginally significant increase in beech wood. Carbon concentrations generally remained in the 450-550 g kg^{-1} range (data not shown). Consequently, C:N and C:P ratios decreased along with the increases in N and P concentrations (Tables 2, 3). The C:N ratio in wood decreased more than the ratio in bark (Fig. 2). By 16Y wood C:N ratios remained greater than bark, but the magnitudes of C:N in wood and bark were similar. The N:P ratio increased significantly in sugar maple and yellow birch bark, but there was no clear pattern in wood.

Bark K concentrations decreased significantly in all species (Table 2). In many cases, these decreases were quite large; sugar maple bark experienced a decrease of more than 80% by 16Y. The concentration of K also decreased significantly in all sampling years in beech wood and at 16Y in yellow birch wood (Table 3). Calcium and magnesium behaved differently in wood and bark. The concentrations of both elements decreased significantly in sugar maple and yellow birch bark by 16Y, and Mg decreased significantly in beech bark as well (Table 2). In wood, however, Ca concentration increased significantly by 16Y in all species. Magnesium concentrations tended to increase in wood as well, but at 16Y only sugar maple showed a marginally significant increase (Table 3). The concentration of Ca in fresh tissues was 15-30 times greater in bark than in wood, while the multiple for Mg was 2.1-3.3.

Because of the small sample sizes and the high variability in concentrations, we did not attempt to develop combined power-exponential models (Equation [2]) for each species individually. The fitted models for wood and bark of all species are shown in Fig. 3, while the estimated model parameters are given in Table 4. The trajectories of the fitted models are

consistent with the statistically significant changes we observed in nutrient concentrations (Tables 2, 3). The models predict steadily increasing N concentrations and decreasing K concentrations in wood and bark, as well as the gradual increase in P concentrations. Despite high variability, the fitted models explained up to 61% of the variation in nutrient concentrations, though three of the models had R^2 values below 0.10 (Table 4).

Nutrient Pools in Decomposing Boles

The fractional changes in the standing stocks of nutrients in decomposing boles (wood + bark) are shown in Fig. 4. Values above 1.0 indicate a net increase in the amount of the nutrient compared to the amount in the fresh bole, suggesting an external source. Although there were a few cases where the mean fraction was greater than 1.0, none of these were statistically significant ($P > 0.05$). By 16Y the fractions for all nutrients were significantly less than 1.0. For the most part, the three tree species followed similar trajectories (Fig. 4). Potassium pools declined faster than the mass decay curve, consistent with the rapid decrease in K concentrations (Tables 2, 3). In contrast, the trajectories for N, P and Ca pools generally stayed above the decay curve due to the increased concentrations in wood and bark. For these three elements, the trajectory of beech was the closest to the decay curve. Pools of Mg and Mn tended to follow the mass loss curve for all species.

Discussion

Decomposition of Wood and Bark

First-order exponential decay models effectively describe the decomposition of beech, sugar maple and yellow birch boles at Hubbard Brook (Fig. 1). However, individual boles decayed at highly variable rates, resulting in considerable variation in mass loss. While first-

order exponential decay is the most widely used model for CWD decomposition, a variety of alternative models have been suggested based on conceptual (Manzoni et al. 2012) and statistical (Freschet et al. 2012) considerations. Because of the high variation in mass loss among individual boles in this study, it is difficult to evaluate conclusively whether the exponential model is better than linear, sigmoidal, or other decay models.

Variation in mass loss was greatest at six (6Y) and ten (10Y) years of incubation, suggesting that individual boles vary greatly in initial susceptibility to decomposition. Mass loss was expected to be related to the initial diameter of the bole (Harmon et al. 1986; Hyvönen et al. 2000). However, our data showed no relationship between initial bole diameter and mass loss after 16 years, despite a three-fold variation in diameter (12 – 32 cm; Fig. 1). The average length of the incubated boles was 1.46 m, so edge effects associated with small 'cookie' samples cannot explain the absence of a diameter-mass loss relationship.

Environmental factors that could explain the high variation in mass loss among individual boles include wood temperature and moisture, initial density, and fungal community characteristics (Liu et al. 2013). The boles were incubated in two moderately sloping locations approximately 200 m apart, so significant differences in temperature and moisture conditions are unlikely. We did observe a weak relationship between initial density and percent mass remaining at 16Y (Mass Remaining [%] = 102.2·Density [Mg m^{-3}] – 29.46; R^2 = 0.114). However, the range of initial density values of the boles used in this study was small (0.51 – 0.63 Mg m^{-3} with three outliers), so variation in initial density can explain only a small fraction of the variation in decay rates. Several studies have found that initial decay rates in CWD are related to the nature and degree of fungal colonization in the biomass at the onset of decomposition (Parfitt et al. 2010; Lindner et al. 2011). As decomposition progresses in boles lying in close proximity, fungal

community structure is likely to become more homogeneous (Liu et al. 2013). Though we have no data with which to examine this hypothesis, it would potentially explain the very high variation in mass loss, especially at 6Y and 10Y.

The decay rates that we observed in this study, and the rate constants derived from them, are generally similar to values estimated in other studies at Hubbard Brook and in similar climatic regions. Arthur et al. (1993) measured the mass and nutrient content of CWD on watershed 2 (W2) at the HBEF 14 and 23 years after an experimental clear-cut in 1965. They reported an overall k_d value of 0.096 yr^{-1} for boles of all species (wood+bark), which is on the upper end of our range (Table 1). Consequently the W2 mass-remaining observations lie on the lower end, but well within, the range of values shown in Figure 1. After clear-felling, W2 was kept free of vegetation for three years by the application of a chemical herbicide. Those three years of exposure to higher levels of solar radiation and lower interception of precipitation may have resulted in somewhat higher decomposition rates than under the intact forest canopy. Arthur et al. (1993) did not estimate decay rates for individual species, but they did conclude, based on an analysis of decay classes, that the decay rates followed the sequence beech > sugar maple > yellow birch. Our decay rate data confirm this pattern. Based on non-overlapping confidence intervals, the k_d value for beech was significantly greater than the value for yellow birch, with sugar maple intermediate (Table 1). However, the rate constants for wood of the three species all had overlapping confidence intervals. Therefore, the differences in bole decomposition rates between species are largely due to differences in the rates of bark decomposition.

