SUBSTRATE LIMITATIONS TO *TSUGA CANADENSIS* AND *BETULA ALLEGHENIENSIS* SEEDLING ESTABLISHMENT

By

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ABSTRACT

SUBSTRATE LIMITATIONS TO *TSUGA CANADENSIS* AND *BETULA ALLEGHENIENSIS* SEEDLING ESTABLISHMENT

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In this dissertation, I provide evidence that the distribution of hemlock (*Tsuga canadensis*), yellow birch (*Betula allegheniensis*), and sugar maple (*Acer saccharum*) decaying wood maintains two patterns of tree distribution in Upper Michigan: the eastern hemlock-northern hardwood patch structure and the hemlock/yellow birch spatial association. Patches (3-30 ha) of hemlock with scattered yellow birch have remained hemlock-dominated and the same size for over 3000 years, even when adjacent to patches of northern hardwood forest usually dominated by sugar maple. Across both patch types, hemlock are most closely spatially associated with yellow birch, an association that makes little sense from a life history perspective, since yellow birch is a gap-phase hardwood and hemlock is a late-successional often slow-growing conifer. However, both hemlock and yellow birch seedlings are most abundant on wood and, I demonstrate here, in particular on hemlock wood. I show that hemlock wood is the most favorable substrate for hemlock and yellow birch seedling establishment (seedling density = 0.42 hemlocks /m^2, 0.60 birches /m^2), followed by yellow birch wood (0.21, 0.15), and that sugar maple wood (0.08, 0.10) and undisturbed soil (0.01, 0.01) are less suitable and support few to no hemlock and yellow birch seedlings older than three years. Sugar maple seedlings, in contrast, do not establish on any species of decaying wood (sugar maple seedling density = 0.03 to 0.09 /m^2 across wood species). Hemlock and yellow birch wood are rare everywhere, but are most abundant in hemlock patches where they cover 2.8% of the forest floor, reinforcing the hemlock-northern hardwood patch structure and the spatial association between hemlock and yellow birch.

I combine field studies of seedling demographics, wood distribution, seed rain, and decaying wood properties in three field sites in Upper Michigan, USA with greenhouse studies of seedling growth, ectomycorrhizal colonization, and nutrient content to determine why hemlock wood and to a lesser extent yellow birch wood support higher densities of hemlock and yellow birch seedlings than either sugar maple wood or soil. Hemlock logs are more favorable for hemlock and yellow birch seedling establishment for several reasons, among them lower pH, sufficient nitrogen and phosphorus supply, a tendency to decay more slowly than hardwood logs and to be attacked by brown rot rather than white rot decay fungi, and a tendency to lose bark cover and develop moss cover. A greater ability to provide ectomycorrhizal inoculum to seedlings and the relative absence of sugar maple seedlings on hemlock logs may also contribute to the higher survival rates of hemlock and birch seedlings. The full text of this dissertation is available free of charge until at least 2010 at www.lauramarx.net.

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My parents say that they knew I was going into science when I became inseparably devoted to a millipede as a toddler. Since then, and quite possibly before, they have provided incredible support and advice, as well as a first-rate college education, for which I thank them. I also thank my brother Steve, who may prefer computers to trees but helped me rebuild a cat skeleton and allowed himself to be dragged to such horrible places as Acadia National Park, Yosemite, and the Everglades on family vacations. All of the Marxes have been examples of how to live a fulfilling, kind, and honest life.

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Many researchers grow to dislike their field sites after spending so much time battling mosquitoes, heat, boredom, and outright futility in them. I still feel privileged to have spent so much time in old growth hemlock-hardwood forests, and to have learned so much about such large, old trees by studying seedlings on such a small part of the forest floor beneath them.

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CHAPTER ONE

INTRODUCTION

General introduction

Let me begin by explaining the title without forest ecology terms. This is a study of substrate limitation to eastern hemlock and yellow birch establishment, or a study of the "preference," if seedlings could choose, of hemlock and birch seedlings to grow on only certain parts of the forest floor (substrates), parts that are so rare that their scarcity limits the numbers of those seedlings that are able to survive more than one year (establishment). The substrates I am particularly interested in are pieces of decaying wood (logs, downed branches, and stumps).

