

Abstract of Thesis

BASE CATION CONCENTRATION AND CONTENT IN LITTERFALL AND WOODY DEBRIS ACROSS A NORTHERN HARDWOOD FOREST CHRONOSEQUENCE

Forest floor calcium (Ca) declines in northern hardwood forests are of interest because Ca availability may limit future forest growth. In the 1990s investigations into Ca pools and fluxes across a northern hardwood forest chronosequence showed decreases across stand age in the mass of forest floor base cations and litterfall cation concentrations. I undertook a study of factors that influence litterfall chemistry to develop a better understanding of base cation biogeochemistry in developing northern hardwood forests. Although Ca, potassium (K), and magnesium (Mg) concentrations in litterfall significantly declined with stand age, species composition and soil nutrient availability also influenced litterfall chemistry. The interplay between these factors, such as the distribution of species with different nutrient demands in areas of base cation availability or limitation, influences forest floor chemistry and may impact the time in which soil Ca depletion occurs.

Additionally, I examined the quantity and qualities (species composition, decay class, size, and nutrient concentrations and contents) of woody debris across the same northern hardwood forest chronosequence. The objectives of this study were to quantify cation pools in woody debris, describe how the qualities of these woody debris pools change with stand development, and establish a baseline for long-term measurements of woody debris accumulation and chemistry with stand age. Decomposition of woody debris transfers base cations to the forest floor, and may be partially responsible for forest floor Ca gains in young stands. Calcium and K pools in woody debris were most strongly influenced by woody debris biomass, whereas Mg content was influenced by both woody debris biomass and species composition. In young stands, woody debris pools were strongly influenced by management practices during harvest. By 20 years since harvest woody debris pools reflected processes of stand development. For example, from 20 to nearly 40 years since harvest woody debris biomass and species composition was dominated by mortality of early successional species. Woody debris in more mature stands reflected small-scale stochastic disturbances including disease and single-tree mortality. Litterfall and woody debris are each components of within-stand cation cycling that will be critical to future forest growth with limited Ca availability.

Keywords: Litterfall, Woody debris, Northern hardwood forest, Calcium, Stand age

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BASE CATION CONCENTRATION IN LITTERFALL AND WOODY DEBRIS
ACROSS A NORTHERN HARDWOOD FOREST CHRONOSEQUENCE

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BASE CATION CONCENTRATION AND CONTENT IN LITTERFALL AND
WOODY DEBRIS ACROSS A NORTHERN HARDWOOD FOREST
CHRONOSEQUENCE

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of
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By

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2006

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General Introduction

The philosophical outlook:

Forest ecosystems are inherently dynamic. With changes to the physical structure of forests come alterations to the ways in which organisms relate to their environment—how they grow, what litter they leave behind, what resources they consume and redistribute, etc. Changes in forest patterns (which can range from the distribution of species across the landscape to the distribution of fungal spores through the atmosphere or atoms of potassium through the soil) always elicit changes in nutrient cycling. Whether such changes are cyclical, components of feedback loops, or unprecedented is likely to intrigue humans throughout time, but when these questions relate to the sustainable future of resources on which humans depend, it is surprising that this isn't front page news.

In the 1960's, the beginning of long-term measurements of biogeochemical attributes of a handful of hydrologically tight watersheds in the White Mountains of New Hampshire coincided with a period of declining calcium (Ca) availability that has been attributed to intensive land management and acid rain. During the first 30 years of research at the Hubbard Brook Experimental Forest, Ca deposition declined 75% (Likens and Bormann, 1995). The majority of this decline was seen before 1975. Since then, the changes have been less dramatic. These and other related trends from Hubbard Brook, including long-term changes in the Ca concentration of streamflow (Federer et al. 1990) and declines in forest floor cation concentrations (Yanai et al. 1999), provided a basis for two important developments: (1) broad-scale investigations of acid rain and of other ways humans have (un)wittingly tinkered with the global-scale cogs, and (2) analyses of landscape-scale trends by interpreting patterns and processes together in long-term perspectives.

Research at Hubbard Brook is invaluable because the lessons learned there have influenced the direction of many modern scientists and have improved public awareness of how people fit into a global community from a biogeochemical perspective. Many scientists use concepts developed at Hubbard Brook, such as analyzing the inputs and outputs to and from a natural system to understand processes within the system. Additionally, results from Hubbard Brook research gave scientists as well as the general public quantitative connections between forest sustainability and global-scale industrial patterns. For example, the discovery of acid rain in North America brought together

hydrological, atmospheric, and industrial disciplines to build a new vision of how ecosystems function.

The Hubbard Brook Experimental Forest is a small site that has hosted a great deal of research. The current study, as a component of a broader investigation, aims to provide context through investigations across a broader landscape for lessons learned at Hubbard Brook with regard to base cation cycling. While Ca declines were being investigated at Hubbard Brook, the stands were all aging synchronously. Separating the effects of stand age from those of environmental changes (e.g., acid rain, decreased Ca deposition, etc) can contribute to the development of our understanding of ecosystem dynamics and responses to a changing environment. By examining aspects of the biogeochemistry of forest stands covering a range of ages, we can better comprehend how stand age and age-related changes in forest structure and composition impact nutrient storage and cycling.

Nutrient fluxes and pools change through stand development and through time. Changes over time have been associated with acid rain and timber harvesting. Acidic deposition (Likens and Bormann, 1995), increased mineral weathering rates (Driscoll et al. 2001), and removal of large nutrient pools by intensive timber harvesting (Arthur et al. 2001) decrease the availability of base cations. Over time, the combined effects of these factors may limit base cation availability. Through stand development, changes in the Ca, K, and Mg cycling patterns may be expected. Certain tree species that are more abundant in young stands, such as pin cherry and yellow birch, have high Ca concentrations in their leaves (Hamburg et al. 2003). As the quality of litterfall changes across stand age, so may the availability of nutrients in the forest floor.

All stands with similar management and rates of acidic deposition might be expected to exhibit similar base cations losses from forest floors, but this has not been observed. Repeated measures along a forest chronosequence in New Hampshire revealed stand age-related trends in the changes of base cation concentrations in forest floors and litterfall (Yanai et al. 1999, Hamburg et al. 2003). The three oldest stands in the chronosequence each showed slight declines in forest floor Ca concentration; stands roughly 30 to 55 years old appeared to have significant declines; and stands <30 years old

gained Ca in the forest floor. Base cation concentrations in litterfall, measured in the same set of stands at the same time, were highest in these young stands.

Two factors, shifting species composition and nutrient uptake from easily-weatherable minerals, have each been proposed as causes of the unexpected Ca gains in forest floors of young northern hardwood forests (Hamburg et al. 2003). I propose that woody debris may also influence the base cation status of forest floors. Shifts in species composition from relatively Ca-rich species, such as pin cherry (*Prunus pensylvanica*) and yellow birch (*Betula alleghaniensis*), toward species with moderate to low Ca concentrations (i.e., beech (*Fagus grandifolia*), white birch (*Betula papyrifera*)) occur in developing northern hardwood stands (Hamburg et al. 2003). Certain species may also be associated with mycorrhizae that have a greater potential for active weathering of non-silicate minerals (Blum et al. 2002). As these trees reach mortality, their wood falls to the forest floor and decomposes, potentially offering a gradual but sustained nutrient flux to the forest floor.

This thesis is a component of a larger study that aims to clarify the effects of stand age on the pools and fluxes of base cations in the northern hardwood forest. I examined the mass, chemistry, and species composition of woody debris and litterfall in northern hardwood stands 15 to ~129 years since harvest. I related the nutrient pool in woody debris and the nutrient flux in litterfall to forest floor nutrients and attempted to identify which soil nutrients (by horizon and by pool type) most strongly influence litterfall chemistry.

The first objective of this study was to determine whether the nutrient pool in woody debris was of sufficient size to impact forest floor base cations. I hypothesized that shifts in the properties of woody debris occur through stand development and that with these shifts, we would also see shifts in the magnitude and distribution of nutrients stored on the forest floor. It was reasonable to expect woody debris to play an important role in the cycling of base cations in the northern hardwood forest because wood contains a large fraction of aboveground Ca, roughly 20 times as much as is in leaves (Whittaker et al. 1979). The wood of early-successional species are particularly Ca-rich (Likens and Bormann, 1970), and pin-cherry, the dominant early-successional tree species, tends to die and fall to the forest floor over a short time period in young stands (Marks, 1974).

The second objective of this study was to identify how litterfall chemistry is related to stand age, species composition, and the chemistry of different soil horizons. I hypothesized that the concentrations of available base cations in different soil horizons may be useful predictors of litterfall chemistry, which is the main avenue through which biotic controls on forest floor chemistry are exerted.

This work will help to clarify how aspects of base cation cycling in the northern hardwood forest are altered in different age forest stands. With such an understanding, we can better recognize how anthropogenic air pollution and forest management have impacted forest sustainability. Improving forest management relies on cultivating this kind of understanding.

Chapter 1
**Base cation concentrations and contents in litterfall:
Interactions with stand age, species composition, and soil nutrient concentrations**

Introduction

In the northern hardwood forest, long-term declines in soil and forest floor cation concentrations are driven by intensive management (Federer et al. 1989) and environmental (i.e., nitrogen deposition) and biotic processes (Hamburg et al. 2003). Acidification of soils in the northeastern US by industrial and automobile emissions accelerates base cation leaching by decreasing cation exchange capacity and increasing mineral weathering rates (Baes and McLaughlin, 1984; Johnson and Todd, 1990; Shortle and Bondietti, 1992). The combined effects of soil acidification and timber harvesting (i.e., aboveground nutrient removal) were predicted to deplete soil Ca (Federer et al. 1989). However, instead of showing signs of Ca depletion, such as poor tree growth and health (DeHayes et al. 1999, Horsley et al. 2002), forest floors in young stands (<30 years old) recovering after harvest appear to have increasing calcium concentrations (Yanai et al. 1999, Hamburg et al. 2003). Whether sufficient pools of base cations remain available for forest growth may depend on how these nutrients are cycled on the stand level.

Availability of forest floor Ca is mediated largely through nutrients returned to the forest floor in leaf litterfall, as well as root turnover. Conversely, the concentration and content of Ca and other nutrients in plants is determined by nutrient availability in the forest floor and mineral soil (Facellie and Pickett, 1991). Across a northern hardwood chronosequence, litterfall calcium concentration was found to decline with stand age (Hamburg et al. 2003). This may be due to differences in nutrient demand among species (Fujinuma et al. 2005), combined with a shift in species composition with stand age. Alternatively, changes in belowground processes related to stand age, and perhaps species composition, may allow young stands to better access certain nutrient pools in the soil (Hamburg et al. 2003). It is also possible that the previously observed decline in Ca concentration with stand age was partially an artifact of subtly varying soil Ca concentrations among stands. Calcium and other cations occur in the soil in multiple forms, which vary in availability to plants (Blum et al. 2002). These pools can be defined

operationally as exchangeable, easily-weatherable, and tightly-bound. The nutrient concentrations vary with depth and across the landscape, reflecting variation in soil substrate chemistry as well as the weathering history of the site. Previous analyses of litterfall nutrient concentration and content in the context of a northern hardwood forest chronosequence were limited by a lack of both soil nutrient data and an understanding of the various pools of nutrients that might be available to plants. The implementation of a new study designed to evaluate the importance of the 'easily-weatherable' nutrient pool in supplying cations, especially Ca, to young forests, offered the opportunity to evaluate litterfall chemistry in the context of soil nutrient availability.

In this study, I evaluated litterfall base cation concentrations and contents across the same northern hardwood forest chronosequence to compare them to the availability of each form of Ca, K, and Mg in different soil horizons, as well as to the age and species composition of the stands. The primary objective of this study was to describe the relationship between litterfall nutrient concentrations and contents and stand age, species composition, and soil nutrient availability. I hypothesized that the soil concentrations of exchangeable (NH_4Cl extractable) and easily-weatherable (cold HNO_3 extractable, e.g., calcite and apatite) base cations were better predictors of litterfall chemistry than was stand age alone. In particular, I hypothesized that the concentration of exchangeable and easily-weatherable cations in deep soil horizons would more strongly predict litterfall cation concentration than would more shallow horizons based on the potential importance of apatite and the depth of unweathered apatite pools (Blum et al. 2002, Hamburg et al. 2003). Finally, I hypothesized that species composition would also be important in determining base cation concentrations in litterfall because species vary in the plasticity of their response to soil nutrient availability (Juice et al. 2006).

Methods

Litterfall mass and chemistry were measured in a northern hardwood forest chronosequence with 14 stands. The stands, aged 15 to ~129 years since harvest, were in the White Mountain National Forest, and included stands in the Bartlett and Hubbard Brook Experimental Forests. The soils were moderately- to well-drained soils derived from granitic glacial till with relatively thick forest floors (Federer, 1984). Annual

precipitation is roughly 130 cm, with less than 45 cm falling as snow (Likens and Bormann, 1995). Basal area of young stands (<35 years) was dominated by pin cherry (*Prunus pensylvanica*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and white birch (*B. papyrifera*). Stands between 35 and 65 years were dominated by American beech, sugar maple (*Acer saccharum*), yellow birch, and white birch. Older stands were composed mainly of American beech, sugar maple, and red maple (*A. rubrum*).

Litterfall was collected in fifteen 0.23 m² baskets per stand from August 2003 to August 2005. Autumn litter was sorted by species; twigs and other non-leaf material were removed, and all components were dried and weighed. Leaf litterfall samples collected from baskets during a rain-free period in October, 2004, were used for nutrient analysis. Leaf samples from all 15 baskets per site were sorted, dried, weighed, and pooled by species for nutrient analysis. For the 2004 nutrient samples, the major species (beech, pin cherry, red maple, sugar maple, white birch, and yellow birch) were analyzed independently for all sites in which they were present. Additionally, those species whose litterfall comprised $\geq 10\%$ of the autumn litterfall dry mass at a site were analyzed independently. All other species, which included basswood (*Tilia americana*), eastern hophornbeam (*Ostrya virginiana*), mountain maple (*Acer spicatum*), and northern red oak (*Quercus rubra*) were proportionally pooled and analyzed as a composite sample. Dried litter samples were ground, dissolved in 1M nitric acid using microwave digestion, and analyzed using inductively coupled plasma-optical emission spectroscopy.

Mean nutrient concentrations were estimated for each site by mass-weighting by species using the average mass of each species of litterfall from 2003 and 2004 and nutrient concentrations from 2004. Litter was collected for the entire litter year (Aug-Aug) for both 2003 and 2004, but laboratory complications limited the utility of collections from August, 2005. Ninety to 95% of the annual litterfall mass fell in autumn in past years in this chronosequence, so this likely introduces only a small level of error.

I used litterfall mass to describe species composition rather than the basal area because I was interested in the effective composition of litterfall inputs to the forest floor. Snags and other such oddities in basal area data may obfuscate the influence of individual species to stand-level litterfall chemistry.

Linear regression models using a backwards stepwise process were used to analyze the influence of species composition and soil chemistry on litterfall chemistry. The effects of species composition and soil chemistry were analyzed in separate stepwise regressions. Response variables were Ca, K, and Mg concentrations and contents in litterfall. For the analysis based on soil chemistry, I developed models in which only the concentrations of the respective nutrients in soil and litterfall were analyzed (i.e., Ca concentrations in soil were used to develop models of litterfall Ca concentration and content).

Soil samples for chemical analysis were obtained from soil pits dug at each site. In 2003, three quantitative soil pits were dug at each of six sites. Soil subsamples were collected from 0 – 10 cm depth, 10 - 20 cm, 20 - 30cm, beyond 30cm and from the underlying C horizon regardless of the depth. The horizons within each sample were recorded. In 2004, qualitative soil pits were dug at the eight remaining sites. Subsamples were collected from each soil horizon on a single exposed face of the pit. Nutrient analyses of the soil samples were done using sequential extractions starting with a 1-M NH_4Cl (pH = 7) solution to remove exchangeable cations. Cold extractions with 1-M HNO_3 removed the nonsilicate minerals (easily-weatherable minerals, e.g., apatite, calcite) and were followed by hot extractions with 1-M HNO_3 to extract remaining cations, which were assumed to be primarily in a tightly-bound form in silicate minerals (Nezat et al. in press). Solutions were analyzed using inductively-coupled plasma-atomic emission spectroscopy. Throughout this paper I will refer to the exchangeable, easily-weatherable, and tightly-bound nutrient pools, which were each defined by the above extractions.

Statistical relationships were analyzed using regression analyses. I used both first degree linear regressions and stepwise linear regressions to build models explaining variation in litterfall nutrient concentrations and content. The stand was considered the experimental unit. Significance was determined using $\alpha = 0.05$ and analyses were conducted using SAS software, Version 9.1 for Windows (SAS, 2004).

RESULTS

Stand Age

Litterfall Ca, K, and Mg concentrations tended to decline with increasing stand age. This trend was nearly significant for Ca ($R^2 = 0.25$, $p = 0.07$), but was nonsignificant for K ($R^2 = 0.12$, $p > 0.1$) and Mg ($R^2 = 0.08$, $p > 0.1$, Fig 1.1). Similar trends were observed in past measurements on this chronosequence from 1993 to 1996, when Ca concentrations were shown to decline significantly and linearly with increasing stand age (Hamburg et al. 2003). During that same period, nonsignificant negative trends were observed for K and Mg concentrations (M. Arthur, unpublished data). Taking the averages of each measurement period (1993 to 1996 and 2003 to 2004), and combining both periods in a regression analysis, I found significant negative linear relationships between litterfall Ca, K, and Mg concentrations and stand age that explain 30%, 24%, and 18% of the variation in these concentrations, respectively (Fig 1.2). Litterfall nutrient content was independent of stand age.