Müller-Using and Bartsch (2009) estimated k_d values for wood and bark of European beech (*Fagus sylvatica* L.) of 0.089 yr^{-1} and 0.109 yr^{-1}, respectively, in the Solling forest in Germany. These estimates are both within the 95% confidence intervals of our values for

American beech (Table 1). Alban and Pastor (1993) estimated a k_d of 0.080 yr^{-1} for quaking aspen (*Populus tremuloides* Michx.) boles (wood+bark) in Minnesota, a value similar to ours for sugar maple and between beech and yellow birch. Our k_d values are greater than hardwood decay rates measured in cooler boreal forests in eastern Canada. For example, Brais et al. (2006) estimated a k_d value of 0.060 yr^{-1} for trembling aspen in northern Québec.

We estimated higher decay rates for bark than for wood in sugar maple and beech (Table 1). This finding is consistent with work done in a beech forest in Germany (Müller-Using and Bartsch 2009) and a radiata pine (*Pinus radiata* D. Don) forest in New Zealand (Ganjegunte et al. 2004). The barks of beech, sugar maple and yellow birch have lower carbohydrate content and greater content of lignin, suberin and other resinous compounds than wood (Johnson et al. 2005). One might therefore expect that bark decomposition would be slower than wood decomposition. However, the fungi responsible for CWD decomposition must penetrate the bark in order to attack wood tissues. Also, bark, which is exposed throughout the life of the tree, may already be host to fungal, bacterial, and microarthropod communities at the time a tree becomes CWD, giving it a head start in decomposition. Finally, the higher N concentrations in bark tissue (5-6 times greater than wood: Tables 2, 3) may help to promote faster bark decomposition as well (Harmon et al. 1986).

Yellow birch has a resinous, paper-like bark which is resistant to decomposition. It is common to find tubes of yellow birch bark in the forest with little or no woody material inside. The k_d value estimated for yellow birch bark through 10Y was 0.054 yr^{-1}, lower than the value for wood. However, through 16Y the bark k_d value increased to 0.074 yr^{-1} (Table 1). Thus, it appears that there may be a 'tipping point' in the decomposition of yellow birch bark, which proceeds very slowly (half-life: 18.5 yr) for at least the first 10 yr, then rapidly increases.

Nutrient Dynamics

The concentrations of nutrients in fresh and decomposing tissues exhibited very high variability (Fig. 3). This variability, in concert with the small number of boles collected at each sampling date, made it a challenge to detect statistically even large changes in nutrient concentrations. For example, the average N concentration in beech wood after 10 years of decomposition was more than twice the average in the paired fresh samples (2880 mg kg^{-1} vs. 1310 mg kg^{-1}), yet the difference was not significant. Nevertheless, we observed many significant changes in tissue chemistry (Tables 2, 3). The number of statistically significant changes increased with time of decomposition. We noted 12 significant results ($P \leq 0.05$) in the 2Y data among the 54 tests carried out for wood and bark. In 10Y and 16Y, the number of significant changes increased to 17 and 32, respectively. The paired nature of this study resulted in a large number of statistical tests. Using a level of significance of 0.05, the 162 tests represented in Tables 2 and 3 are expected to produce 8 falsely significant results, a relatively small fraction of the 61 we observed.

We observed large and significant increases in the concentration of N in decomposing CWD, especially wood and bark of sugar maple and yellow birch (Tables 2, 3). This phenomenon has been observed in many studies of CWD decomposition (e.g., Alban and Pastor 1993; Arthur et al. 1993; Laiho and Prescott 2004; Brais et al. 2006). Phosphorus concentrations also increased significantly during decomposition, especially in wood (Table 3). Because of the increases in N and P concentrations, the C:N and C:P ratios in wood and bark decreased significantly during decomposition (Fig. 2; Tables 2, 3). Initial C:N and C:P ratios were very high, especially in wood. Despite the large declines, C:N ratios in both wood and bark after 16 years of decomposition are still considerably greater than soil C:N ratios. The lowest C:N ratios

in decomposing wood and bark at 16Y were approximately 100 and 40, respectively. The mean C:N ratio in Oi-horizon soil at Hubbard Brook, which includes recent litter, is 27.2 (Balaria et al. 2009). Means et al. (1992) found a similar pattern in an old-growth Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest in Oregon, where the most decomposed logs had C:N ratios of about 250, while forest floor soil had C:N of approximately 50. Based on the N concentration trajectories (Fig. 3, Table 4), and assuming that decomposing tissues continue to contain approximately 50% C, we estimate that the C:N ratios in bark and wood will reach the Oi-horizon C:N value around year 45 and 80, respectively. In both cases, this convergence occurred at greater than 99% mass loss.

Despite the increases in N and P concentrations, we did not observe significant increases in the amount of N or P in decomposing boles, as some studies have documented (e.g., Alban and Pastor 1993). Diazotrophic bacteria are capable of atmospheric N fixation in high C:N substrates like CWD (Mooshammer et al. 2014). In addition, mycelia of some wood-decaying fungi have been shown to transfer N and P from forest floor soils to CWD, supplementing the N and P in the CWD and improving C:N:P ratios for decomposers. (Wells and Boddy 1990; Boddy and Watkinson 1995; Mooshammer et al. 2014). Several investigators have reported that N:P ratios in decomposing CWD converge to a mass-ratio value of about 20 (equivalent to a molar ratio of 44) (Laiho and Prescott 1994; Saunders et al. 2011), suggesting a strong, biologically mediated linkage between N and P retention mechanisms. Our data do not show any convergence in N:P ratios during decomposition. In bark, the molar N:P ratio averaged 49-62 in fresh tissue and increased significantly in sugar maple and yellow birch, to values of 75 and 81, respectively. In wood, initial molar N:P ratios ranged from 41 (sugar maple) to 57 (yellow birch) and few significant changes were observed during decomposition (Table 3). Thus, it appears that

microbial activity in CWD at Hubbard Brook does not drive N:P ratios towards a common value as in some other ecosystems.