Organization of the dissertation

I begin with a literature review and my own observations concerning the natural history of hemlock/northern hardwood forests in Upper Michigan. I'll cover where hemlock and yellow birch grow and why this is an interesting pattern to research. Then I will list and explain some possible explanations for the distribution of hemlock and yellow birch.

Chapter 2 can be thought of as the patterns chapter. This chapter, and chapter 3 as well, contains a draft of a manuscript that will be submitted for publication. In chapter 2, I show numerical evidence for the patterns of hemlock and yellow birch distribution described in the introduction. I also describe the distribution of decaying hemlock, birch, and sugar maple wood in my field sites.

Chapter 3 is a mechanisms chapter. I cover the various factors that I tested to see which factor(s) could explain why certain species of decaying wood support more hemlock and yellow birch seedlings than do others. These factors include: light levels, seed rain, pH, nitrogen and phosphorus content, potential for mycorrhizal inoculation of seedlings, wood moisture content, decay "pattern", and residence time of wood. Some of these factors were measured in the field, while others were examined in the greenhouse using planted hemlock and birch seedlings.

Chapter 4 is a list of detailed methods not included in other chapters, including a key to identification of decaying wood to the species level, and chapter 5 is a general conclusion.

Historical context

Forests containing eastern hemlock (*Tsuga canadensis* (L.) Carr.) covered most of Upper Michigan and northern Wisconsin until the end of the 19th century (Comer et al. 1998). Although hemlock is now much rarer, covering an estimated 0.5% of the landscape in 1980 (Eckstein 1980) and declining at least slightly since then (Woods 2000), it is still an ecological dominant in the forests in which it occurs. Hemlock is a long-lived canopy tree and has strong effects on the light availability and soil chemistry beneath the canopy (Finzi et al. 1988b, Ferrari 1999). Hemlock seedlings, however, have high mortality rates in the first year (Potzger and Friesner 1932 *in* Friesner and Potzger 1944) and grow very slowly, causing potential for problems with hemlock regeneration. This contrast between adult canopy trees that are relatively hardy and survive even when perched on boulders, steep hillsides, or stumps, and seedlings that are killed by relatively mild weather events and even by hardwood litter has brought more attention to hemlock than might be expected of a tree that has never been a particularly valuable timber species (Tubbs 1995). Frederick Clements (Clements *in* Rogers 1978), Henry David Thoreau (1854), and Aldo Leopold (1938) are among the early observers of hemlock forest natural history, while Sarah Harlow discussed the physiology and requirements of hemlock seedlings as early as 1900.

Yellow birch (*Betula alleghaniensis* Britton) is similar to hemlock in distribution and seedling requirements, but is an economically valuable timber species and less of an ecological dominant than hemlock. Much of the research concerning birch (I use "birch" rather than "yellow birch" throughout -- other birch species are mentioned only in Chapter 3) has been related to forest management, and there is abundant information about its nutritional and site requirements (Tubbs 1969, USDA Forest Service 1969, Canavera 1978, Peterson and Facelli 1992). Birch is firmly in the middle of many gradients used to group tree species (Sutherland et al. 2000) and so studies of its regeneration ecology under old-growth conditions, or its natural history in general, are slightly more difficult to find (Stearns 1951, Reif 1992, Peterson 2000, Woods 2000). Yet many researchers who explicitly studied only hemlock, as even I did in the first few months of designing this study, have included observations about birch in their introduction or discussion sections (Hough 1936, Rogers 1980, Frelich et al. 1993).

Natural history of eastern hemlock and yellow birch

In Michigan's Upper Peninsula, hemlock occurs either in hemlock-dominated stands or hemlock-hardwood (often dominated by sugar maple, *Acer saccharum* Marsh.) stands (Pastor and Broschart 1990). In old growth forests such as the Sylvania Wilderness, small patches of these two stand types often border one another, and the boundaries of each patch have changed little in the past 3,000 years (Davis et al. 1993). There are several ways in which hemlock patches could have originated in the Upper Peninsula. One way is by replacement of white pine with hemlock in those areas with suitable soil conditions for pine growth, possibly after fire (Davis et al. 1995, Davis et al.