Species Composition

I used simple linear regressions to analyze changes in the proportion of each species to total litterfall mass across stand ages. With increasing stand age, pin cherry declined, and then disappeared. The percentage of the total litterfall mass comprised of white birch decreased linearly with increasing stand age ($R^2 = 0.40$, $p = 0.02$, Fig 1.3). Conversely, the proportion of beech litterfall increased linearly with stand age ($R^2 = 0.38$, $p = 0.02$) and the proportion of litterfall comprised of red maple was positively, but less significantly related to stand age ($R^2 = 0.26$, $p = 0.06$, Fig 1.3). Notably, pin cherry had high Ca, K, and Mg concentrations; white birch had a low Ca concentration, but relatively high K and Mg concentrations (Table 1.1). Low base cation concentrations in beech and red maple litterfall may decrease stand-level litterfall base cation concentrations. Cation-rich species, such as yellow birch and striped maple, are common in young stands, whereas aspen, which has a low Mg concentration, a moderate Ca concentration, and the highest K concentration was most abundant in stands 45 to 69 years old.

To test the potential influence of species composition on species mass-weighted litterfall nutrient concentrations and nutrient contents, I used backwards stepwise linear regressions. Ten independent variables were initially included in each stepwise regression; these were the percentages of total litterfall mass made up of pin cherry, beech, white birch, yellow birch, striped maple, red maple, sugar maple, ash, aspen, and composite samples of minor species of litterfall. Minor species included basswood (*Tilia americana*), eastern hophornbeam (*Ostrya virginiana*), mountain maple (*Acer spicatum*), and northern red oak (*Quercus rubra*). The proportion of each species (as a percent of the total annual litterfall mass) explained a large portion of the variation in species-weighted litterfall Ca concentration ($R^2 = 0.71$, $p = 0.02$), and litterfall Ca contents ($R^2 = 0.75$, $p = 0.01$), but only a small amount of variation in litterfall Mg concentrations ($R^2 = 0.33$, $p = 0.03$) (Table 1.2). Litterfall Ca concentration and contents were each modeled by the percentages of beech, pin cherry, sugar maple, and white birch, whereas the model for Mg concentration was based solely on the percentage of aspen litterfall. Species composition did not explain litterfall Mg contents, nor litterfall K concentrations or contents.

Soil Nutrient Concentrations

The soils in this study were all derived from glacial till, which is inherently heterogeneous. Pockets of minerals rich in base cations (e.g., Ca in apatite) may be abundant in certain locations. In all stands in the chronosequence, the Oa horizon had the highest concentrations of exchangeable Ca, K, and Mg (Fig 1.4). However, within the mineral soil, the highest concentrations of Ca were in easily-weatherable pools, which are likely important sources of base cations to trees in the northern hardwood forest (Blum et al. 2002). The highest concentrations of K and Mg were in the tightly-bound pools, the concentrations of which increased with depth (Fig 1.4).

To test the hypothesis that exchangeable cations and easily-weatherable minerals were the primary sources of Ca, K, and Mg for litter, I first tested the influence of the concentrations of nutrients in these pools within the C, B, upper mineral, and Oa soil horizons on species mass-weighted litterfall nutrient concentrations using backwards stepwise linear regressions. The models resulting from the stepwise regressions were

relatively simple with 1 to 4 variables remaining (Table 1.3). Exchangeable and easily-weatherable base cation concentrations in the soil explained less of the variation in litterfall Ca concentration and more of the variation in litterfall Mg concentration compared to species composition. A moderate amount of the variation in litterfall K concentration was explained by soil K. Specifically, litterfall Ca concentration was linearly related to the concentration of exchangeable Ca in C horizon soils ($R^2 = 0.37$, $p = 0.02$). Easily-weatherable K concentrations in the B and C horizons explained variation in litterfall K concentrations ($R^2 = 0.46$, $p = 0.03$). A more complex model that explained the variation in litterfall Mg concentrations included the easily-weatherable concentrations of Mg in C horizon and upper mineral soils as well as the exchangeable Mg concentrations in B and C horizon soil ($R^2 = 0.82$, $p < 0.01$). (Table 1.3).

Exchangeable and easily-weatherable cation concentrations also explained variation in litterfall Ca and Mg contents ($R^2 = 0.32$, $p = 0.03$; $R^2 = 0.60$, $p < 0.01$, respectively, Table 1.3) based on simple models. Litterfall calcium content was modeled by the easily-weatherable concentration of Ca in B horizon soil. The model explaining litterfall Mg content was based on the exchangeable Mg concentrations in B and C horizon soils (Table 1.3). No significant model resulted from the stepwise process to explain variation in litterfall K content.

To assess the importance of tightly-bound base cations in soils for explaining litterfall chemistry, the same backwards stepwise regressions as above were used with the addition of the tightly-bound concentrations of each base cation in C, B, upper mineral, and Oa soil horizons. Tightly-bound base cations in the soil helped to explain a great amount of variation in litterfall K ($R^2 = 0.997$, $p = 0.02$) and Mg concentrations ($R^2 = 0.99$, $p < 0.001$). These stepwise regressions were notably more complex with 8 and 11 significant variables remaining in the resulting models, respectively, which included exchangeable, easily-weatherable, and tightly-bound nutrient concentrations in multiple soil horizons (Table 1.4). Models of litterfall Ca concentration were not improved by the inclusion of tightly-bound nutrient concentrations.

Tightly-bound soil nutrient concentrations helped to explain large amounts of variation in litterfall base cation contents. These models were also relatively complex, including 4 to 8 significant variables that represented each of the nutrient forms and

horizons. Nonetheless, 69% of the variation in litterfall K content was explained by the resulting model based on soil chemistry ($p = 0.02$). An even greater portion of the variation in litterfall Ca content ($R^2 = 0.94$, $p < 0.01$) and Mg content ($R^2 = 0.997$, $p < 0.01$) were explained by soil chemistry.

Discussion

Declines in litterfall cation concentration in plant tissues with stand age have been identified in association with declining forest floor cation concentrations (Arthur and Yanai, 2000; Hamburg et al. 2003). Lower concentrations of Ca, K, and Mg in litterfall over time may be indirect responses to soil acidification (Miller et al. 1993; Likens et al. 1998; Watmough and Dillon, 2003) or to processes related to stand aging (Yanai et al. 1999, Hamburg et al. 2003), which include shifting species composition (Berendse, 1998). Across a forest chronosequence, I evaluated three factors that may influence litterfall chemistry; stand age, species composition of the litterfall, and soil nutrient concentrations.

Stand age was negatively correlated with litterfall nutrient concentrations, but this was only significant when litterfall chemistry was considered over two measurement periods (1993 to 1996 and 2003 to 2004). Within a single measurement period, only litterfall Ca concentration in the 1990's showed a significant correlation with stand age (Hamburg et al. 2003). The small amount of variation in litterfall cation concentrations explained by stand age suggests that other factors may be important. Stand age was not correlated with litterfall Ca, K, or Mg contents.

In the northern hardwood forest, overstory species composition shifts as stands mature. The shift from pin cherry dominance in young stands toward mixed hardwoods more typical of mature northern hardwood forests is the most pronounced shift in species composition in these stands and has been previously described (Marks, 1974; Hughes and Fahey, 1994). The relative abundance of other species also changes through stand development. In this chronosequence, the percentages of litterfall comprised of beech and red maple increased as stands aged, whereas white birch and pin cherry litterfall decreased. Both pin cherry and white birch were generally cation-rich species, whereas beech and red maple tended to have lower cation concentrations. Likewise, other cation-

rich species, such as yellow birch and striped maple, are abundant in young stands. Therefore, dynamics in species composition could lead to significant alterations in litterfall chemistry through stand development. Changes in the relative abundance, as opposed to the mass, of species are important to litterfall nutrient concentrations because they elicit changes in the species-weighted litterfall nutrient concentrations. Changes in litterfall mass that may occur during a productive year, on the other hand, would not necessarily lead to differences in nutrient concentrations, if species proportions do not change.

Stand age is not the only driver of species composition. Land-use history can strongly impact species composition (Goodale and Aber, 2001; Lorimer, 2001). Likewise, other factors, such as soil fertility or historical disturbances, are also influential. Two stands in this study, each ~129 years old and located tens of meters from each other on similar landscape positions, were dominated by different species; red maple in one and sugar maple with ash in the other. These stands vary in their species-weighted litterfall Ca and K concentrations, but have very similar litterfall Mg concentrations.

Because changes in species composition often occur with stand age, I analyzed the influence of species composition on litterfall nutrient concentrations separately from the influence of stand age. Species composition was strongly correlated with litterfall Ca concentration, as well as litterfall Ca content. Both the concentration and content of Ca in litterfall were predicted by the proportions of beech, pin cherry, sugar maple, and white birch litterfall. The proportions of three of these species, beech, pin cherry, and white birch, were linearly related to stand age, suggesting that the influence of these species on litterfall chemistry is synonymous with the effects of stand age. Indeed, the abundance of at least some of these species, particularly pin cherry, is inextricably tied to stand age (Marks, 1974; Hughes and Fahey, 1994). The increase in the proportion of beech litterfall with increasing stand age was somewhat surprising given that mature beech trees are more susceptible to beech bark disease (Rhoads et al. 2002), however small overstory gaps, even those created by a dead beech tree, often yield a patch of dense beech regeneration in the understory (Hane, 2003), which may explain why beech litterfall increases with stand age even in the face of ongoing infection by the beech scale insect. The proportion of sugar maple litterfall was not linearly related to stand age, but

varied considerably among stands from nearly complete absence to near dominance. Sugar maple's wide range of relative abundance, and/or its plasticity in response to Ca availability (Dijkstra and Smits, 2002; Bailey et al. 2004, Juice et al. 2006) may be why this species was important to litterfall Ca concentration and content.

Interestingly, species composition was less important to the concentrations and contents of K and Mg than of Ca. Neither litterfall K concentration nor content was significantly related to species composition. Litterfall Mg concentrations, on the other hand, were significantly correlated with the proportion of aspen, but not of other species. Although this was significant, it only explained a moderate proportion of the variation in litterfall Mg concentration. Aspen litterfall had low base cation concentrations. In a related study (chapter 2), aspen woody debris was also found to have very low Mg concentrations. This species may have a low demand for Mg, potentially giving it an advantage in cation-poor sites. Further investigation into the role of aspen in Mg cycling is merited.

Litterfall chemistry has been shown to be strongly tied to nutrient availability in the soil (Dijkstra, 2003), and in the glaciated soils of the White Mountains the distribution of nutrients in different pools within each soil horizon and across the landscape is likely unpredictable without direct measures (Watmough et al. 2005). I found that Ca, K, and Mg concentrations in litterfall were significantly related to soil nutrient concentrations. Litterfall Ca concentration was linearly related to the concentration of exchangeable Ca in the C horizon soil, while litterfall Ca content was linearly related to the concentration of easily-weatherable Ca in the B horizon soil. This supported our hypothesis that available nutrient concentrations (the sum of exchangeable and easily-weatherable nutrients) in deeper soil horizons were important to litterfall Ca concentrations. Likewise, it corroborates other work that points to the importance of available Ca in deep soil horizons to foliar chemistry (Finzi et al. 1998; Dijkstra, 2003).

Nutrient concentrations in deep soil horizons were also linearly correlated with the concentrations of K and Mg in litterfall. Litterfall K concentration was modeled by the concentrations of easily-weatherable K in B and C horizons, which points to mineral weathering as a source of K for trees. Litterfall Mg concentrations were linearly associated with the exchangeable Mg concentrations in B and C horizon soil as well as

the easily-weatherable concentrations of Mg in C horizon and upper mineral soils. Nutrients in deep soil horizons were important to litterfall Mg content, as well. Exchangeable Mg concentrations in B and C horizon soils explained much of the variation in litterfall Mg contents through a complex relationship mainly based on B and C horizons, again pointing to the importance of nutrient concentrations in deeper soil horizons.

Available base cation pools in deep soil horizons were also shown to be important in European beech forests (Fitcher et al. 1998). They identified Mg deficiencies in trees growing on soils with low Mg contents in deep soil horizons. Nutrients in deep soil horizons are likely important, because even in young stands, roots successfully grow into the C horizon (Yanai et al. 2006). Deep soil horizons have low root abundance and low available base cation concentrations. Tightly-bound K and Mg concentrations in deep horizons, however, tended to be relatively high.

Cation concentrations in silicate minerals were estimated with the final leach of the soil samples (hot HNO₃ extraction) and were referred to as the tightly-bound soil nutrient concentrations. Tightly-bound soil nutrient concentrations helped to explain variation in litterfall chemistry. These models explained very large portions of the variation in litterfall K and Mg concentrations and in litterfall Ca, K, and Mg contents. The complexity of these models, limited their utility for identifying nutrient forms or soil horizons most influential to litterfall chemistry. Tightly-bound Ca concentrations did not help to explain litterfall Ca concentration. Interestingly, the inclusion of tightly-bound soil Ca improved the model of litterfall Ca contents, but did not improve the model of litterfall Ca concentration. With tightly-bound concentrations, soil Ca explained nearly three times as much variation as did the available Ca concentrations. Concentrations of tightly-bound K were helpful in explaining variation in litterfall K content, which was not significantly modeled by the available K concentrations in soil. Litterfall Mg concentrations and content were each strongly correlated with available soil Mg concentrations, so little variation remained to be explained by tightly-bound Mg.

Concentrations of tightly-bound K and Mg increased with soil depth, whereas tightly-bound Ca concentration decreased with depth. Additionally, concentrations of tightly-bound K and Mg were much higher than the exchangeable or easily-weatherable

concentrations of these nutrients in mineral soil horizons. Tightly-bound Ca concentrations were lower than easily-weatherable Ca concentrations in each soil horizon. The greater contribution of tightly-bound soil nutrients to K and Mg concentrations in litterfall is not surprising given the relative abundance of tightly-bound K and Mg, but the mechanism and rate by which they are released from the tightly-bound form has not been entirely elucidated or quantified.

Conclusion

Acid deposition and intensive timber harvests each help to reduce the availability of Ca, and potentially of other base cations, in the northern hardwood forest. Therefore, nutrient return to the forest floor in annual litterfall is an important component of base cation cycling. This study provided an opportunity to examine the influence of stand age, species composition and soil chemistry (with the inclusion of deep soil horizons) on litterfall chemistry in the northern hardwood forest. Litterfall nutrient concentrations declined with stand age, but both species composition and concentrations of available soil nutrients were more important to litterfall Ca concentration and content. The relative abundance of aspen was an important factor for litterfall Mg concentrations. Available soil nutrient concentrations were also important predictors of litterfall Mg concentration and content, while available and tightly-bound soil K concentrations were the best predictors of litterfall K concentration and content. In conclusion, species composition and soil nutrient concentrations were strong predictors of litterfall chemistry. Continued acidification of soils in the northern hardwood forest appears likely to deplete Ca resources because of the relative importance and moderate concentrations of easily-weatherable minerals. Conversely, the higher concentrations of tightly-bound K and Mg that appeared accessible to plants may help to slow the effects of acidification on these nutrients in plant tissues.

Nutrient	Pin Cherry	Beech	White Birch	Yellow Birch	Striped Maple	Red Maple	Sugar Maple	Ash	Aspen	Other	Average	
Ca	mg/g (n, sd)	11.4 (7, 4.4)	9.1 (14, 2.5)	9.7 (13, 2.6)	14.0 (14, 1.9)	14.2 (2, 2.7)	10.7 (14, 1.9)	10.3 (13, 2.5)	10.6 (4, 5.8)	9.9 (1, 0)	4.0 (14, 1.3)	9.9 (96, 3.8)
K	mg/g (n, sd)	3.6 (7, 2.0)	4.2 (14, 2.0)	5.5 (13, 1.5)	4.0 (14, 1.2)	5.0 (2, 0.1)	3.8 (14, 1.1)	4.7 (13, 1.0)	3.5 (4, 1.2)	6.4 (1, 0)	3.5 (14, 1.3)	4.2 (96, 1.4)
Mg	mg/g (n, sd)	1.9 (7, 0.8)	1.4 (14, 0.5)	1.8 (13, 0.7)	2.4 (14, 0.7)	1.8 (2, 0.0)	1.5 (14, 0.5)	1.2 (13, 0.4)	1.3 (4, 1.0)	1.0 (1, 0)	0.6 (14, 0.3)	1.5 (96, 0.8)

Table 1.1 Average base cation concentrations (mg/g) of each species of litterfall. Sample number and standard deviation are given in parentheses (n, sd).

Litterfall Response Variable	R ²	p	Intercept	Ash	Aspen	Beech	Pin Cherry	Red Maple	Sugar Maple	Striped Maple	White Birch	Yellow Birch	Other
Ca concentration	0.71	0.02	-0.17			0.20	0.24		0.16		0.11		
Ca content	0.75	0.01	-0.34			0.07	0.08		0.06		0.04		
K concentration	No significant model												
K content	No significant model												
Mg concentration	0.33	0.03	1.73		-0.07								
Mg content	No significant model												

Table 1.2 Coefficients of determination, p-values, and parameter estimates are given for 1st degree linear models in which litterfall Ca, K, and Mg concentrations and contents were modeled by the percent of annual litterfall mass comprised of each species.

Litterfall Response Variable	Soil Nutrient	R ²	p	Intercept	C Horizon		B Horizon		Upper Mineral Soil		Oa	
					Exchangeable	Easily-Weatherable	Exchangeable	Easily-Weatherable	Exchangeable	Easily-Weatherable	Exchangeable	Easily-Weatherable
Ca concentration	Ca	0.37	0.02	7.89	0.13							
Ca content	Ca	0.32	0.03	2.87				0.002				
K concentration	K	0.46	0.03	4.36		0.05		-0.07				
K content	K	No significant model										
Mg concentration	Mg	0.82	0.002	1.12	-0.04	-0.01	0.15			0.01		
Mg content	Mg	0.6	0.006	0.37	-0.01		0.04					

Table 1.3 Coefficients of determination, p-values, and parameter estimates and are given for 1st degree linear models in which Ca, K, and Mg concentrations and contents of litterfall were modeled by concentrations of the respective nutrient in exchangeable and easily-weatherable soil pools. Blank cells indicate variables that were eliminated during the stepwise process.