Potassium concentrations declined sharply during decomposition (Fig. 3; Tables 2, 3), and the loss of K from decomposing logs outpaced mass loss (Fig. 4). This finding, which is consistent with other studies (Alban and Pastor 1993; Arthur et al. 1993; Ganjegunte et al. 2004), reflects the high mobility of K in plant tissues (Gosz et al. 1973; Krankina et al. 1999).

The Ca concentration in bark decreased during decomposition, by as much as 54% (yellow birch; Table 2). On the other hand, the Ca concentration in wood increased significantly, more than doubling in all species (Table 3). Thus, the concentrations in wood and bark converged during decomposition, though bark concentrations continued to exceed wood concentrations throughout the study period. Ganjegunte et al. (2004) also observed increasing Ca concentrations in wood and decreasing concentrations in bark during the decomposition of radiata pine CWD in New Zealand. The fraction of Ca remaining in wood was never significantly greater than one for any species at any time in our study (data not shown), indicating that wood was never a net sink for Ca. Therefore, it is not clear to what degree the increase in Ca concentration in wood was the result of retention of Ca that was originally in the wood versus immobilization of Ca leached from decomposing bark.

The change in wood Ca concentration during decomposition was significantly correlated with the change in P concentration (Fig. 5), a finding also observed in coniferous forests by Laiho and Prescott (2004). Cord-forming saprophytic fungi can transfer P into and within decaying wood during decomposition, thereby increasing the wood P concentration (Wells and Boddy 1990). While these fungi do not appear to accumulate large amounts of Ca in their

fruiting bodies (Harmon et al. 1994), their activity promotes decay, resulting in increased Ca concentrations in the residual wood (Shortle et al. 2012).

Modeling Nutrient Dynamics in CWD

The high variability in nutrient concentrations at each sampling resulted in considerable scatter around the fitted power-exponential relationships (Fig. 3). In some cases (e.g., P in bark) model R^2 values were very low, suggesting that there is little or no relationship between concentration and time of decomposition. In other cases the change in concentration could be described by a simpler model form. For example, the concentration of N appears to increase approximately linearly during decomposition of both wood and bark (Fig. 3). It would be appropriate to model each nutrient-tissue combination using the most parsimonious model for that combination. However, there is also merit in using a single, flexible model form such as the power-exponential equation for multiple nutrients to maintain overall model simplicity.

The power-exponential relationships may result in poor estimates of the changes in nutrient concentrations for a single bole. However, they may provide adequate predictions of nutrient dynamics in a stand-replacing event, where a large population of boles is subject to decomposition. To test the usefulness of our relationships we used them to model the change in the nutrient content of boles on W2 at Hubbard Brook 23 years after clear-felling, using the results of Arthur et al. (1993) for validation.

Since the nutrient pool in CWD is the product of mass and concentration, equations [1] and [2] can be multiplied to model the pool size, P_t, at time t (yr):

$$P_t = M_t \cdot Y_t = M_0 \cdot a \cdot (t+1)^b \cdot e^{(k_n - k_d) \cdot t} \qquad [3]$$

Arthur et al. (1993) reported an initial felled bolewood mass of 116.5 Mg ha^{-1}, which was distributed in the following proportions: sugar maple, 33%; beech, 29%; yellow birch, 25%,

other, 13%. We allocated the mass of "other" species to maple, beech and birch in proportion to their abundances, then applied the measured bark:wood ratios from our fresh boles to estimate the initial masses (M_0, in Mg ha^{-1}) of bark and wood for each of the three species. We then applied equation [3] using the parameter values in Tables 1 and 4 to calculate the amounts of N, P, K, Ca and Mg remaining after 23 years of decomposition.

The predicted nutrient pools remaining in W2 were in good agreement with the measured pools reported by Arthur et al. (1993) (Fig. 6). Nitrogen, P and K were underestimated by equation [3] while Ca and Mg were overestimated. Percent error ranged from 6% (Mg) to 37% (K). The correspondence of our estimates with the measured pools is remarkable considering both the scatter in the fitted concentration trajectories (Fig. 3) and the uncertainties in the field measurement and collection of CWD on W2 after 23 years. The allocation of the masses of "other" species to sugar maple, beech and yellow birch, and the herbicide treatment that was applied in the first three years after W2 was cut are additional sources of uncertainty that may have contributed to the discrepancies in Figure 6. The fit that was achieved despite all of these uncertainties suggests that this approach may be useful for estimating nutrient dynamics after stand-replacing events such as clear-cutting, ice storms or hurricanes.

Implications for Forest Sustainability

In forest systems with nutrient-poor soils, falling trees can deliver a large pulse of nutrients to the soil, especially in major disturbances. The relatively slow decomposition of CWD results in the release of these nutrients over many years, providing resources to trees in various stages of stand development. For example, after 16 years of decomposition the N and P content of decomposing hardwood boles was about half of the initial amount (Fig. 4), despite an average mass loss of 73%. As decomposition proceeds, the remaining bole wood and bark will

be gradually incorporated into forest floor soils and humus, where more than 50% of fine-root biomass is located at Hubbard Brook (Fahey and Hughes 1994). In a changing climate, potential increases in CWD decomposition rates may result in more rapid release of nutrients, increasing nutrient availability in early stages of regeneration but reducing availability later.