Litterfall Response Variable	Soil Nutrient	R ²	p	Intercept	C Horizon			B Horizon			Upper Mineral Soil			Oa			
					Exchangeable	Easily-Weatherable	Tightly Bound	Exchangeable	Easily-Weatherable	Tightly Bound	Exchangeable	Easily-Weatherable	Tightly Bound	Exchangeable	Easily-Weatherable	Tightly Bound	
Ca concentration	Ca	0.37	0.02	7.89	0.13												
Ca content	Ca	0.94	0.003	5.17	0.02		-0.09	0.02	0.008		0.004		0.01	-0.00008			
K concentration	K	0.997	0.02	-9.2	0.68	-0.08	-0.02	0.06	-0.14	0.02	-0.13	0.23	0.03			-0.02	-0.04
K content	K	0.69	0.02	0.99			-0.001			0.002		0.01				-0.004	
Mg concentration	Mg	0.99	0.001	1.46	-0.04	-0.01		0.14	0.003			0.02	0.0004		-0.01	0.01	
Mg content	Mg	0.997	0.0001	0.43		-0.002	0.0001		0.002	0.0001		0.002	0.0002		-0.002	0.003	-0.0001

Table 1.4 Coefficients of determination, p-values, and parameter estimates and are given for 1st degree linear models in which Ca, K, and Mg concentrations and contents of litterfall were modeled by concentrations of the respective nutrient in exchangeable, easily-weatherable, and tightly bound soil pools. Blank cells indicate variables that were eliminated during the stepwise process.

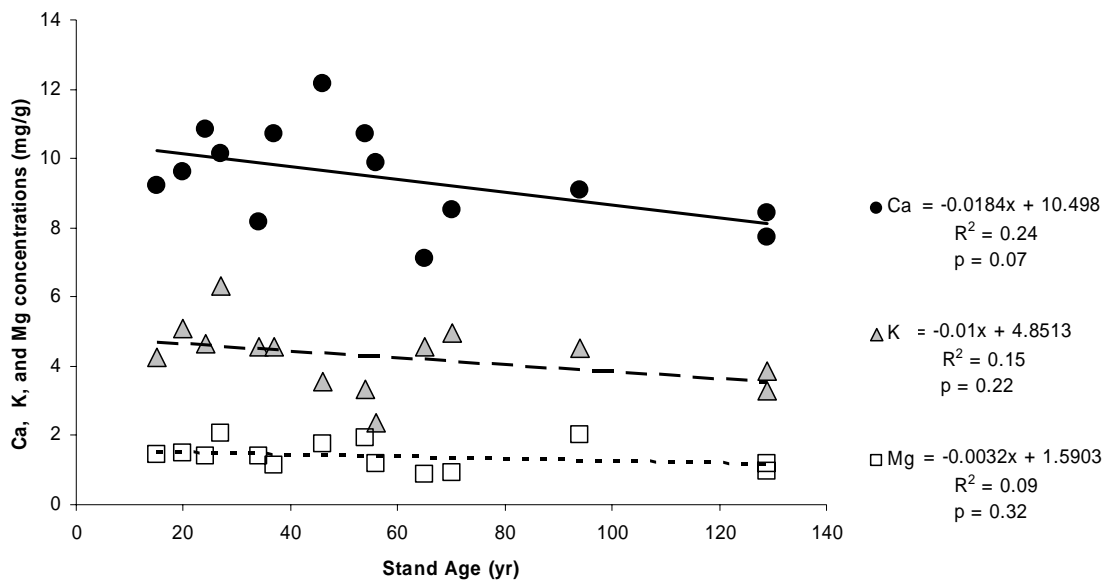


Figure 1.1 Nutrient concentrations in litterfall mass-weighted for the proportion of each species based on 2003 and 2004 litterfall data.

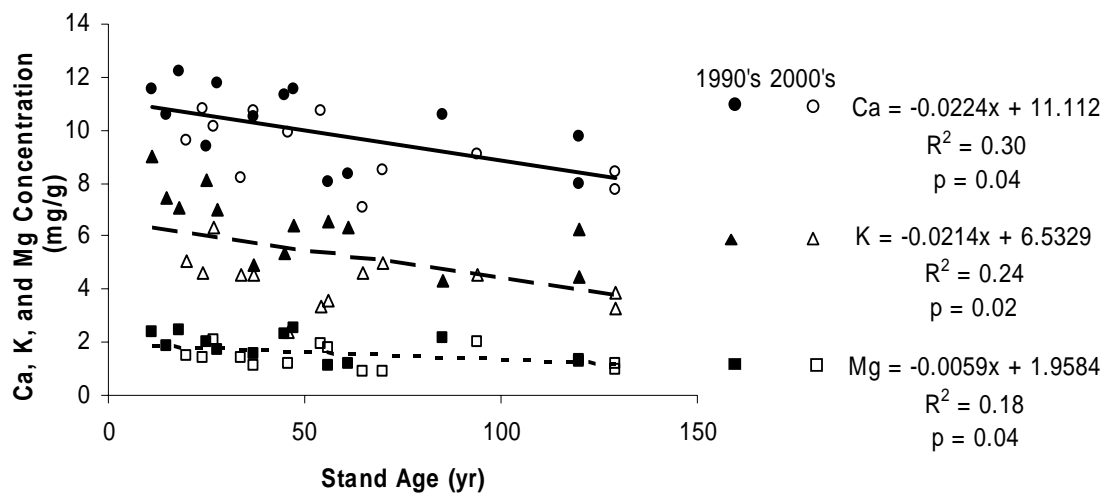


Figure 1.2 Concentrations of base cations in leaf litterfall. Dark symbols are data collected in 1993-1996 (Hamburg et al. 2003) and open symbols are from 2003-2004.

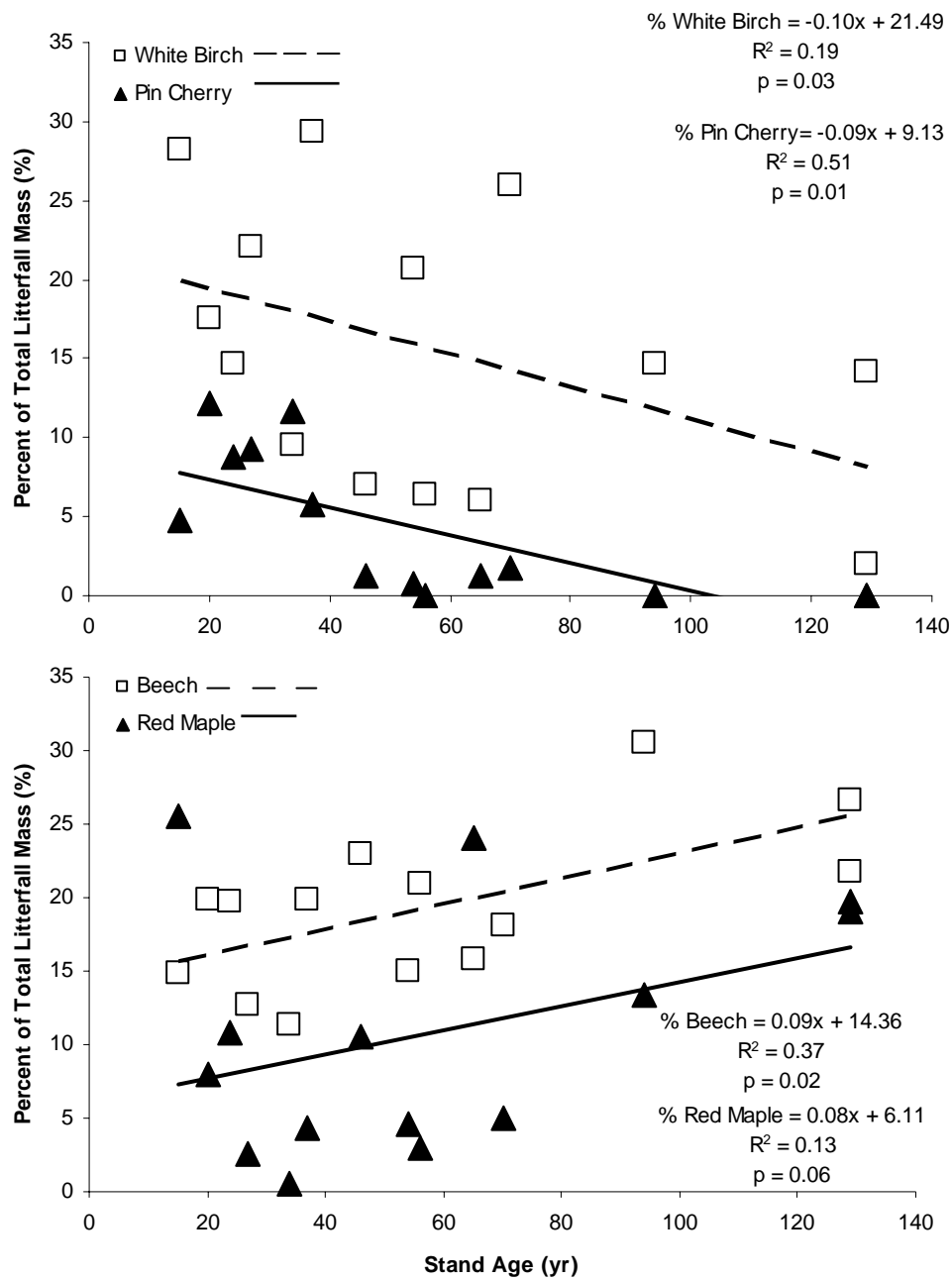


Figure 1.3 The percentage of litterfall comprised of pin cherry and white birch declined with increasing stand age (upper panel), while beech and red maple increased with stand age (lower panel).

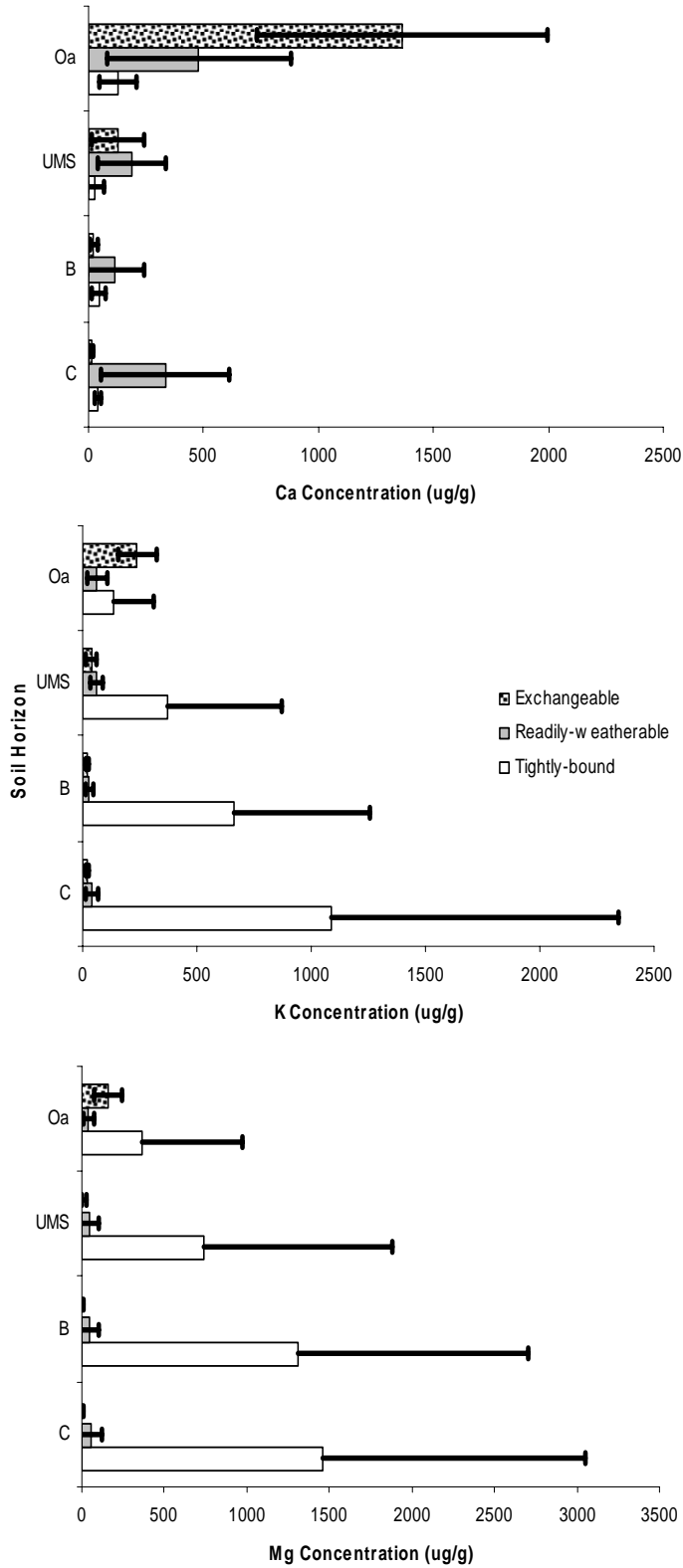


Figure 1.4 Mean (\pm sd) exchangeable, easily-weatherable, and tightly bound concentrations of Ca (upper panel), K (middle), and Mg (lower panel) in C, B, upper mineral (UMS), and Oa soil horizons. Only positive standard deviations are shown for tightly bound concentrations of K and Mg.

Chapter 2
**Base cation concentrations and contents in woody debris
across a northern hardwood forest chronosequence**

INTRODUCTION

Base cation content in northern hardwood forest floors has declined in recent decades (Federer et al. 1989). These changes in forest floor chemistry have been attributed to acid rain (Baes and McLaughlin, 1984; Johnson and Todd, 1990; Shortle and Bondietti, 1992) and intensive timber harvests (Bormann and Likens, 1979), but there also appear to be biotic influences on the biogeochemistry of base cations in developing forests. In a recent analysis of a northern hardwood forest chronosequence in New Hampshire, forest floor calcium (Ca) concentration was shown to increase in the years following a full harvest (Yanai et al. 1999). This contradicts the idea that all stands are losing base cations from the forest floor and that stands regenerating after harvests should have even greater rates of base cation loss due to rapidly growing trees accumulating nutrients.

Major sources of Ca to the forest floor come from decomposing roots, litterfall, and woody debris (Likens et al. 1998). The magnitudes of these nutrient pools and fluxes can have large spatial and temporal variations (Likens et al. 1998; Whittaker et al. 1979; Yanai et al. 1999). Notably, the quantity and quality of woody debris varies across the landscape as a function of stand development, disturbance, and interactions between these. For example, an intense ice storm in New Hampshire created larger pools of woody debris in mature stands and stands with more beech than in young stands where damage tended to be minimal (Rhoads et al. 2002).

Throughout secondary succession of managed northern hardwood forests, woody debris inputs to the forest floor are dynamic. Initially, inputs are driven by management decisions, which favor complete removal of economically valuable tree species. Over time, further woody debris inputs are likely to reflect successional changes in overstory composition. For example, in the northern hardwood forest, a pulse of pin cherry wood is contributed to the woody debris pool as this species dies out of stands 25 to 35 years old (Marks, 1974). As the size, amount, and species composition of woody debris changes, the pools of nutrients stored in wood on the forest floor also change.

The potential influence of woody debris pools on the biogeochemistry of base cations has not been adequately described in the northern hardwood forest. Woody debris may have a significant influence on forest floor chemistry if the flux of nutrients from woody debris occurs at a significant rate and the amount of nutrients in the woody debris is sufficiently large. In a recent study of the effects of woody debris on soil properties, leachate from woody debris had significantly higher concentrations of Ca, K, and Mg than did throughfall or litter leachate (Hafner et al. 2005), demonstrating that the flux rate can be high. The pool sizes of base cations in woody debris, however, have been described only in broad terms for the northern hardwood forest. Two studies that measured the content of base cations in woody debris (Lang and Forman, 1978; Arthur et al. 1993) showed, among other things, that the properties of woody debris affect the nutrient pools within woody debris. Different size classes of woody debris had different chemistry (Lang and Forman, 1978) as did different decay classes of woody debris (Arthur et al. 1993).

Analyses of the biomass and species composition of woody debris in the northern hardwood forest have shown varying magnitudes of debris between stands in different successional stages and across the landscape. Immediately following harvest, large pools of woody debris have been observed (Tritton, 1980; Gore and Patterson, 1986; Arthur et al. 1999), but in later stages of succession, the woody debris pool has been simply described as “non-slash” (Tritton, 1980). A comprehensive study of woody debris mass and nutrients across a broad range of stand ages has not been conducted in developing northern hardwood forests. We hypothesized that three distinct types of woody debris would each correspond to a particular phase of secondary succession in the northern hardwood forest and that each phase would have distinct characteristics with regard to species composition and distribution of biomass among decay classes and sizes. We further hypothesized that the nutrient content of woody debris would be primarily related to woody debris biomass with minor influences due to species and decay class. To test these hypotheses, we used a space-for-time substitution with 15 stands in a northern hardwood forest chronosequence.

The objectives of this study were to (1) describe the biomass and volume of woody debris in the context of stand development, and to (2) compare the species composition, decay classes, diameters, and Ca, K, and Mg concentrations and contents of woody debris in the different phases of stand development. Although previous research investigated the dynamics of dead

wood in developing northern hardwood forest stands, we can more precisely describe woody debris pools during stand development using a chronosequence approach with 15 stands from 15 to ~129 years since harvest. Tritton (1980) used 8 stands from 10 years since harvest to “old”; Gore and Patterson (1986) used 4 stands from 1 to 100 years since harvest plus one old-growth and one uneven-aged managed stand. The more extensive nature of this sampling scheme can help to describe woody debris in each successional stage.

METHODS

Stand Description

Woody debris was examined on a chronosequence of 15 northern hardwood stands in the White Mountain National Forest, New Hampshire (Table 2.2.1). Stands were located in Bartlett Experimental Forest (BEF; 6 stands; 44° 03' N, 71° 17' W), Hubbard Brook Experimental Forest (HBEF; 1 stand; 43° 56' N, 71° 44' W), and in the surrounding White Mountain National Forest (8 stands). These were even-aged northern hardwood stands on which previous research had been conducted (Federer, 1984; Taylor et al. 1999; Yanai et al. 1999, 2000; Arthur et al. 2001; Hamburg et al. 2003; and Yanai et al. 2003). The stands were between 320 and 630 m elevation and were harvested between ~1875 and 1990. Although changes in the methods and removal intensity of harvests have varied over this period, the chronosequence approach offers comparisons across stand ages that are otherwise unavailable to all but the longest-running investigations. The soils were moderately- to well-drained soils derived from granitic glacial till with a mor-type forest floor (Federer, 1984). Annual precipitation at HBEF is 130 cm, less than 45 cm of which falls as snow (Likens and Bormann, 1995). Basal area of young stands (<35 years) was dominated by pin cherry (*Prunus pensylvanica*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and white birch (*B. papyrifera*). Stands 35 to 65 years were dominated by American beech, sugar maple (*Acer saccharum*), yellow birch, and white birch. Older stands were composed mainly of American beech, sugar maple, and red maple (*A. rubrum*). Throughout this paper, stand ages refer to the years since the last harvest.

Stand Survey

Stand surveys conducted during summer, 2003, included measurements of tree species and diameter at breast height (dbh). In each stand, we conducted a vegetation survey using five

sets of plots along each of five 50 m transects. We measured dbh and species of trees ≥ 2.0 and < 10.0 cm dbh in twenty-five 25 m² plots and trees ≥ 10.0 cm dbh in five 500 m² plots. We used this design in every stand, except for the 16 year old stand and the 65 year old stand where stand dimensions did not allow for 50 m transects. In the latter, the transects were 30 m long and the subplots were sized to allow for the same number of plots; we measured trees ≥ 2.0 and < 10.0 cm dbh in 15 m² plots, and trees ≥ 10.0 cm dbh in 300 m² plots. Measurement plots in the 16 year old stand were from another related study in which the stands were gridded instead of using a transect-based plot design. In this stand, a nested design was used for the vegetation measurements with the same definitions of size classes. We used ten 25 m² plots for trees ≥ 2.0 and < 10.0 cm dbh and two 900 m² plots for trees ≥ 10.0 cm dbh. In all stands, dead trees ≥ 2.0 cm dbh were noted, and their species and dbh recorded.

The biomass of standing dead wood ≥ 2.0 cm dbh (snags) was calculated using species-specific allometric equations (Table 2.2; Jenkins et al. 2004). We assumed snags to be boles without crowns. Specific allometric equations for each species were selected because (1) they could be used to calculate the biomass of the bole only, and (2) the diameter ranges used to develop the allometrics closely matched those measured in the current study. When multiple equations met the first two criteria, the equation with the highest coefficient of determination and sample number was selected.

Woody Debris

We measured the volume of downed woody debris using line-intersect sampling (LIS) (Van Wagner, 1968; DeVries, 1974; Waddell, 2001). In each stand, we installed three permanent clusters of transects adapted from the protocols for woody debris sampling from the USFS Forest Inventory Analysis (PNW FIA, 2002). Each cluster had three 25 m transects radiating out from a center point. To avoid over-sampling the center of each cluster, we took no measurements on the first 5 m of each transect. Fine woody debris (FWD) was defined as having a diameter at intersection with the transect ≥ 3.0 cm and < 7.6 cm and was at least 1 m long. Coarse woody debris (CWD) had a diameter at intersection ≥ 7.6 cm and was also at least 1 m long. On the second 5 m of each transect (from 5 to 10 m along the transect), we measured FWD. From 5 m to 25 m along each transect, CWD was measured. In smaller stands, such as the 16, 46, and 65 year old stands, three clusters could not be fit into the stand, so a box of

transects with a pair of perpendicular transects crossing in the center of the stand were installed. This satisfied the need for equal lengths of transects extending in different directions to account for a non-random distribution of woody debris (Waddell, 2001). For FWD, species, decay class, length, and diameter at intersection were recorded. Coarse woody debris measurements included the same parameters, as well as the large- and small-end diameters of intersected material to minimize error in calculating woody debris volume (Waddell, 2001). All diameter measurements were taken perpendicular to the length of the wood. The relative state of decay of each log was recorded using a common, but subjective, 5-class scale in which 1 is fresh and 5 is very well decayed (Pyle and Brown, 1998). Woody debris was included in this survey if it met three criteria: it was of sufficient size where it crossed the transect, it was at least partially above the soil surface, and it was leaning at an angle $<45^\circ$ from the ground. Throughout this paper, the term “woody debris” will refer to the sum of FWD and CWD.

This study was designed to accommodate long term measurements. Cluster centers and transect endpoints were marked with flagging and fiberglass posts. All CWD measured in this survey was labeled with a numbered aluminum tag for future identification. It was assumed that FWD, which was not tagged, would decompose within the timeframe of the next sampling.

In each stand, we collected samples from the first piece of CWD of each species and decay class combination encountered along each transect. Common combinations of species and decay class were sampled multiple times from each stand. Samples were collected by cutting a disc roughly 5 to 10 cm thick with a bow saw or chainsaw. Each sample was sealed in a labeled plastic bag, and upon return to the lab was vacuum-sealed and frozen. We measured the volume of the vacuum-sealed woody debris discs by water displacement. Sealing the subsamples prevented water from infiltrating the wood and allowed the volume estimate to incorporate pore spaces and voids in the wood structure. A calibration process, in which we measured the volume of sealed and unsealed objects, revealed that regardless of the object's size or shape, the vacuum bag added 30 mL of volume to the measurement. We assumed standard temperature and pressure to convert the displaced water from mL to cm^3 and assumed that the displaced volume minus 30 cm^3 (for the bag) equaled the sample volume. The samples were removed from the vacuum bags, dried in paper bags at 60°C for 4+ days, and weighed. The volume and dry mass were used to calculate wood density (g/cm^3).

Stand-level estimates of woody debris biomass were calculated using field measurements of woody debris volume scaled by the average density of each species and decay class combination. The volume of a single piece of CWD was calculated as:

$$X_i = \frac{\left(\frac{\pi}{8}\right)(D_{Si}^2 + D_{Li}^2)(l_i)}{10,000} \quad (\text{A})$$

where X_i = the volume (m^3/ha) of the i th piece of woody debris, D_{Si} = small-end diameter (cm), D_{Li} = large-end diameter (cm), and l_i = the length (m). The term 10,000 accounts for the use of cm for diameter and m for length. Only one diameter was recorded for each piece of FWD, so the volume of a single piece of FWD was calculated as

$$X_i = \frac{\left(\frac{\pi}{4}\right)(D_i^2)(l_i)}{10,000} \quad (\text{B})$$

where X_i = the volume (m^3/ha) of the i th piece of woody debris, D_i = diameter (cm) at intersection for that piece of woody debris and l_i = the length of that piece (m). The volume of woody debris was summed as follows:

$$\text{Volume} \left(\frac{\text{m}^3}{\text{ha}} \right) = \left(\frac{\pi}{2L} \sum \frac{X_i}{l_i} \right) \times (10,000) \quad (\text{C})$$

where L = the length (m) of the transect, X_i = the volume (m^3) of each piece of woody debris, and l_i = the length (m) of each piece of woody debris. Equations A, B, and C are described in further detail by Waddell (2002). Finally, the volume (m^3/ha) and wood density (g/cm^3) were multiplied to calculate woody debris biomass (Mg/ha).

Some types of dead wood were not addressed by our research protocol. These included fine woody debris < 3.0 cm diameter and wood below the forest floor surface. Stumps would have been included in the survey had the transects crossed any.

The woody debris discs, cut from logs in the field, were also used for nutrient analysis. Wood samples and NBS apple leaves were ground, ashed at 500°C , dissolved in 6M HNO_3 , and analyzed for Ca, Mg, and K on an atomic absorption spectrophotometer. The average nutrient concentration for each species and decay class combination across all stands was used to develop stand-level estimates of nutrient pools in woody debris.

Statistics

The stands were considered the experimental units and data from all transects within a stand were added together to estimate biomass, volume, and nutrient content. Of primary interest were relationships between woody debris properties (biomass, volume, etc.) and stand ages, which were analyzed using linear regressions ($\alpha = 0.05$). For analyses of woody debris size, stands were grouped by age using woody debris species composition to define groups. Differences between groups were analyzed using ANOVA and independent t-tests. The first group was the two youngest stands, followed by the group from 20 to 37 years old that had more pin cherry woody debris, and the stands ≥ 46 years old, which had a diverse mix of species, were the third group. Statistical analyses were performed using SPSS (SPSS Inc, 2004).

RESULTS

Volume and Biomass

Although stand age did not explain a statistically significant amount of the variation in woody debris volume ($p = 0.07$) or biomass ($p = 0.12$), other important patterns emerged. Woody debris volume ranged from 6.4 to 80.9 m³/ha (Fig 2.1) with a mean (\pm sd) of 30.6 (\pm 22.5) m³/ha. Woody debris biomass ranged from 1.0 to 26.1 Mg/ha (Fig 2.1) with a mean of 8.8 (\pm 6.1) Mg/ha. The minimum volume and biomass of woody debris was in a 20 year old pin cherry stand with $> 10,000$ live stems/ha in which slash was absent and early succession mortality had not begun. From this low point, there was a positive linear association between woody debris volume and stand age in stands 20 to 46 years old ($R^2 = 0.83$, $p = 0.01$, $n = 6$). The same relationship existed between woody debris biomass and stand age ($R^2 = 0.77$, $p = 0.02$, $n = 6$). The largest pool of woody debris volume was in a \sim 129 year old stand (80.9 m³/ha), whereas the largest pool by biomass was in a 54 year old stand (26.1 Mg/ha) with a patch of relatively undecayed CWD from recent storm damage.

Density

Wood density, based on measurements from dominant species in decay classes 1 – 3, ranged from 0.23 g/cm³ to 0.54 g/cm³ (Table 2.3). Direct measures of wood density for samples in decay classes 4 and 5 were rejected because the vacuum sealer compressed these low density samples, artificially inflating the calculated density. An estimate of 0.14 g/cm³ was used for decay classes 4 and 5 based on results by Arthur et al. (1993) and Adams and Owens (2001).

This value likely approximates the density of decay class 4, but possibly overestimates the density of decay class 5 woody debris. Because the sum of the decay class 5 woody debris biomass for all stands was low (< 1.9 Mg/ha), this potential overestimation of density would not significantly change the results of this study and a better estimate is not available.

In the first three decay classes, density was influenced by species as much as it was by decay class. Sugar maple and white birch tended to be the most dense in each of these decay classes (Table 2.3).

Decay Class and Size

Across all stands, biomass was nearly normally distributed among decay classes, but within each stand, the distribution was more erratic. Decay classes 2, 3, and 4 were observed in nearly every stand (Fig 2.2), and decay class 3 accounted for $> 50\%$ of the woody debris biomass in 9 out of 15 stands. Debris in the youngest stands (aged 15 and 16) tended to be well-decayed—93% of the woody debris biomass in these stands was in decay classes ≥ 3 (Fig 2.2). Fresh or relatively undecayed woody debris was associated with stem exclusion in young stands and disturbances in older stands. In stands 24 to 54 years old ($n = 6$), 64% of the woody debris biomass was in decay classes 1 or 2, which reflects the contribution of new stems from stem exclusion in stands < 46 years old and disturbances in the 46 and 54 year old stands. In stands > 54 years old ($n = 6$), decay class 3 was the most abundant, accounting for 58% of the woody debris biomass.

Fine woody debris biomass was most abundant in the stem exclusion stands, 20 to 37 years old ($n = 5$), while the remaining stands ($n = 10$) had less FWD and larger-diameter CWD. Biomass of FWD was negatively correlated with stand age ($p = 0.01$) and stands ≤ 37 years old had significantly higher FWD biomass than did stands > 37 years old ($p = 0.05$) (Fig 2.1). The largest pools of FWD were up to 2.4 Mg/ha (Table 2.4). The mean large-end diameter of CWD in stands 20 to 37 years old (12.4 ± 4.5 cm) was significantly smaller than in younger (17.4 ± 8.9 cm, $p < 0.001$) and older stands (17.1 ± 8.9 cm, $p = 0.001$).

Species Composition

Stand age-related trends in the species composition of woody debris showed three distinct groups of stands (Fig 2.2). The youngest stands (aged 15 and 16) had a high proportion (~50%) of woody debris that was coniferous, including eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*), and a somewhat greater diversity of hardwood species compared to the second group. Woody debris in stands aged 20 to 37 years old had a lower species diversity than did either of the other groups. These stands were dominated by pin cherry woody debris (41 to 92% by mass) with the bulk of the remainder being birches. The third group, containing stands ≥ 46 years old, had woody debris of a diverse mix of hardwood species. Coniferous woody debris was over 20% of the woody debris pool in two of the three oldest stands.

Species diversity within each of the three groups described above reflects the stand that contributed to each woody debris pool. The younger and older groups of stands ($n = 10$) received woody debris typical of at least moderately mature northern hardwood stands. These stands averaged more than 7 species of woody debris per stand. The most species rich woody debris pool was in the 54 year old stand with recent storm damage; 13 species were observed. Stands 20 to 37 years old ($n = 5$) received woody debris due to mortality of early successional trees, mainly pin cherry. A mean of 4 species of woody debris were observed in these stands.

Beech bark disease (BBD) was evident in most stands, but was greatest in the oldest stands, where it appeared to be a cause of mortality. Beech woody debris was rather limited throughout the chronosequence with the exception of two of the oldest stands. In the 94 and one of the ~129 year old stands, 6.5 Mg/ha and 3.3 Mg/ha of beech woody debris were observed (Fig 2.2). Standing dead beech trees were most abundant in the 94 year old stand, which had 27.9 Mg/ha of beech snags. All other stands had an average of $1.6(\pm 2.0)$ Mg/ha of beech snags (Fig 2.3).

Although maples (red + sugar) accounted for an average of 25% of the live basal area, maples generally represented a small portion of the woody debris biomass. In most stands ($n = 12$), maples comprised 5% of the woody debris biomass (Fig 2.2). In stands 56, 65, and 70 years old, maples accounted for 50%, 65%, and 19% of the woody debris biomass, respectively. Although they were a major portion of the overstory basal area in every stand > 37 years old, maples were not a large part of the woody debris pool. Maple snags were most abundant in

stands ≥ 56 years old ($n = 6$), four of which had 5 to 20 Mg/ha of maple snags (mainly sugar maple). No maple snags were observed in stands < 20 years old, and stands 20 to 54 years old had small amounts of standing dead maples (< 0.75 Mg/ha).

Birches (yellow + white) averaged 27% of the woody debris biomass across all stands and accounted for at least 10% of the woody debris biomass in 11 stands. There appear to be no age-related trends for the abundance of white birch woody debris, which was identified in 12 out of 15 stands. Pools of yellow birch woody debris were observed in stands 24 to 34 years old, as well as sporadically throughout the rest of the chronosequence (Fig 2.2). White birch snags were dotted throughout stands ≥ 46 years old, but yellow birch snags mainly appeared during the stem exclusion phase.

Nutrient Concentration and Content

Nutrient concentrations varied both by species and by decay class. The highest Ca and K concentrations tended to be in the lower decay classes (Table 2.5). There was an inverse trend between decay class and Ca and K concentrations that was significant for K ($p = 0.02$, Fig 2.4), but not for Ca ($p = 0.10$). On average, the concentration of Ca in decay class 5 woody debris was 32% lower than in decay class 1, and the concentration of K in decay class 5 woody debris was 26% lower than in decay class 1 (Fig 2.4). The concentration of Mg in woody debris varied between decay classes differently than did the other nutrients. The highest Mg concentrations in woody debris were in decay class 3, and the lowest Mg concentrations were in decay classes 1 and 5 (Fig 2.4). Still, Mg concentrations in decay class 5 woody debris averaged more than 150% as high as in decay class 1 woody debris. Significant differences in the Mg concentration between decay classes were not observed.

The mean (\pm sd) nutrient content of woody debris was 36.8 (± 26.8) kg/ha for Ca, 21.0 (± 15.8) kg/ha for K, and 1.8 (± 1.2) kg/ha for Mg. Nutrient content of woody debris ranged from 7.5 to 111.6 kg/ha of Ca, 2.5 to 64.7 kg/ha of K, and 0.3 to 4.3 kg/ha of Mg.

The nutrient pools of Ca and K closely reflected woody debris biomass. The nutrient content of woody debris in the two youngest stands did not deviate from the overall mean for each nutrient across all stands. Small amounts of each nutrient were observed in the 20 year old stand where woody debris biomass was very low. As stands progressed through stem exclusion (20 to 37 years old, $n = 5$) linear trends of increasing Ca ($p = 0.02$), Mg ($p < 0.001$), and K ($p <$

0.001) content were steeper than the accumulation of woody debris biomass during this phase. In stands > 37 years old, both biomass and nutrient content of woody debris fluctuated around the mean under the influence of stand dynamics (e.g., storm damage, disease, mortality).

The content of Mg in woody debris was more strongly influenced by species composition and decay class than were the other nutrients. For example, a small pool of woody debris Mg was observed in the 54 year old stand that had the largest pools of woody debris biomass, and Ca and K content. Aspen, which had a low Mg concentration, was abundant in the woody debris pool in the 54 year old stand (Fig 2.5). The largest pools of woody debris Mg were in two of the oldest stands with more beech and conifers.

DISCUSSION

Volume and Biomass

Few other studies have reported the volume of woody debris in eastern deciduous forests. The average woody debris volume reported in this and six other studies ranged from 16.8 m³/ha (Goebel and Hix, 1996) to 86.0 m³/ha (Idol et al, 2001) (Fig 2.6) with a mean of 35.8 m³/ha, which corroborates the results of the current study in which a mean woody debris volume of 30.6 m³/ha was measured.

Woody debris biomass has been reported more frequently for eastern deciduous forests, including some stands in the northern hardwood forest (Fig 2.6). The average woody debris biomass reported in nine studies in eastern deciduous forests was 27.0 (± 24.0) Mg/ha. The most woody debris was in recently clearcut stands (137.2 Mg/ha (Idol et al, 2001) and 86.4 Mg/ha (Gore and Patterson, 1986)) where large pools of residual woody debris are to be expected. Every stand >10 years old had woody debris biomass < 50 Mg/ha. Seventeen stands from five studies had < 10 Mg/ha of woody debris. Of these, 12 stands were part of the current study.

Although the biomass of woody debris reported in this study tended to be lower than that reported by others in the northern hardwood forest, we believe our results to be accurate for a number of reasons. First, the volume of woody debris reported in this study is in line with other studies (Fig 2.6). We calculated volume directly from field measurements and this was the basis for calculating biomass and nutrient content. Second, reported densities of decaying hardwoods vary greatly and this can dramatically alter a study's results. The density values used in this study were moderate and fell in the middle of the ranges from most of the other studies (Fig 2.6).