The dynamics of Ca in decaying wood have important implications as well for the acid-base chemistry of forest soils that have been depleted of Ca by chronic acid deposition. We observed large, significant increases in Ca concentrations in wood during decomposition at Hubbard Brook (Table 3). Similarly, Shortle et al. (2012) documented large and significant increases in the concentration of Ca in red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marshall) wood after 8 years of decomposition. They also measured the concentration of exchangeable Ca in the decomposing wood and found that over time it converged to the exchangeable Ca concentration in the forest floor. Because wood has very low Al concentrations, decomposing wood provides a medium with high Ca:Al ratio, favorable for good tree growth (Shortle et al. 2012). In base-poor soils like those at Hubbard Brook, Ca dynamics in CWD may therefore promote tree regeneration by providing microenvironments where conditions are more favorable than the soil as a whole.

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Study. The Hubbard Brook Experimental Forest is administered by the USDA Forest Service, Northern Experiment Station, Newtown Square, PA.

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Table 1. First-order decay constants (k_d) and estimated half-lives for the decomposition of northern hardwood boles at the Hubbard Brook Experimental Forest, NH. Uncertainties shown in the table are standard errors.

Species/Component	Decay constant, k_d (yr^{-1})	95% Confidence Interval	Half-life (yr)
American Beech	0.097 ± 0.009	0.077 – 0.116	7.18
Wood only	0.095 ± 0.009	0.075 – 0.115	7.30
Bark only	0.141 ± 0.029	0.076 – 0.205	4.92
Sugar Maple	0.079 ± 0.007	0.064 – 0.094	8.76
Wood only	0.076 ± 0.008	0.060 – 0.092	9.17
Bark only	0.116 ± 0.009	0.096 – 0.135	6.00
Yellow Birch	0.065 ± 0.006	0.053 – 0.077	10.7
Wood only	0.064 ± 0.006	0.050 – 0.077	10.9
Bark only	0.074 ± 0.007	0.060 – 0.089	9.35

Table 2. Changes in nutrient concentrations and ratios in decomposing bark tissues. The means and standard deviations for fresh tissues are shown in the 'Fresh' column. Other columns show the average change in the concentration or ratio after 2, 10 or 16 years of decomposition. Values in **bold** face are statistically significantly different than zero ($P < 0.05$). Values in *italics* had P-values between 0.05 and 0.10, and are referred to as "marginally significant" in the text. Data are not shown for cases where $P > 0.10$.

(next page)

Parameter	Fresh	2Y	10Y	16Y
	---------- American Beech Bark ----------			
Nitrogen, mg kg^{-1}	8263 ± 946			
Phosphorus, mg kg^{-1}	302 ± 55			
Potassium, mg kg^{-1}	1344 ± 229			**-876**
Calcium, mg kg^{-1}	22600 ± 4110			
Magnesium, mg kg^{-1}	421 ± 92			**-132**
Manganese, mg kg^{-1}	215 ± 36			
C:N, molar ratio	68.0 ± 9.0			
C:P, molar ratio	4164 ± 653	**+802**		
N:P, molar ratio	61.6 ± 8.8	**+22.9**		
	---------- Sugar Maple Bark ----------			
Nitrogen, mg kg^{-1}	5915 ± 803		**+4867**	**+5301**
Phosphorus, mg kg^{-1}	263 ± 33		**+182**	**+80**
Potassium, mg kg^{-1}	2288 ± 357		**-1362**	**-1936**
Calcium, mg kg^{-1}	15070 ± 7100			**-3830**
Magnesium, mg kg^{-1}	506 ± 135	*+71*		**-315**
Manganese, mg kg^{-1}	278 ± 65			*-92*
C:N, molar ratio	99.0 ± 13.0		**-47.2**	**-43.9**
C:P, molar ratio	4917 ± 587		**-1814**	**-1013**
N:P, molar ratio	50.2 ± 7.1	*+10.1*		**+22.5**
	---------- Yellow Birch Bark ----------			
Nitrogen, mg kg^{-1}	6767 ± 685			**+3407**
Phosphorus, mg kg^{-1}	328 ± 101	**-90**		
Potassium, mg kg^{-1}	1337 ± 406	**-914**	*-1380*	**-862**
Calcium, mg kg^{-1}	12160 ± 2550	**-2760**		**-6530**
Magnesium, mg kg^{-1}	413 ± 89		**-135**	**-236**
Manganese, mg kg^{-1}	209 ± 37			
C:N, molar ratio	88.8 ± 9.1			**-21.9**
C:P, molar ratio	4352 ± 1292	**+2290**		
N:P, molar ratio	48.7 ± 11.8	**+24.2**	*+23.9*	**+28.7**

Table 3. Changes in nutrient concentrations and ratios in decomposing wood tissues. The means and standard deviations for fresh tissues are shown in the 'Fresh' column. Other columns show the average change in the concentration or ratio after 2, 10 or 16 years of decomposition. Values in **bold** face are statistically significantly different than zero ($P < 0.05$). Values in *italics* had P-values between 0.05 and 0.10, and are referred to in the text as "marginally significant." Data are not shown for cases where $P > 0.10$.