Some extremely high densities for decaying hardwoods have been used elsewhere (Idol et al, 2001). Third, some studies employed different formula for calculating and summing the volume and/or biomass of woody debris (e.g., Hura and Crow, 2004). We used the standard equations published by Waddell (2001). Fourth, differences in the biomass of woody debris exist within forest types and stand histories can have a large effect (Goodburn and Lorimer, 1998; Currie and Nadelhoffer, 2002).

Different processes appeared to regulate the patterns of woody debris biomass in three groups of stands. The youngest stands (15 and 16 years old) had average sized pools of woody debris that had likely spiked after the timber harvest (year 0) (Bormann and Likens, 1979) and declined while logging residue and other debris from the previous stand decomposed. The regrowing forest did not appear to contribute to the woody debris pool for the first 20 years of stand development.

During overstory stem exclusion, the regrowing forest began contributing to the woody debris pool. In forest ecosystems where early successional species grow in dense numbers and are short-lived, like pin cherry in the northern hardwood forest, stem exclusion causes a pulse of woody debris biomass. In this chronosequence during the stem exclusion phase, the biomass of woody debris increased linearly with stand age and rose almost to the mean woody debris biomass for all stands, which was 8.8 Mg/ha. The species composition of a regrowing stand can affect the actual amount of woody debris during stem exclusion. For example, most of the aboveground biomass in a pure pin cherry stand would be expected to become woody debris by the middle of the 4th decade, whereas longer lived species in early successional stands have some percentage of survival through stem exclusion. Also, decomposition rates of different species may determine the magnitude of woody debris accumulation resulting from stem exclusion.

In older stands inputs to the woody debris pool appeared to be more stochastic. Small scale within-stand disturbances, which included single tree mortality, storm damage, pests, and diseases, added woody debris to the forest floor. In our chronosequence, most stands > 40 years old had woody debris pools that were similar to or slightly smaller than the mean for all stands. Small disturbances in the remaining stands were reflected in the woody debris pools. Disturbances apparent in this chronosequence were storm damage and disease (e.g., BBD). Each

of the three stands in which disturbances were evident had larger than average pools of woody debris.

Density

Wood density is infrequently reported in woody debris studies in eastern deciduous forests. We compared our density results to those for decaying hardwoods from seven other studies. From studies in which density was not directly reported, we inferred it when both biomass and volume were reported. Although there is a large range of reported densities of decaying wood in eastern deciduous forests, our values were within the ranges defined by most of the studies (Fig 2.7). It is important to note that techniques for measuring density of woody debris vary significantly in methods, repeatability, and precision. These methods merit further attention (Creed et al. 2004).

Differences observed in the density of the first three decay classes for each species were small. This may indicate that either little mass is lost during the initial stages of decomposition, or that the subjectivity of decay class assignment allows for occasional misidentification of decay classes.

Decay Class and Size

Patterns of the distribution of woody debris biomass through the decay classes varied in different age stands. The youngest stands (aged 15 and 16) had generally well-decayed woody debris because these stands were not receiving woody debris inputs from the regrowing stand and most of the debris on the ground had been there since the last harvest, if not longer. These pools of well-decayed woody debris developed from what were likely large pools of fresh (decay class 1 or 2) woody debris from timber harvests.

The woody debris biomass in the first three decay classes increased during the stem exclusion phase of forest development, 20 to 37 years old. Fresh woody debris is input to the forest floor during this stage as small-diameter logs, which decompose faster and therefore likely progress through the decay classes more quickly than the large-diameter logs in other phases of secondary succession. The potential for quick decomposition of these small logs is important because it likely accelerates the nutrient flux from woody debris (Likens et al. 1998), potentially

making these smaller pools in young stands at least as important to forest floor chemistry as are the larger pools in older (and the youngest) stands.

Three groups of stands were identified by the mean large-end diameters of woody debris and the abundance of FWD. The first group, which included the two youngest stands (aged 15 and 16 years), and the third group, which included stands ≥ 46 years old, had similar mean large-end diameters of CWD. Significantly smaller CWD was observed in stands 20 to 37 years old. In these stands, residual CWD, which is material from the stand that grew prior to the recent harvest and debris from the harvest, had already decomposed. This pool of woody debris was composed entirely of branches and small stems deposited on the forest floor during stem exclusion.

Nutrient Concentration and Content

Three pools of woody debris have different properties with regard to their nutrient contents. Residual woody debris pools may be large initially following harvests (Tritton, 1980; Gore and Patterson, 1986), but by the middle of the second decade of stand development, woody debris pools were moderate. The nutrient pools we observed in residual woody debris were similar to the mean nutrient content of woody debris across stands of all ages.

During stem exclusion when early succession woody debris accumulated on the forest floor, the woody debris nutrient pools also accumulated. Although nutrient pools in woody debris only built up to a moderate level during stem exclusion, pin cherry, which dominated this pool, had high concentrations of Ca, K, and Mg and potentially rapid decomposition rates. The rates at which nutrients move from woody debris to the forest floor during this stage of forest development could be of importance to the cycling of base cations in young forests.

The largest pools of nutrients in woody debris were in the mid succession woody debris pool found in the more mature stands (≥ 46 years old). In these stands, the higher species diversity and stochastic distribution of small-scale disturbances appeared to determine the size and composition of the woody debris pool. For example, storm damage produced a large pool of woody debris in the 54 year old stand, nearly half of which was aspen. This stand had a much smaller pool of Mg in woody debris than was found in the more mature stands with beech and hemlock in the woody debris pool. On the other hand, aspen and the other species in the woody

debris pool in the 54 year old stand had moderate to high concentrations of Ca and K, making this the largest pool of Ca and K measured in the chronosequence.

In young northern hardwood stands (< 30 years), forest floors appear to be a sink for Ca, while stands > 30 years are losing Ca from forest floors (Hamburg et al. 2003). To determine whether woody debris in young stands could influence forest floor base cation pools, I estimated the annual flux of Ca from woody debris. Woody debris ≥ 3.0 cm in young stands averaged 4.9 Mg/ha and ranged from 1.0 to 10.0 Mg/ha with 7.5 to 39.3 kg/ha of Ca. Exponential decay rates (k) were 0.096/year for dead boles (Arthur et al. 1993) and are likely higher for small-diameter woody debris. I conservatively applied $k = 0.096/\text{year}$ to all size classes of woody debris and calculated annual Ca fluxes from woody debris in young stands to average 1.9 kg/ha/yr and range from 0.7 to 4.5 kg/ha/yr. Forest floor pools of Ca in this chronosequence ranged from 200 to 640 kg/ha, thus the expected flux of Ca from woody debris in young stands is 0.1% to 2.25% of the forest floor pool. In northern hardwood stands, forest floors appear to be a sink for 34 kg/ha of Ca per year in young stands and a source of 22 kg/ha/yr in stands > 30 years old (Yanai et al. 1999). The expected flux from woody debris in young stands is 2.1% to 13.2% of the Ca accumulating in young stands.

The above estimates are conservative because they (1) do not account for any woody debris < 3.0 cm diameter, which appears to be abundant in young stands; (2) are based on exponential decay rates developed for a mix of hardwood species and larger-diameter woody debris than is seen in most of the young stands. Pin cherry wood, which dominates the woody debris pools in young stands appears to decompose faster than most other species, even faster than similarly sized pieces of other species. Pools and fluxes of very fine woody debris were measured in young northern hardwood stands where roughly 1.1 Mg/ha of woody debris ≤ 1.6 cm diameter fell per year (Hughes and Fahey, 1994). Conservatively, an additional megagram of woody debris would bump the upper estimates from above by 10%. Realistically, decay rates of these very fine pieces of woody debris are likely much faster than the value of $k = 0.096/\text{year}$ used above.

Although decomposition of woody debris does not appear to be solely responsible for the unexpected gains in forest floor Ca observed in young stands, woody debris seems likely to account for a significant portion of that flux. Further investigations into the pools of very fine woody debris (< 3.0 cm diameter) and the nutrient fluxes associated with the decomposition of

this material may clarify the influence of woody debris on Ca cycling in young northern hardwood forest stands.

CONCLUSION

We observed three kinds of woody debris in 15 northern hardwood stands from 15 to ~129 years old: residual, early-succession, and mid-succession woody debris. Residual woody debris, characteristic of the youngest stands had high proportions of decay-resistant and economically undesirable species such as hemlock and fir. Residual woody debris tended to be well-decayed because ≥ 15 years had elapsed since the time of harvest and residual woody debris had been on the ground at least that long.

Small-diameter pin cherry and birch logs dominated the early-succession woody debris, characteristic of stands roughly 20 to 40 years old. This coincided with natural thinning of the regenerating stand as live tree densities dropped from $\sim 12,000$ trees/ha at age 20 to $< 4,000$ trees/ha by age 46. Pin cherry wood, which had particularly high nutrient concentrations, accumulated on the forest floor during the stem exclusion phase, but was nearly absent from stands ≥ 46 years old.

Stands ≥ 46 years old had variable amounts of woody debris that apparently reflected within-stand dynamics. Patches of storm damage produced pulses of woody debris inputs. Pests and diseases, like BBD, affect both the size and composition of woody debris in some stands (Rhoads et al. 2002). Within our chronosequence, pulses of beech woody debris were seen in two of the most mature stands, in what we called the mid-succession woody debris. This pool had a diverse species composition and the widest range of woody debris diameters.

There was a lack of large-diameter woody debris throughout the chronosequence. Woody debris with a diameter ≥ 40 cm is a feature of old growth northern hardwood forests (Hura and Crow, 2004) and uneven aged managed northern hardwood forests (Spears et al. 2003). In our chronosequence, 20 pieces of woody debris > 30 cm diameter were observed; very few were > 40 cm. Of these, 16 pieces were in stands ≥ 46 years old. The other four pieces were in stands ≤ 20 years old; there was no large CWD in the stem exclusion stands. The largest live trees measured were > 60 cm dbh and were found in each stand > 70 years old. Eventually, these large stems will become part of the woody debris pool and their presence will define a late-successional woody debris pool. Based on our chronosequence, it appears that late-successional

woody debris is not produced in the first 130 years of stand development in even-aged northern hardwood stands.

Tritton (1980) distinguished between the characteristics of two pools of woody debris in the northern hardwood forest: slash and non-slash. This study builds on her work by further describing the non-slash as a pool of early-succession woody debris followed by mid-succession woody debris. Further, I proposed that each of three pools of woody debris seen during the first 130 years of stand development of northern hardwood forests have unique characteristics. I also found that pools of base cations in woody debris are small relative to the forest floor pools. We hypothesize that the decomposition of woody debris in young stands may significantly contribute to the accumulation of base cations in young stands that is not seen in older stands. Additional investigations into the nutrient pools, input rates, and turnover times of all size classes of woody debris in young stands may help to clarify the patterns of base cation cycling.

Stand Age in 2004	Year of Last Harvest	Elevation (m)	Aspect	Slope (%)	Location
15	1989	330	flat to NW	6	WMNF-Saco RD
16	1988	340	NE	15-30	WMNF-Saco RD
20	1984	330	NNE	12	WMNF (BEF)
24	1979-80	540	WNW	19	WMNF-Saco RD
27	1976-77	630	SSW	28	WMNF-Saco RD
34	1970	520	SSW	21	WMNF (HBEF)
37	1967	360	NNE	18	WMNF (BEF)
46	1958	540	ESE	14	WMNF-Saco RD
54	1949-50	460	NNE	9	WMNF-Saco RD
56	1948	550	NNE	13	WMNF-Saco RD
65	1939	320	flat	2	WMNF (BEF)
70	1933-35	350	NNE	18	WMNF (BEF)
94	1910	580	SSW	26	WMNF-Saco RD
~129	~1875	320	flat	3	WMNF (BEF)
~129	~1875	320	flat	5	WMNF (BEF)

Table 2.1 Stand information. (BEF – Bartlett Experimental Forest, HBEF – Hubbard Brook Experimental Forest, SACO RD – Saco Ranger District, WMNF – White Mountain National Forest)

Species	Source
American Beech	Whittaker et al. 1974
Balsam Fir	Young et al. 1980
Eastern Hemlock	Hocker and Early, 1983
Eastern Hobhornbeam, Ironwood	Hocker and Early, 1983
Hardwoods (general)*	Sollins et al. 1973
Mountain Maple	Hocker and Early, 1983
Pin Cherry	Hocker and Early, 1983
Quaking Aspen	Ker, 1984
Red Maple	Clark et al. 1985
Red Spruce	Ker, 1984
Striped Maple	Hocker and Early, 1983
Sugar maple	Young et al. 1980
White Ash	Clark and Schroeder, 1986
White Birch	Ker, 1984
Yellow Birch	Whittaker et al. 1974

Table 2.2 Original citation for the allometric equations used to calculate the biomass of each species of snag.

Species	Decay Class		
	1	2	3
Ash		0.41 (1,)	0.26 (2, 0.03)
Aspen		0.34 (3, 0.07)	0.23 (4, 0.08)
Beech		0.32 (1,)	0.34 (10, 0.10)
Pin Cherry	0.43 (3, 0.02)	0.34 (7, 0.08)	0.32 (9, 0.08)
Red Maple	0.54 (1,)		0.36 (3, 0.08)
Sugar Maple	0.38 (3, 0.14)	0.35 (2, 0.15)	0.36 (8, 0.07)
White Birch	0.32 (1,)	0.49 (5, 0.01)	0.36 (10, 0.08)
Yellow Birch		0.31 (1,)	0.34 (9, 0.09)
Conifer	0.37 (3, 0.08)	0.32 (2, 0.01)	0.28 (9, 0.05)
Other	0.37	0.32 (3, 0.13)	0.28 (5, 0.08)

Table 2.3 Density (g/cm^3), number of samples, and standard deviation (n, sd) of each species or species group and each decay class. Empty cells indicate that the particular combination of species and decay class was not observed in the coarse woody debris pool of any stand. A density of 0.14 g/cm^3 was assumed for all species in decay classes 4 and 5.

Stand Age	CWD	FWD	% FWD
15	7.8	0.1	1
16	9.5	0.4	4
20	0.9	0.1	11
24	1.0	1.7	63
27	2.3	0.7	22
34	5.3	2.1	29
37	3.8	2.4	39
46	6.4	0.3	5
54	25.7	0.4	1
56	6.4	0.8	11
65	7.6	0.3	4
70	5.4	0.0	1
94	14.5	0.2	2
~129	6.4	0.1	2
~129	19.2	0.1	0

Table 2.4. Biomass (Mg/ha) of CWD and FWD

	Ca (mg/g)					K (mg/g)					Mg (mg/g)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
PC	6.0 (5, 5.5)	4.8 (12, 0.8)	4.8 (14, 2.0)			4.67 (5, 7.32)	3.08 (12, 3.24)	3.27 (14, 4.62)			0.25 (5, 0.08)	0.24 (12, 0.11)	0.17 (14, 0.10)		
BE		4.2 (1,)	3.6 (16, 1.8)	2.6 (4, 1.2)	4.2 (1,)		0.62 (1,)	2.71 (16, 1.34)	1.30 (4, 0.56)	1.24 (1,)		0.09 (1,)	0.36 (16, 0.21)	0.38 (4, 0.28)	0.14 (1,)
WB	4.5 (1,)	3.8 (7, 1.5)	5.0 (9, 3.1)	8.0 (4, 3.6)	4.3 (1,)	2.12 (1,)	3.82 (7, 3.75)	2.58 (9, 2.35)	2.27 (4, 2.20)	1.31 (1,)	0.00 (1,)	0.11 (7, 0.09)	0.16 (9, 0.09)	0.31 (4, 0.44)	0.11 (1,)
YB		3.7 (2, 1.3)	5.1 (14, 1.9)	4.9 (5, 3.1)	2.8 (1,)		1.76 (2, 0.69)	1.57 (14, 0.62)	1.38 (5, 0.56)	0.83 (1,)		0.19 (2, 0.10)	0.37 (14, 0.30)	0.28 (5, 0.32)	0.00 (1,)
STM		3.6 (3, 1.8)	3.9 (2, 0.1)				2.12 (3, 0.29)	1.19 (2, 0.03)				0.49 (3, 0.19)	0.26 (2, 0.03)		
RM	5.9 (2, 0.0)		3.4 (5, 0.9)	3.9 (1,)	1.3 (1,)	2.09 (2, 0.00)		2.74 (5, 2.37)	1.15 (1,)	1.61 (1,)	0.08 (2, 0.11)		0.27 (5, 0.07)	0.17 (1,)	0.20 (1,)
SM	4.2 (4, 1.0)	6.2 (2, 0.7)	3.0 (8, 1.7)	6.1 (3, 0.8)	2.0 (1,)	1.73 (4, 0.29)	1.57 (2, 1.24)	1.56 (8, 0.62)	0.70 (3, 0.03)	1.93 (1,)	0.19 (4, 0.18)	0.63 (2, 0.17)	0.19 (8, 0.06)	0.17 (3, 0.05)	0.32 (1,)
ASH		2.4 (4, 0.1)	2.9 (2, 2.0)	2.9 (2, 0.4)			1.80 (4, 0.28)	1.24 (2, 0.32)	1.74 (2, 0.06)			0.23 (4, 0.06)	0.36 (2, 0.00)	0.18 (2, 0.08)	
ASP	3.4 (1,)	5.3 (2, 0.4)	6.1 (4, 2.9)	5.1 (2, 0.1)		2.46 (1,)	2.00 (2, 0.09)	3.99 (4, 4.86)	3.53 (2, 2.67)		0.10 (1,)		0.16 (4, 0.18)	0.06 (2, 0.08)	
CONIFER	2.3 (5, 0.6)	4.8 (4, 1.4)	4.3 (10, 2.5)	3.3 (1,)		1.75 (5, 0.14)	1.38 (4, 0.29)	2.71 (10, 2.55)	1.41 (1,)		0.17 (5, 0.09)	0.17 (4, 0.09)	0.27 (10, 0.19)	0.26 (1,)	
OTHER		3.6 (1,)	3.8 (4, 0.8)	2.5 (5, 0.8)	4.4 (3, 1.4)		1.14 (1,)	1.25 (4, 0.48)	1.41 (5, 0.23)	1.28 (3, 0.53)		0.10 (1,)	0.25 (4, 0.13)	0.15 (5, 0.10)	0.35 (3, 0.12)

Table 2.5 Average nutrient concentration (mg/g) in woody debris for each decay class and species or species group. Values are averaged for all observations of a species-decay combination across all stands. Zeroes indicate values lower than our measurement threshold. Blank cells indicate that a species x decay combination was not observed during the coarse woody debris survey.

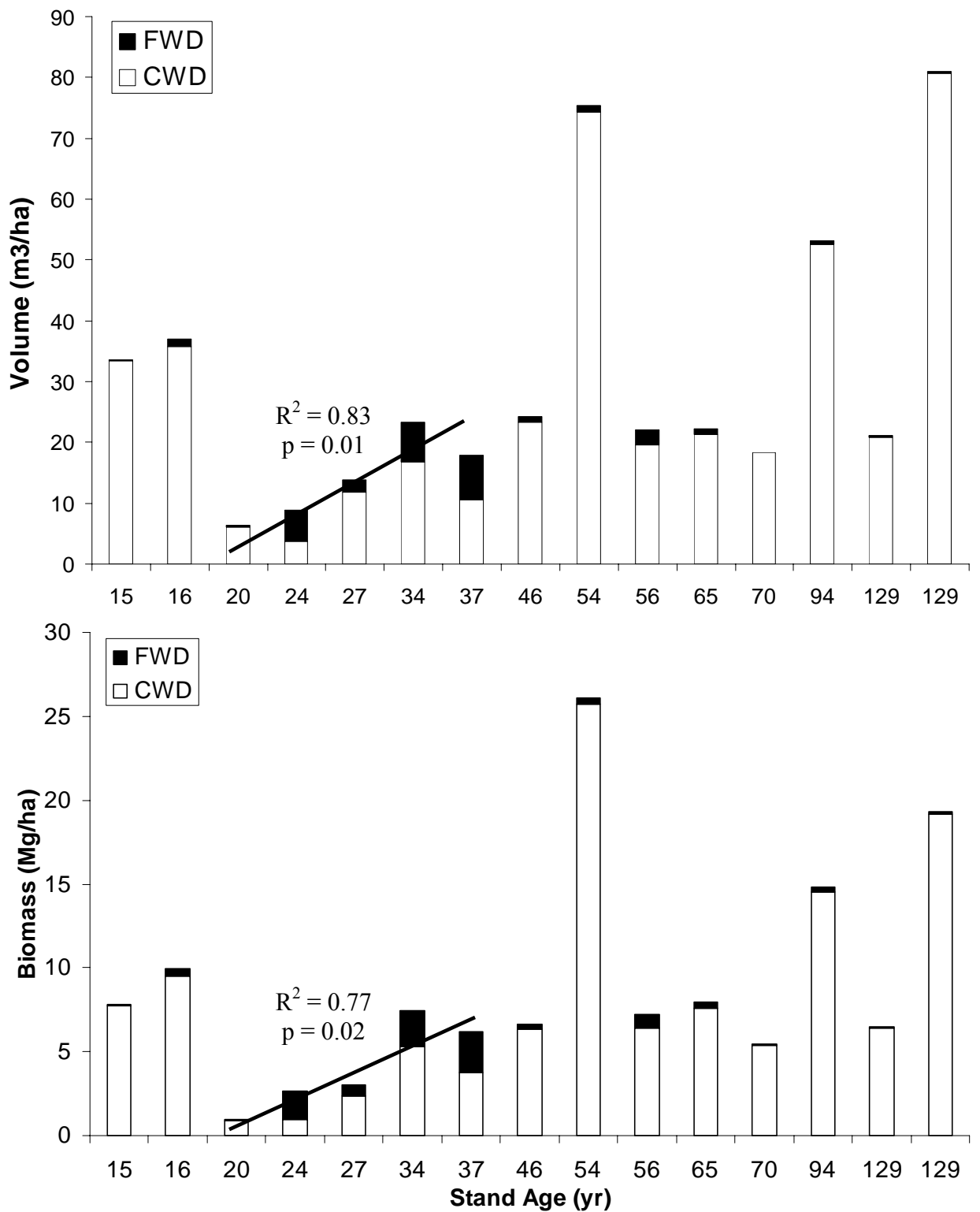


Figure 2.1 Volume (m³/ha) and biomass (Mg/ha) of fine and coarse woody debris across the chronosequence.

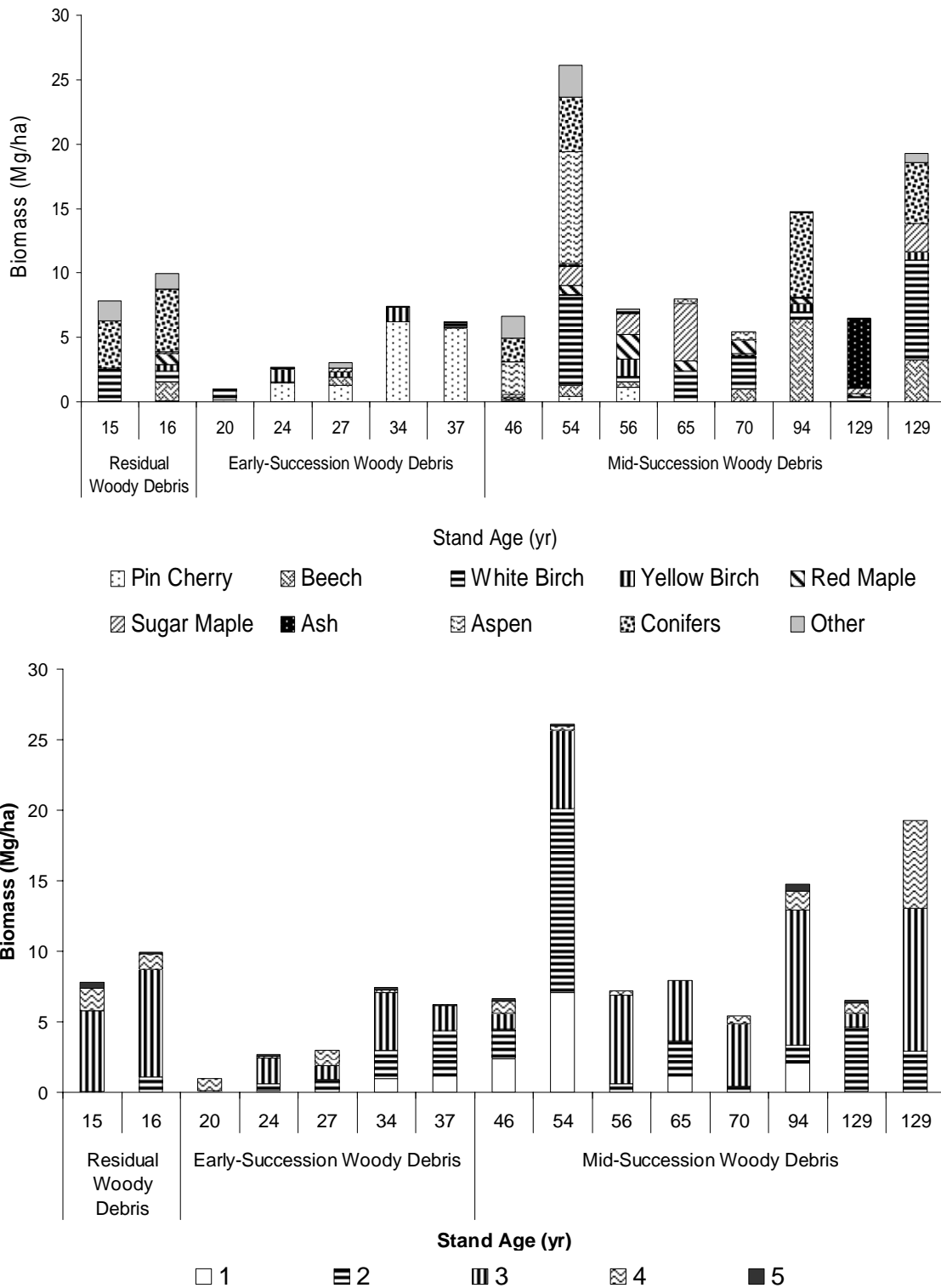


Figure 2.2 Biomass (Mg/ha) of each species (upper panel) and decay class (lower panel) of woody debris across the chronosequence. Three different pools of woody debris are identified across stand age: residual, early-succession and mid-succession woody debris.

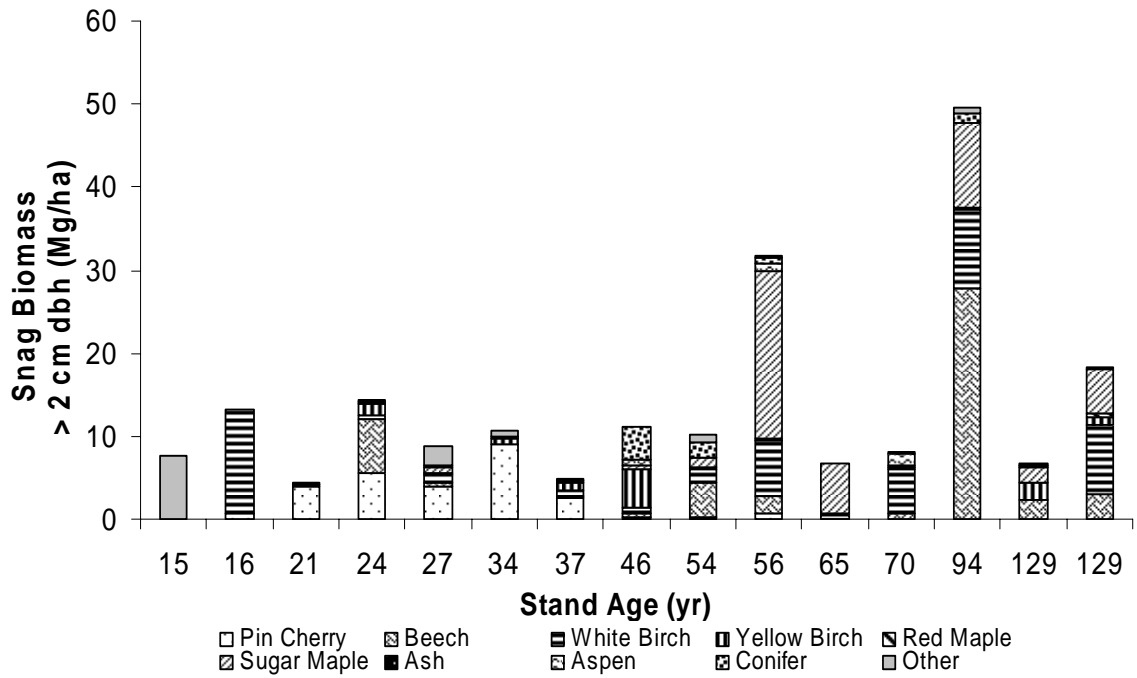


Figure 2.3 Snag biomass (Mg/ha) by species across the chronosequence

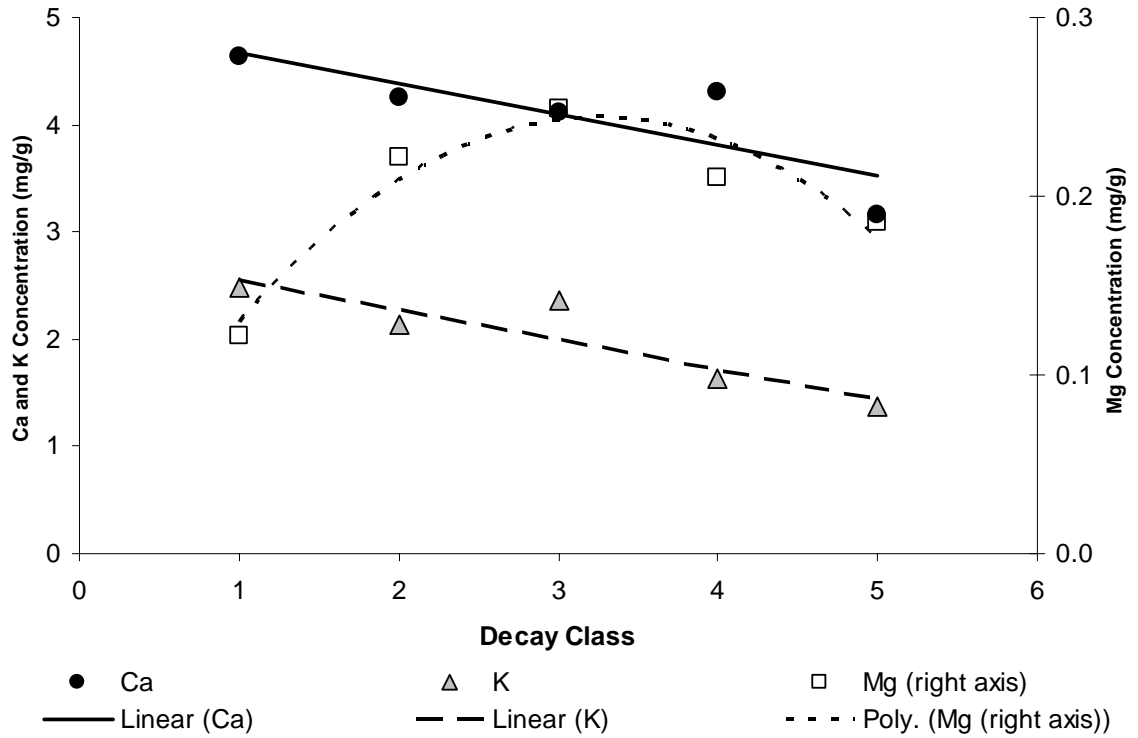


Figure 2.4. Average nutrient concentrations (mg/g) for each decay class of woody debris. The coefficient of determination for each regression is: $R^2_{Ca} = 0.68$, $R^2_K = 0.82$, $R^2_{Mg} = 0.91$.

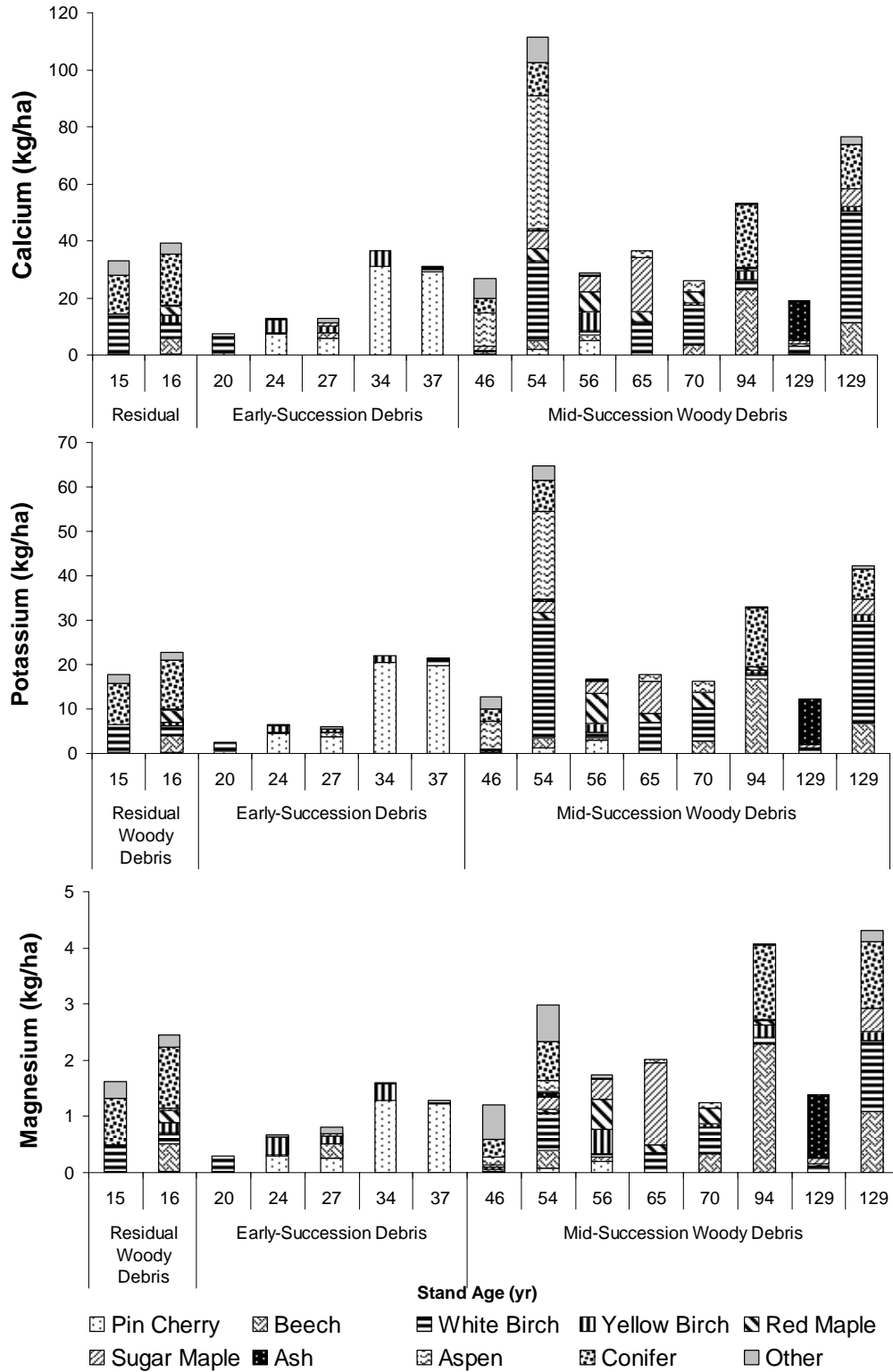


Figure 2.5 Nutrient content (kg/ha) in each species of woody debris across the chronosequence.