(next page)

Parameter	Fresh	2Y	10Y	16Y
	---------- American Beech Wood ----------			
Nitrogen, mg kg^{-1}	1234 ± 182			*+888*
Phosphorus, mg kg^{-1}	55.6 ± 20.9			*+43.8*
Potassium, mg kg^{-1}	812 ± 214	**-205**	**-532**	**-466**
Calcium, mg kg^{-1}	693 ± 187	**+81**	**+1840**	**+986**
Magnesium, mg kg^{-1}	200 ± 67	**+31**	*+100*	
Manganese, mg kg^{-1}	55.8 ± 12.1		**+23.2**	**+35.8**
C:N, molar ratio	463 ± 64		*-187*	*-173*
C:P, molar ratio	25270 ± 9300		**-7310**	*-18100*
N:P, molar ratio	54.4 ± 18.2			*-16.8*
	---------- Sugar Maple Wood ----------			
Nitrogen, mg kg^{-1}	1094 ± 322		**+2350**	**+2160**
Phosphorus, mg kg^{-1}	62.5 ± 13.0			**+90.3**
Potassium, mg kg^{-1}	512 ± 103			
Calcium, mg kg^{-1}	1045 ± 328		**+2820**	**+1500**
Magnesium, mg kg^{-1}	154 ± 44			*+86*
Manganese, mg kg^{-1}	74.2 ± 18.2			
C:N, molar ratio	550 ± 147	**-68**	**-477**	**-286**
C:P, molar ratio	20660 ± 4280		**-9630**	**-13100**
N:P, molar ratio	41.3 ± 18.5		**+17.4**	
	---------- Yellow Birch Wood ----------			
Nitrogen, mg kg^{-1}	1120 ± 186		*+963*	**+1770**
Phosphorus, mg kg^{-1}	50.4 ± 16.8	**+19.6**	**+43.2**	**+81.5**
Potassium, mg kg^{-1}	417 ± 258			**-62**
Calcium, mg kg^{-1}	866 ± 385			**+1050**
Magnesium, mg kg^{-1}	149 ± 57			
Manganese, mg kg^{-1}	61.4 ± 12.1			**+65.9**
C:N, molar ratio	514 ± 76		**-217**	**-300**
C:P, molar ratio	28760 ± 14800			**-22600**
N:P, molar ratio	56.6 ± 29.4			

Table 4. Parameters for combined power-exponential models relating nutrient concentrations to time of decomposition (Equation [2]). Relationships were developed for bark and wood by combining the data for all species.

Nutrient	*a*	*b*	k_n	R^2
	---------- Bark ----------			
Nitrogen, mg kg^{-1}	6863	0.0568	0.0162	0.473
Phosphorus, mg kg^{-1}	293.2	-0.0711	0.0156	0.014
Potassium, mg kg^{-1}	1685	-0.4963	-0.0006	0.612
Calcium, mg kg^{-1}	15906	0.3703	-0.0947	0.220
Magnesium, mg kg^{-1}	450.0	0.0822	-0.0529	0.437
Manganese, mg kg^{-1}	223.7	0.3828	-0.0654	0.060
	---------- Wood ----------			
Nitrogen, mg kg^{-1}	1088	0.2301	0.0223	0.568
Phosphorus, mg kg^{-1}	55.29	0.4256	-0.0238	0.443
Potassium, mg kg^{-1}	560.0	-0.0142	-0.0440	0.265
Calcium, mg kg^{-1}	756.0	0.6766	-0.0517	0.456
Magnesium, mg kg^{-1}	162.4	0.2265	-0.0289	0.058
Manganese, mg kg^{-1}	63.63	-0.1630	0.0657	0.444

Figure Captions

Fig. 1. Mass loss during decomposition of northern hardwood boles (wood + bark) at the Hubbard Brook Experimental Forest, NH. Data for watershed 2 (Arthur et al. 1993) at years 14 and 23 include all species. First-order models derived from our data (Table 1) are shown by: solid line (sugar maple), long dashes (yellow birch), short dashes (American beech). Inset: Mass loss at 16 years was unrelated to initial bole mass.

Fig. 2. Changes in C:N ratios of bark and wood during decomposition. Be: American Beech, SM: Sugar Maple, YB: Yellow Birch.

Fig. 3. Changes in nutrient concentrations during *in situ* decomposition of bark and wood at the Hubbard Brook Experimental Forest, New Hampshire. Data for sugar maple, American beech and yellow birch are combined. The lines in each panel show the fitted power-exponential relationship (Equation [2]), using the parameters in Table 4.

Fig. 4. Fractional gain or loss of nutrients during decomposition of hardwood tree boles (bark+wood). Symbols show the mean ± one standard error. Values above 1.0 (dashed line) indicate a net gain in the mass of the nutrient in the decomposing bole, suggesting an external source. The solid gray line represents the average mass decay rate (Equation [1]), based on the estimated decay rates in Table 1. Trajectories below this line are experiencing nutrient losses that exceed mass loss, while trajectories above this line are preferentially accumulating the nutrient.

Fig. 5. Relationship between the change in Ca concentration and the change in P concentration in decomposing bark and wood at Hubbard Brook. There is no significant relationship in bark, whereas the relationship in wood is highly significant ($P < 0.001$).

Fig. 6. Pools of N, P, K, Ca and Mg remaining in boles on watershed 2 at the Hubbard Brook Experimental Forest, New Hampshire 23 years after clear-felling. Measured values are taken from Arthur et al. (1993). The pools were also estimated using Equation [3] and parameter values given in Tables 1 and 4. See the Discussion for details.

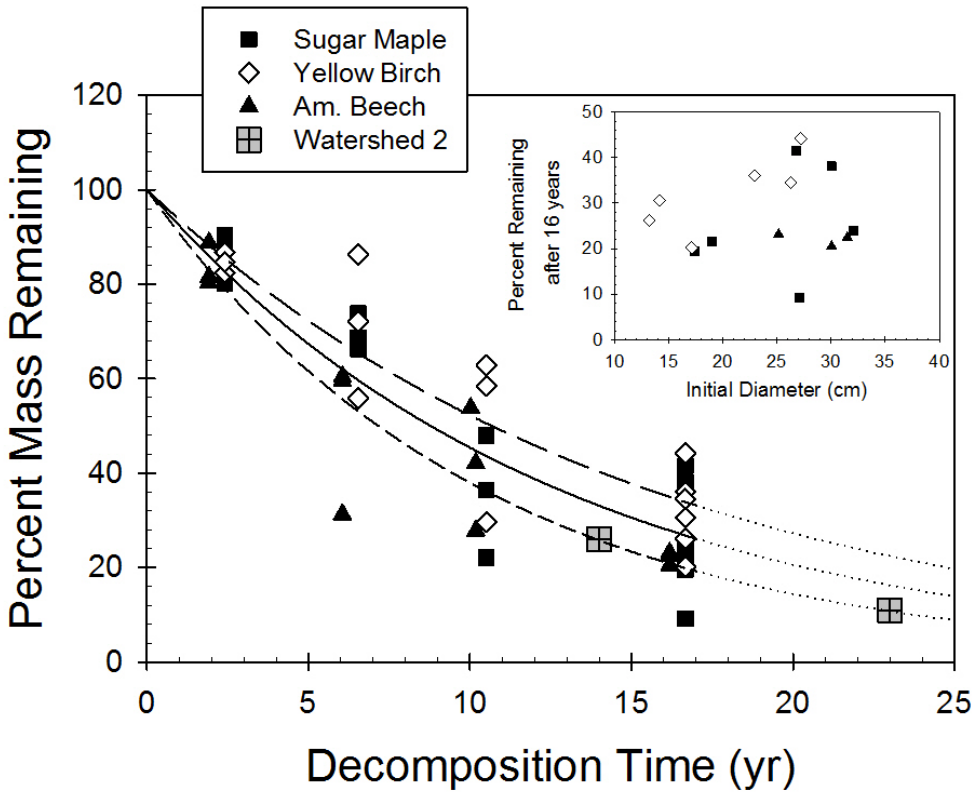
Sugar Maple
Yellow Birch
Am. Beech
Watershed 2
Percent Mass Remaining
Decomposition Time (yr)
0
20
40
60
80
100
120
0
5
10
15
20
25
Percent Remaining after 16 years
Initial Diameter (cm)
0
10
20
30
40
50
10
15
20
25
30
35
40

Figure 1

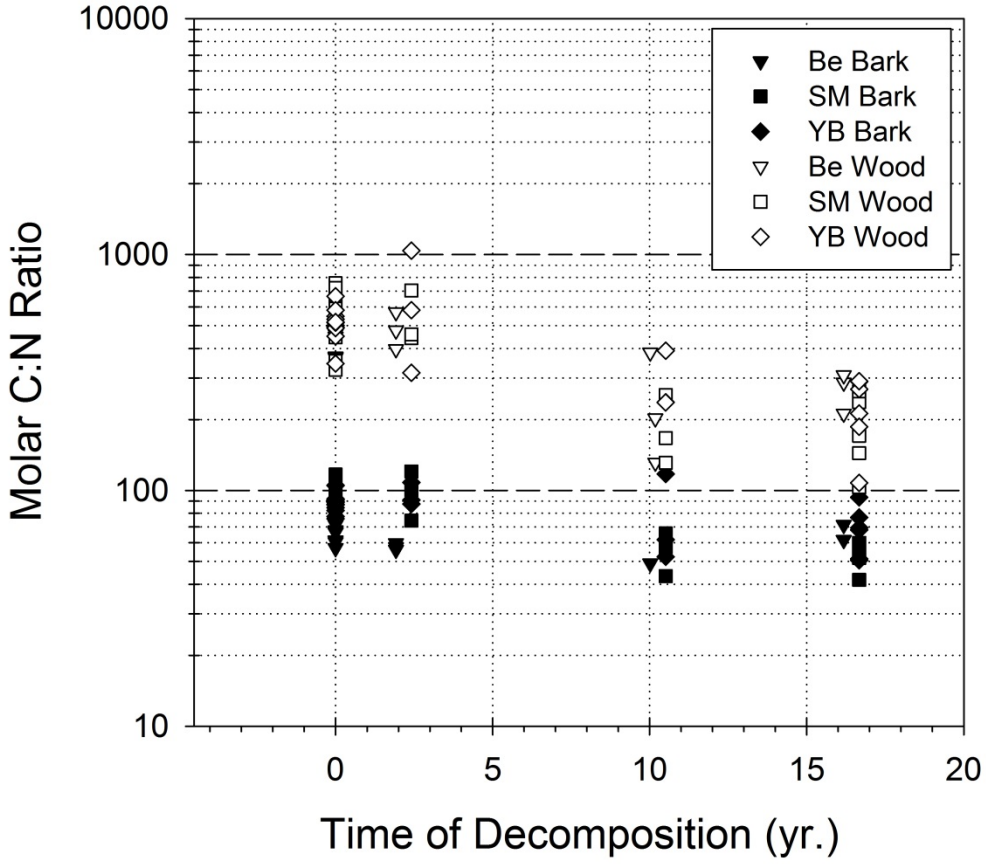
10000
1000
100
10
Molar C:N Ratio
0
5
10
15
20
Time of Decomposition (yr.)
Be Bark
SM Bark
YB Bark
Be Wood
SM Wood
YB Wood