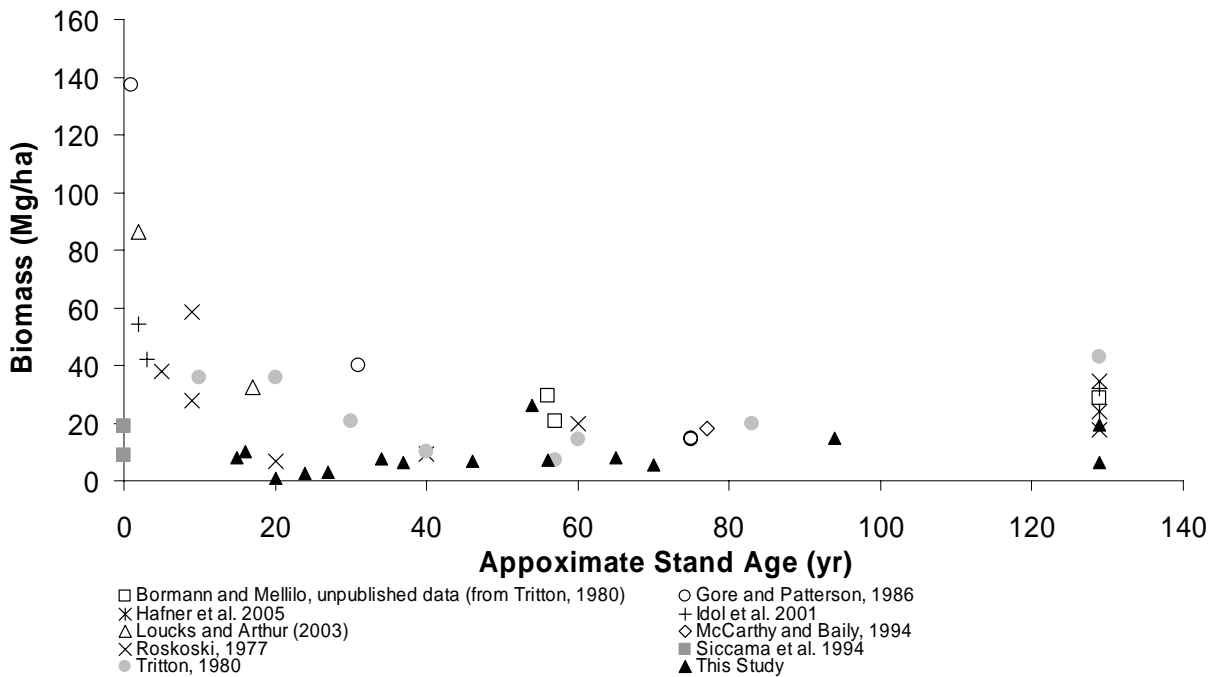
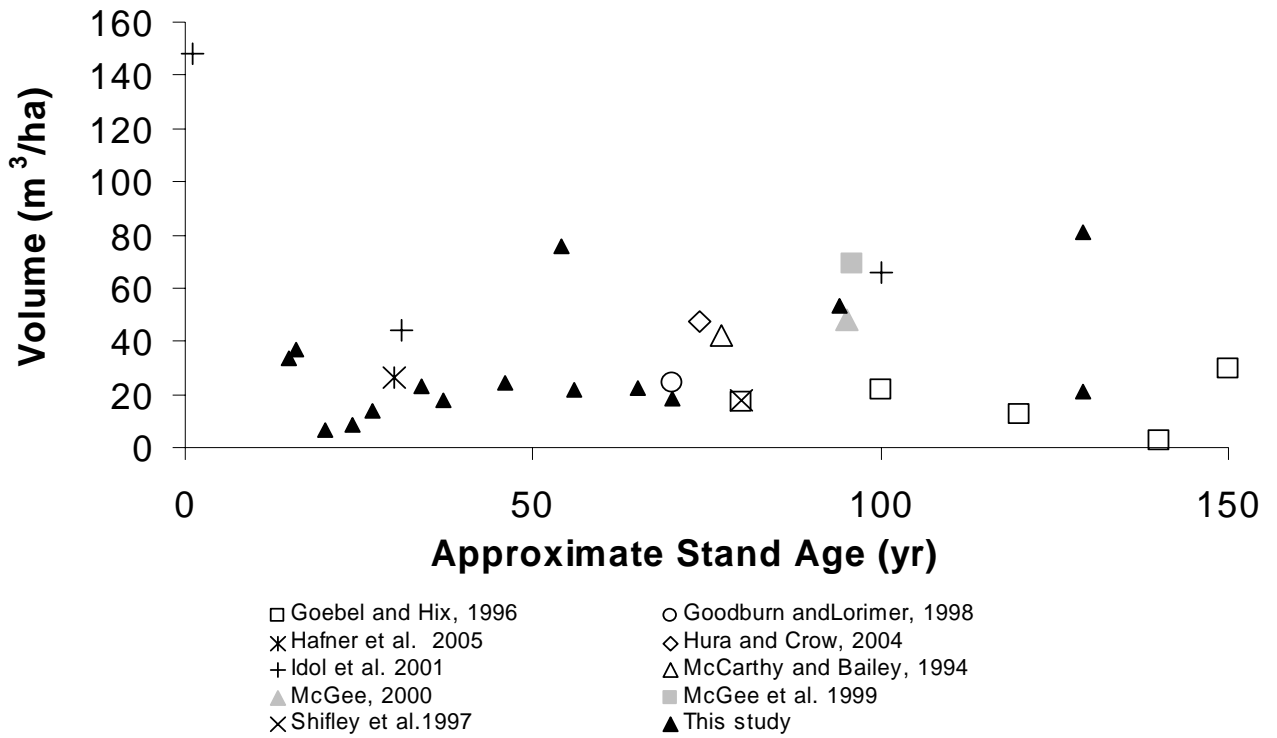


Figure 2.6 Volume (m^3/ha) and biomass (Mg/ha) of woody debris from this and other studies in eastern deciduous forests. Ages for some stands are approximate. Biomass of woody debris in all stands >129 years old were plotted at 129 years for ease of presentation.

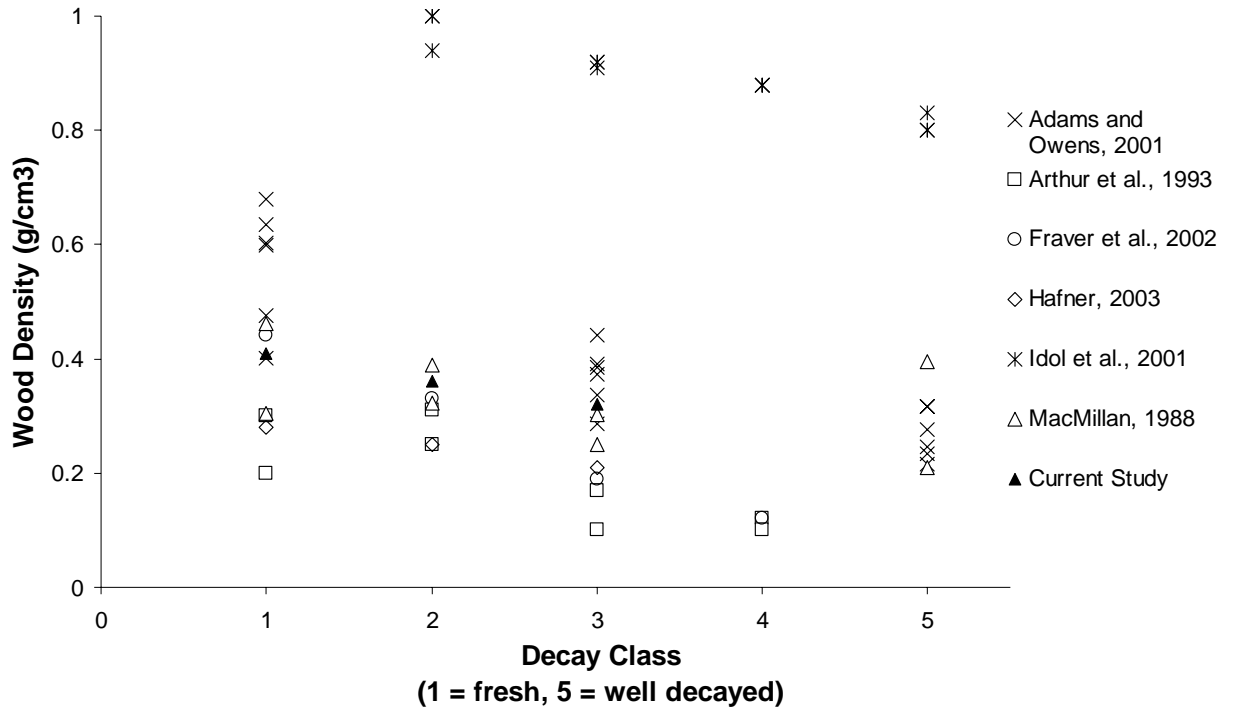


Figure 2.7 Woody debris density from this and six other studies in eastern deciduous forests. Densities of woody debris were either reported directly in the cited paper or inferred from biomass and volume of woody debris published together. The values above are densities for multiple hardwood species. When necessary the decay classes were translated from the scale used in the original article to the system used in this study.

Appendix One: Nitrogen concentration and content of woody debris

INTRODUCTION

Nitrogen was measured in woody debris of a mix of species and decay classes across a chronosequence of northern hardwood forest stands. Nitrogen dynamics in relation to woody debris is the best studied feature of woody debris in the northern hardwood forest. Past research has investigated the rates of N fixation in woody debris (Roskoski, 1977), flux rates of nitrogen leaching from woody debris (Hafner, 2003), as well as stand level nitrogen losses resulting from rapid creation of woody debris (Rhoads et al. 2002). Pools of N in woody debris and in other components of the forest have been measured at Hubbard Brook Experimental Forest (Whittaker et al. 1979; Arthur et al. 1993).

The objective of this appendix is to communicate what we learned about N in woody debris through our investigation detailed in Ch 2. For a site description and explanation of our experimental design, see Methods in Ch 2.

RESULTS & DISCUSSION

In a study investigating the pools of base cations in woody debris, we also measured the N concentration and calculated the N content of woody debris in stands 15 to ~129 years since harvest. Nitrogen concentrations varied both by species and by decay class. The variance of N concentration remained relatively constant between species, but both the average N concentration and the variance of N concentration increased with advancing decay (Fig 3.1).

Species

Few significant differences in N concentration among species of woody debris were observed. Nitrogen concentrations in sugar maple were significantly lower than in yellow birch and the “other” minor species, which include eastern hophornbeam, American basswood, and striped maple in the northern hardwood forest (Table 3.1; Fig 3.1)

Decay Class

Decay class appeared to be more important in affecting N concentrations than was species. Advanced decay classes of woody debris had higher N concentrations than did

the lower classes. Decay class 1 had the lowest N concentrations. Decay classes 2 and 3 were similar to each other, but both had greater N concentrations than decay class 1 and lower N concentrations than decay classes 4 or 5 (Table 3.2).

Nitrogen content

Nitrogen content in woody debris ranged from 3.5 to 47.9 kg/ha with a mean (\pm sd) of 17.5 (\pm 12.3) kg/ha. The amount of N in woody debris was marginally positively correlated with stand age ($p = 0.07$, $R^2 = 0.23$, Fig 2). Because lower decay classes tended to have particularly low N concentrations, the presence of fresh woody debris did not strongly impact the N pools in woody debris. With roughly 1,104 kg/ha of N in the forest floor (Whittaker, 1979), the woody debris N pool is 0.3 to 4.3% as large as the pool of N in the forest floor. In stands with larger pools of well-decayed woody debris, the N pool in woody debris can up to 8% of the N in aboveground biomass (~600kg, Whittaker, 1979).

CONCLUSION

Nitrogen dynamics in woody debris are completely different from the base cations. For example, N concentrations in woody debris increase as decomposition progresses and N content of woody debris is linearly related to stand age, but this is not strongly significant. The pool of N in woody debris is very small relative to the pool of N in the forest floor, but can be a somewhat significant portion of the aboveground N stores; I estimated that woody debris could hold as much as 8% of the aboveground N by mass.

	Ash	Aspen	Beech	Conifers	Other	Pin Cherry	Red Maple	Sugar Maple	White Birch	Yellow Birch
Ash		0.59	0.60	0.23	0.12	0.44	0.32	0.92	0.34	0.19
Aspen	0.59		0.95	0.98	0.16	0.65	0.96	0.28	0.41	0.19
Beech	0.60	0.95		0.95	0.15	0.65	0.99	0.28	0.37	0.15
Conifers	0.23	0.98	0.95		0.05	0.56	0.95	0.05	0.29	0.09
Other	0.12	0.16	0.15	0.05		0.28	0.22	0.00	0.66	0.84
Pin Cherry	0.44	0.65	0.65	0.56	0.28		0.73	0.12	0.58	0.23
Red Maple	0.32	0.96	0.99	0.95	0.22	0.73		0.13	0.51	0.28
Sugar Maple	0.92	0.28	0.28	0.05	0.00	0.12	0.13		0.05	0.01
White Birch	0.34	0.41	0.37	0.29	0.66	0.58	0.51	0.05		0.55
Yellow Birch	0.19	0.19	0.15	0.09	0.84	0.23	0.28	0.01	0.55	

Table 3.1 P-values showing significant differences between the N concentrations of different species of woody debris developed using independent t-tests.

	1	2	3	4	5
1		0.01	0.02	0.00	<0.001
2	0.01		0.09	<0.001	<0.001
3	0.02	0.09		0.01	<0.001
4	0.00	<0.001	0.01		0.06
5	<0.001	<0.001	<0.001	0.06	

Table 3.2 P-values for contrasts of % N in different decay classes of woody debris developed using independent t-tests.

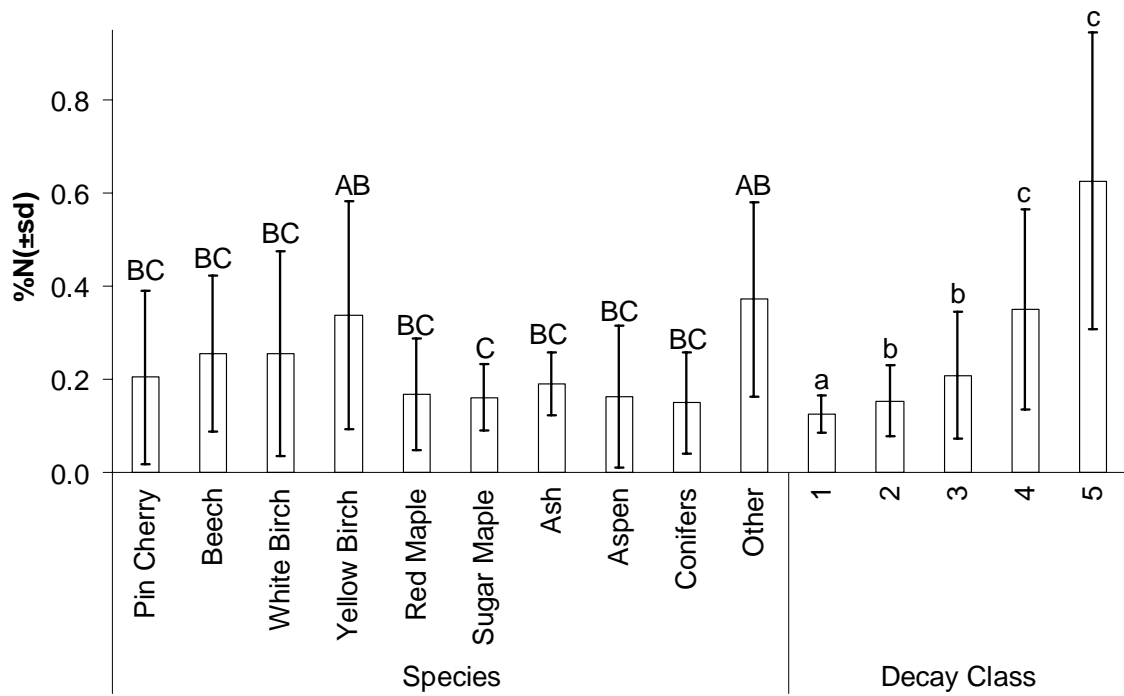


Figure 3.1 Average N concentration (%) in each species and in each decay class of woody debris. Significant differences occurred between species where there are no matching capital letters and significant differences occurred between decay classes where there are no matching lower case letters.

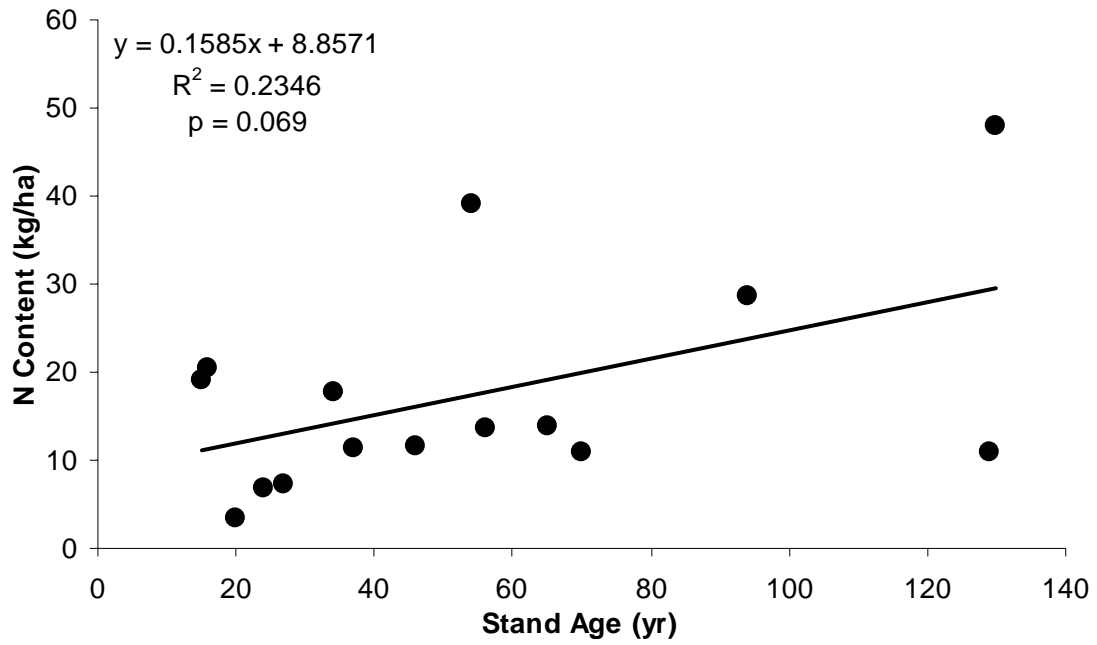


Figure 3.2 Nitrogen content (kg/ha) of woody debris across the chronosequence.