Figure 2

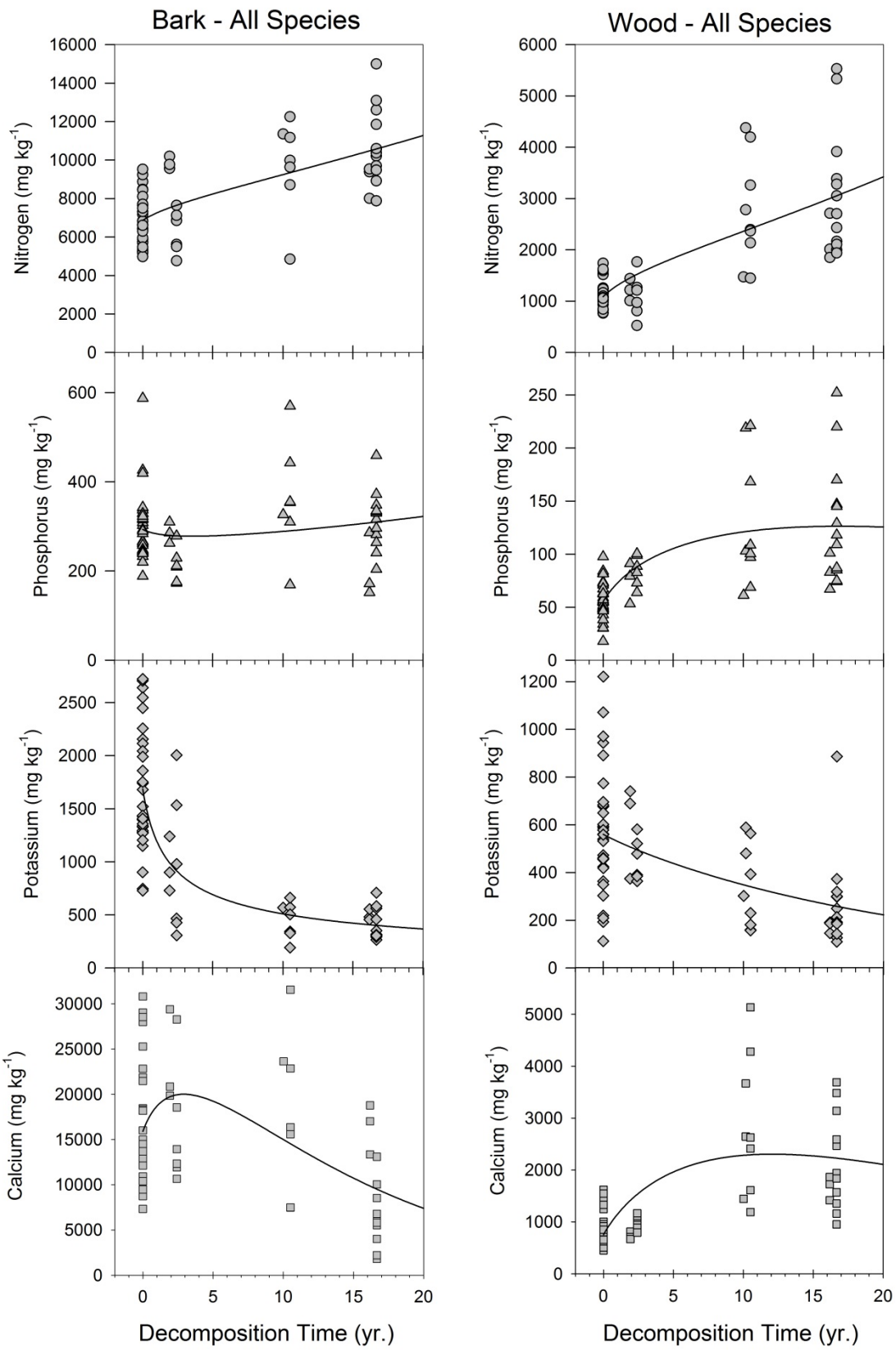
Bark - All Species
Wood - All Species
Nitrogen (mg kg-1)
Phosphorus (mg kg-1)
Potassium (mg kg-1)
Calcium (mg kg-1)
Decomposition Time (yr.)
Decomposition Time (yr.)

Figure 3

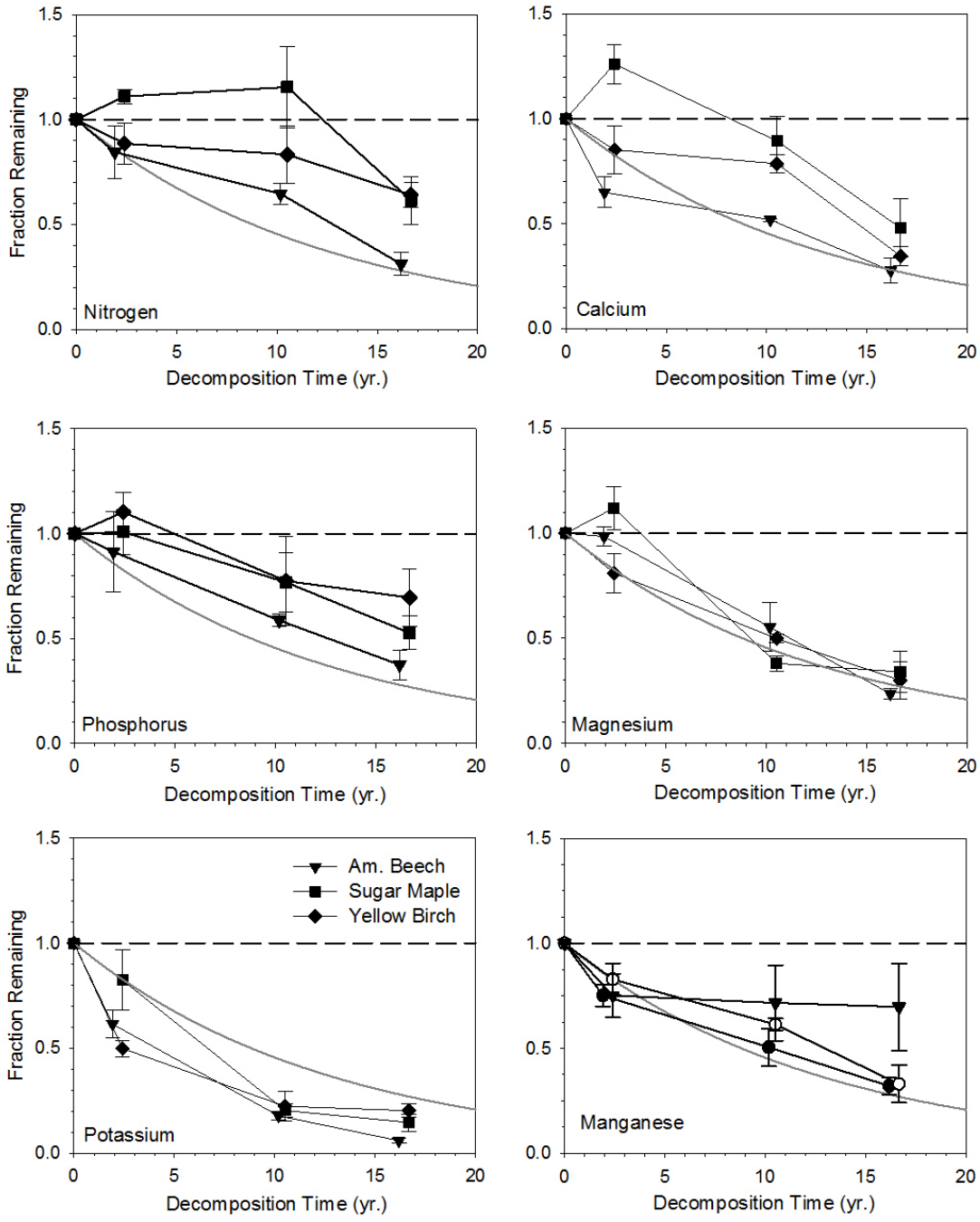
Fraction Remaining
Decomposition Time (yr.)
Nitrogen
Calcium
Phosphorus
Magnesium
Potassium
Manganese
Am. Beech
Sugar Maple
Yellow Birch
0.0
0.5
1.0
1.5
0
5
10
15
20