Appendix Two: Notes and reflections on a woody debris survey.

In July, August, and September of 2004, I measured woody debris along the “Federer chronosequence.” Added to the original chronosequence was CC2 (Taylor et al. 1999), the lowest elevation clearcut from the early 1990’s along Bear Notch Road in Bartlett, New Hampshire, in the Saco District of the White Mountain National Forest adjacent to the Bartlett Experimental Forest. Six of the now 14 sites in the chronosequence are within the BEF; of the remaining 8, one is in the Hubbard Brook Experimental Forest and 7 are in the surrounding White Mountain National Forest. All stands have a history of intensive timber harvest with most recent cutting dates ranging from about 1992 back to the 1870’s.

Woody debris surveys were conducted along transects modeled after the US Forest Service’s Forest Inventory Analysis protocols for woody debris (PNW FIA, 2002). The general model is clusters of transects. I placed three clusters, each with three 25m transects radiating out from a randomly selected center point. Limits on randomization were used mainly to ensure that three clusters would fit in the site. To avoid over sampling the area directly around the center of each cluster, I took no measurements on the first 5m of each transect. The measurement protocol is highlighted in Fig 4.1.

A white post and flagging mark both ends of every transect. Short fiberglass posts were used at most sites, but PVC and CPVC were used at some sites. Either way, a post was placed in the ground to mark the center point of each cluster. Another post was positioned at the end of each transect. There is a piece of black and pink striped flagging on every post and a piece of the same flagging on a nearby tree for every post. The posts were all labeled using a black marker and the following pattern:

ACKER CWD M3-2 240°

This would be the label on the post for the end of the transect that runs 240° from the center of the second cluster at M3. The center post at this same cluster would read:

ACKER CWD M3-2 Center.

The flagging on trees uses the same label scheme, but does not repeat “Acker.” The azimuth always refers to the direction from the center of the cluster to the end of the transect. In the adjusted forms (H1, T20), all posts were lettered instead of being assigned to a cluster. In such cases the azimuth refers to the direction from the lower

letter alphabetically to the next letter, so the azimuth of T20-AB is 75° and the line begins at point A.

Along the 5m to 10m section of each transect, I measured small-diameter woody debris (≥ 3.0 cm diameter at the point of intersection with the transect), which will be referred to as fine-woody debris (FWD). Along the 5m to 25m section of each transect, I measured woody debris ≥ 7.6 cm diameter (CWD) where it crossed the transect. All diameter measurements were taken perpendicular to the length of the wood rather than along the plane of the transect. For CWD, diameters at intersection and of the large-end and small-end of the wood were measured. For FWD, the diameter at intersection was recorded. Length, species, and decay classes were also recorded for all pieces, both FWD and CWD.

All dead wood of sufficient size that crossed the transect and was at least partially above the soil surface, below the canopy, and leaning at less than a 45 degree angle from the ground was counted for this survey.

Some wood pieces had become soil on the bottom, but the section above the soil surface remained intact. When I collected samples of these pieces, I limited the sample to the woody material, leaving the soil behind. Material that was soil, indistinguishable from soil, or mixed in with soil was considered forest floor, not CWD and would be better measured through a study of the forest floor.

From casual observations during the survey, these data appear to be very good representations of the abundance of CWD. This survey did not aim to describe the very fine woody debris, or wood integrated into the forest floor. Each of these features are likely to play roles in the nutrient status of a forest in ways similar to the woody debris that I measured. They are deserving of their own studies as well as being included in broadened definitions of woody detritus.

Below are site-specific notes about how the survey was conducted:

At H1, the 65 year old stand, the 30m vegetation transects and the small area of the stand precluded the use of the transect clusters. At this site a box arrangement with an X in the middle was used with 25m transects as depicted in Fig 4.2.

Just like the transects arranged in clusters, these transects include measurement buffers at the first 5m, where no woody debris is measured. This prevents over sampling

where transects converge with the exception of the intersection of EF and HI. Point A was placed between the orange posts that mark the ends of L1 and L2 from the vegetation measurements. Measurements of CWD were taken along 80m of transect and FWD was measured along 30m of transect. Spatial limitations within this stand prevented additional transects. The transect began at point A, heading toward B, so the first 5m from A to B was skipped. Likewise, the 5m buffer zone was always placed at the end corresponding to the earliest letter of the transect. Tag numbers ranged from 62 to 73.

H2 has a standard arrangement of the standard clusters. Tag numbers at H2 range from 1 to 12.

H3 contains a standard arrangement of transect clusters. Data for H3-1 appears to be missing. Also missing is data for H3-2 300°. When it turns up, I'll add it in. Until data turns up or is added back in, the data for H3 represents only 100m of CWD and 25m of FWD. Tag numbers for H3-2 and H3-3 range from 13 to 26.

At H4 an adjusted cluster system was used to avoid letting one leg of H4-3 wander out of the stand into a road and a recently cut stand. Cluster H4-3 has one leg turned 180° from an expected direction. Tag numbers at H4 ranged from 28 to 40.

Exact cluster centers at H5 were not noted and should be relocated this season. The standard cluster arrangement was used at H5. Tag numbers at H5 ranged from 42 to 60.

At H6 a standard cluster arrangement was used. H6 has a lot of woody debris with a diameter ~1cm. This is fine woody debris that our survey was not designed to detect, but it is worth a mention. Only tag number 27 was used at H6 on H6-2 210°.

At CC2, the same arrangement as at H1 was used (the box with an X in the middle). Again, the box was used to accommodate a small stand. At this site, the point A was as close to the flags marking L1 as possible. The L1 post was not relocated even though it was installed earlier this summer. The vegetation transects are spread out from each other more than I thought, so the woody debris transects cover the area from L1 past L3, maybe L4. Nonetheless, the survey is certainly representative of the stand. Tag numbers ranged from 75 to 84.

M3 has an arrangement of the standard clusters. The lowest tag numbers are at M3-3 180°, and the highest numbered tags are at M3-1 240°. These clusters are all

standard length of 25m total, with 5m buffer zones, and 5m of FWD overlapping 20m of CWD. The only nonstandard feature here is that the litterfall baskets for L4 and L5 were not placed correctly. They extend north from the northern end of the transects, so the woody debris cluster M3-3, on L5, is on the vegetation transect, not near the litter baskets. Tag numbers 194 to 220 were used at M3.

M4 has a standard arrangement. Tag numbers at M4 range from 101 to 139.

M5 has a standard cluster arrangement. Tag numbers at M5 ranged from 401 to 412. This site was measured at the same time as M3, so I took a separate set of tags up to M5, which is why there is a jump over the 300's.

M6 has a standard cluster arrangement. There was very little CWD present and it seemed like the results from the 5m sections of FWD were not accurately describing the level of FWD present on the site, so all FWD sections were extended from 5m to 15m at M6. Total transect lengths were normal, but the extended FWD transects summed to 135m. The CWD transects still totaled 180m. Tag numbers at M6 ranged from 162 to 165. Samples were also collected for some FWD and were given 4-digit sample identification numbers during the nutrient analysis beginning at 4001. This was chosen as the starting number to use the 4000's to indicate samples for which there are no corresponding tag #'s and were collected in 2004.

T20 was the only other stand where the woody debris transects were laid out in a modified box with an X (Fig 4.3). This was done to accommodate the skid road in the middle of the site. The site is typically entered along the skid road shown in the diagram. Walking in along this road, points E and F can be found immediately...that is, these are near the "entrance" to the site. During the measurements, we realized that the box was only sufficient for small sites where space was limited. Because space was not a limiting factor at T20, I added two 25m transects to the side of the box as depicted in Fig 3. Tag numbers at T20 ranged from 85 to 100. Tag numbers 98 and 99 were temporarily misplaced and were not used at all during the woody debris survey. The total length of transects at T20 was 158m.

T30 has a standard cluster arrangement. Tag numbers used at T30 range from 140 to 161.

At 101 there is a standard cluster arrangement. Tag numbers at 101 range from 166 to 193.

The total lengths of all transects are given in Table 4.1 and the azimuth and starting point for transects are given in Table 4.2

Lab Work:

After sample collection, the cookies were vacuum-sealed using a regular food-grade vacuum-sealer. This machine, which uses polyethylene bags, was used to seal the wood cookies in an air-tight space that conforms to the shape of the cookie. The volumes of the vacuum-sealed samples were measured by water displacement. Well-decomposed samples were compressed during the vacuum-sealing process so their density could not be accurately measured. This is an inherent flaw of this method. Samples were then dried, ground, ashed, extracted with 6M HNO₃ and analyzed using atomic absorption spectroscopy in the Arthur lab at UK under the guidance of Milinda Hamilton..

Data Work: Notes on modeling volume from field data

For all pieces of CWD, I recorded the shape of woody debris in terms of cone, cylinder, elliptical, or other. Width and height of elliptical pieces were averaged into a single term that was used as a diameter. The volume of all pieces, then, could be calculated as though they were cones. There were a few circumstances in which the diameter of the large-end was actually smaller than the diameter of the small end. I used large- and small-ends to represent the butt and leader of the log respectively. As decomposition occurs, there may be swelling in some parts of logs or fragmentation of other parts that can result in larger small-ends than large-ends. These are not mistakes, it's just how it goes when you try to classify things into discrete groups in the field.

Site	FWD transect length (m)	CWD transect length (m)
H1	30	80
H2	45	180
H3	45	180
H4	45	180
H5	45	180
H6	45	180
M3	45	180
M4	45	180
M5	45	180
M6	135	180
T20	45	180
T30	45	180
101	45	158
CC2	30	80

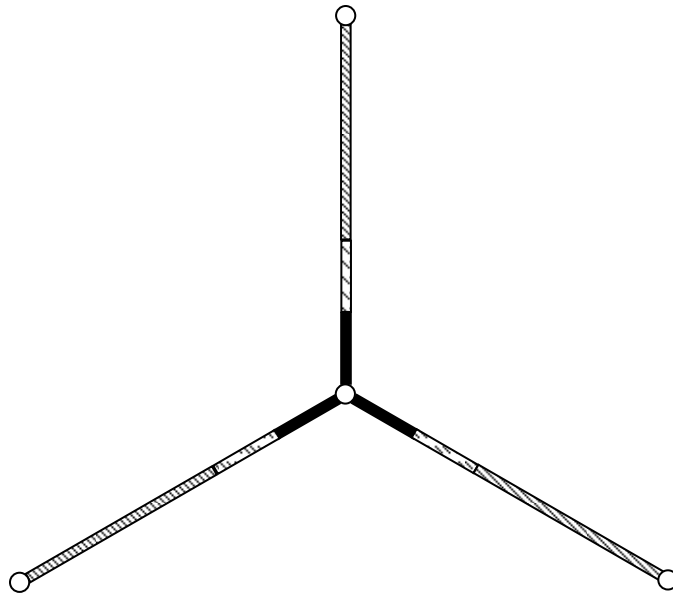
Table 4.1 Sum of CWD and FWD transect lengths at each site

Cluster ID	Cluster Center	Azimuth	Azimuth	Azimuth
CC2-AB	CC2/L1/LF1	360		
CC2-BC		270		
CC2-CD		180		
CC2-DE		45		
CC2-EF		315		
H1-AB	H1/L1/LF1	360		
H1-BC		270		
H1-CD		180		
H1-DE		90		
H1-EF		315		
H2-1	Between H2/L1 and H2/L3 at the west end of the transects	360	120	240
H2-2	Between H2/L2/LF3 and H2/L6/LF1	360	240	120
H2-3	5m N of east end of H2/L5	180	60	300
H3-3	Between H3/L5 and H3/L6	360	120	240
H3-2	5m E of H3/L4/LF2	180	60	300
H3-1	10m W of H3/L3/LF2			
H4-1	Between H4/L1 and H4/L2 about 20 m from the east end of the transects.	90	330	210
H4-2	Between H4/L3 and H4/L4 just more than ½ way down the transects from the east end.	270	30	150
H4-3	H4/L5/LF1	300	360	60
H5-1		260	20	140
H5-2		200	320	80
H5-3		260	20	140
H6-1	5m east of H4/L1	270	30	150
H6-2	Between H6/L2/LF3 and H6/L4/LF3	330	210	90
H6-3	5m SE of east end of H4/L4	270	60	150
M3-3	Middle of M3/L5	180	60	300
M3-2	M3/L3/LF3	360	120	240
M3-1	M3/L2/LF2	360	120	240
M4-1	Between M4/L1/LF2 and M4/L1/LF3	180	60	300
M4-2	15m N of M4/L3/LF2	360	120	240
M4-3	Between M4/L4/LF2 and M4/L4/LF3	60	180	300
M5-1	M5/L3/LF2	360	120	240
M5-2	M3/L4/LF2	360	120	240
M5-3	M3/L2/LF2	60	180	300
M6-2	5m SE of M6/L1/LF3	90	210	330
M6-1	M6/L2/LF2	30	150	270
M6-3	10m NW of M6/L4/LF2	30	150	270

Table 4.2 Available information for relocating woody debris clusters.

Cluster ID	Cluster Center	Azimuth	Azimuth	Azimuth
T20-AB		75		
T20-BC	Skipped 7m across road, but added 7m to total length... CWD = 20m, FWD = 5m, trans = 32m	345		
T20-CD		255		
T20-DA	Skipped 7m across road, but added 7m to total length... CWD = 20m, FWD = 5m, trans = 32m	125		
T20-DE	18m long, CWD = 18m, FWD = 5m, trans = 18m	185		
T20-AF		305		
T20-GH		125		
T20-GI		65		
T30-1	Between T30/L2/LF1 and T30/L2/LF2	360	120	240
T30-2	Between T30/L3/LF2 and T30/L3/LF3	60	180	300
T30-3	Between the two pieces of L5 at the N end.	60	180	300
101-1	101/L2/LF1	240	360	120
101-2	101/L2/LF3	240	120	360
101-3	101/L5/LF3	120	240	360

Table 4.2 continued



- Permanent PVC markers
- No measurements
- ▨ FWD & CWD measurements
- ▩ CWD measurements only

Figure 4.1 Measured properties of CWD included diameter at intersection, large-end and small-end diameter, length, species, decay class, shape, and tag #. Measured properties of FWD included diameter at intersection, length, species, decay class, shape, and tag #. Round metal tags with engraved numbers were nailed to each piece of CWD.

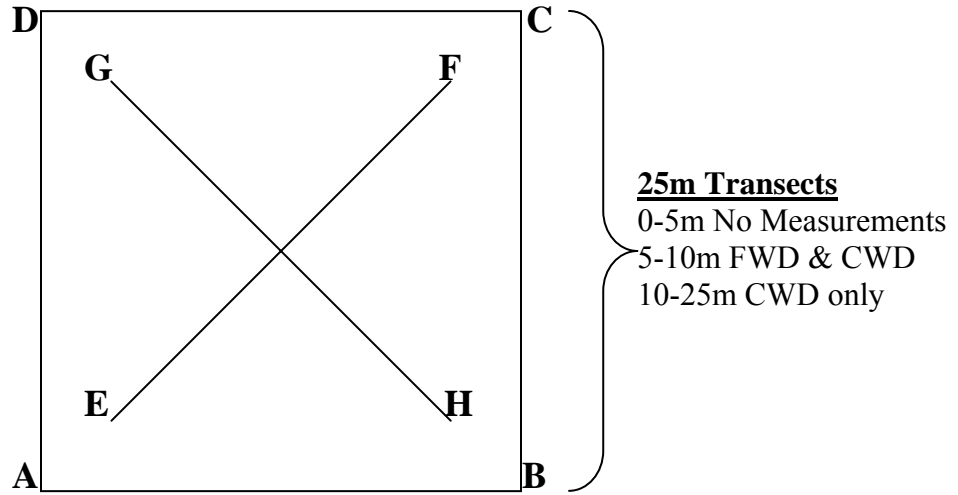


Fig 4.2 The arrangement of woody debris transects at H1, the 65 year old stand was adjusted to fit the stand.

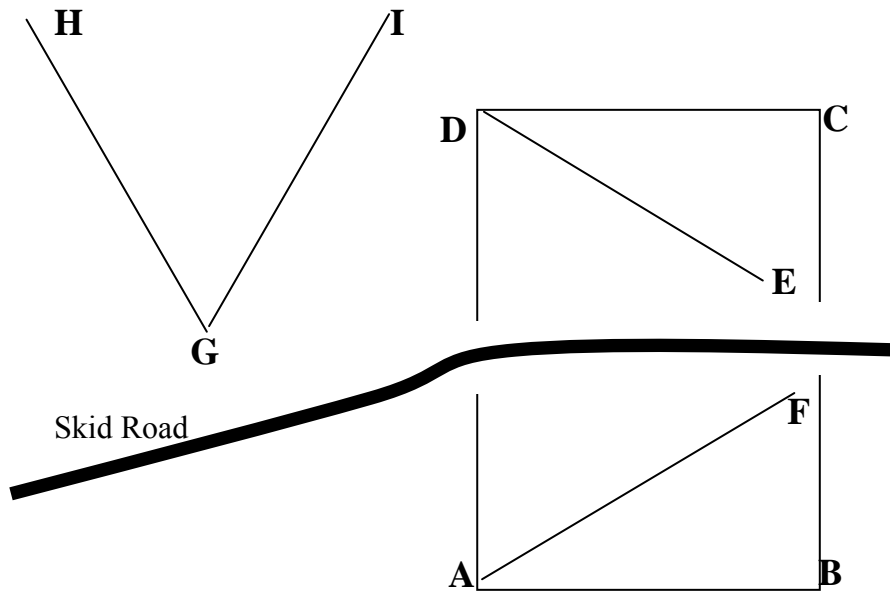


Figure 4.3 Transect arrangement around skid road at T20, the 46 year old stand.

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