Figure 4

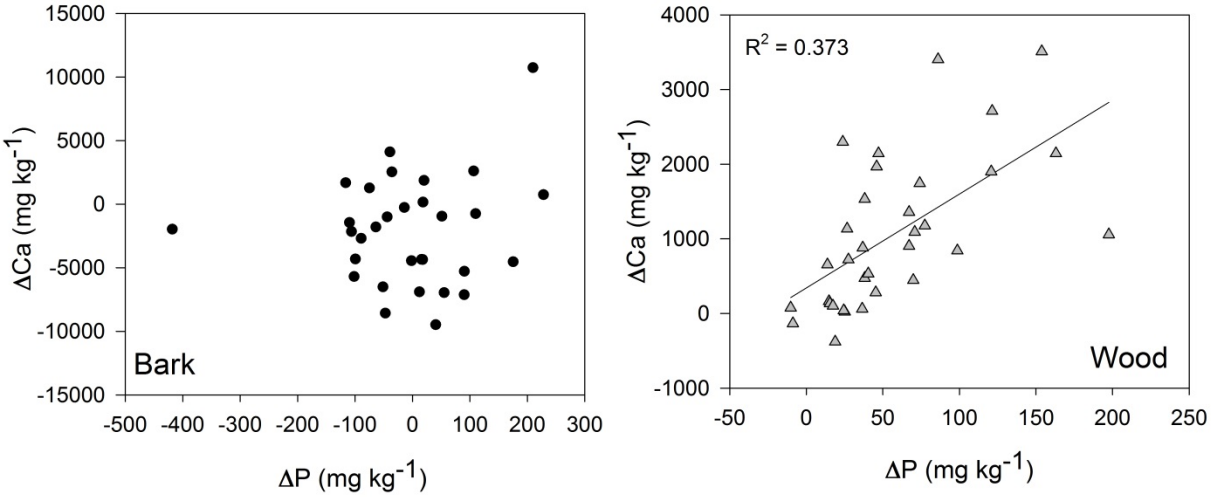
15000
10000
5000
0
-5000
-10000
-15000
ΔCa (mg kg-1)
Bark
-500 -400 -300 -200 -100 0 100 200 300
ΔP (mg kg-1)
4000
3000
2000
1000
0
-1000
ΔCa (mg kg-1)
R2 = 0.373
Wood
-50 0 50 100 150 200 250
ΔP (mg kg-1)

Figure 5

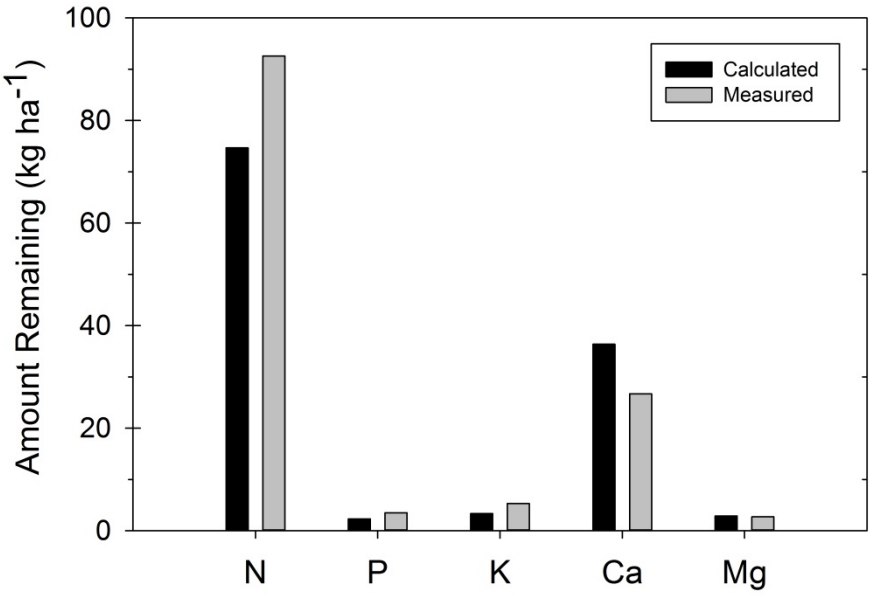
Amount Remaining (kg ha-1)
100
80
60
40
20
0
Calculated
Measured
N
P
K
Ca
Mg

Figure 6