1998). Davis (1995) also speculates that warmer, drier climatic conditions during hemlock invasion of Upper Michigan (approximately 3200 years ago) allowed hemlock to invade areas with adequate moisture, while other areas changed from oak dominance to sugar maple dominance.

One tree species is commonly found in both hemlock and sugar maple patches: yellow birch. Birch is a gap-phase generalist species, but shows a distinct association with hemlock throughout the northern Great Lakes forests, and in both hemlock and hemlock-hardwood patches (Stearns 1951, Forest Service 1965). In an analysis of the 1996 Forest Inventory Analysis data from northern Wisconsin, Kotar et al. (1999) found that hemlock and birch have the highest degree of association out of all 22 species found in these forests. The same studies (Davis et al. 1993, 1995) that show the replacement of pine pollen with hemlock pollen during the formation of hemlock patches show a corresponding increase in birch pollen, and replacement of paper birch macrofossils with yellow birch macrofossils (S. Finkelstein, University of Toronto post-doc, pers. comm. 2005).

From a shade tolerance and life history perspective, the hemlock/birch association is counterintuitive (Crow 1995). Hemlock *should* consistently shade out birch (in low light), or birch should overtop hemlock (in high light), yet the two species not only coexist but often form pairs or triplets of similar-diameter adult trees (Figure 2.6). While the association of adult hemlock and birch trees is difficult to explain, the association at the seedling stage makes more sense. Hemlock and birch are both small-seeded, require the same germination temperature, and need consistently moist substrates in order to reach the sapling stage (Houle and Payette 1990, Tubbs 1995). As many as 88% of hemlock and 74% of birch seedlings that germinate die in the first year (Potzger and

Friesner 1932 *in* Friesner and Potzger 1944, Linteau 1948). Most of these seedlings die when the substrate on which they have germinated becomes dry. Hemlock roots, and birch roots when under dense shade, grow approximately 13 mm (0.5 in) into the soil during the first full year of growth, which means that even mild droughts resulting in drying of the top layer of soil can result in seedling death (Friesner and Potzger 1944, Linteau 1948, Godman and Lancaster 1990, Tubbs 1995). Hemlock and birch seedlings, however, are often able to start growing in the same places, using germination substrates that are not utilized by most hardwood species (see Tubbs 1995 and Rogers 1980 for anecdotal evidence), possibly sharing nutrients through shared mycorrhizal networks (Booth 2004 and in progress), and coexisting on these substrates through the sapling and canopy tree stages.

Maintenance of hemlock and birch distribution

Long-term maintenance of both the hemlock patch structure and the hemlock/birch association must depend on strong feedback mechanisms (Frelich et al. 1993). Below, I introduce five of the mechanisms known to help maintain hemlock and birch distribution along with evidence to support each. I end by proposing my own hypothesis, substrate limitations to the establishment of hemlock and birch seedlings.

1. Slower nitrogen cycling under hemlock canopies (Campbell and Gower 2000)

One form of positive feedback that may maintain hemlock and mixed hardwood patches is vegetation-caused differences in soil nutrient availability and chemistry under hemlock and hardwood canopies. Under current soil moisture and climatic conditions, the only significant differences in cation availability and pH beneath each forest type appear to be directly caused by the plants currently occupying each patch of soil (Bockheim 1997). It is not the case that hemlock and hardwood stands became established on inherently chemically different patches of soil (Frelich et al. 1993, Bockheim 1997). Once hemlocks are established on a site, though, nitrogen mineralization rates tend to be lower under hemlock canopies than under sugar maple canopies, and the high lignin:N ratio in hemlock litter helps to maintain this difference (Ferrari 1999, Mladenoff 1987). In addition, hemlock wood has smaller extractable pools of inorganic N than either birch or sugar maple wood (see Chapter 3), suggesting that both hemlock litter inputs and wood inputs contribute to the slower cycling of N under hemlock canopies. Not all studies have determined that nitrogen mineralization rates are lower under hemlocks, though. The conclusion authors have come to appears to depend on whether nitrogen cycling is measured at the individual tree scale or the forest stand scale.

Mladenoff (1987) measured differences on the scale of canopy trees, comparing the forest floor under hemlock canopies, maple canopies, and gaps in each forest type. Both N mineralization and nitrification rates were higher under sugar maple canopies than under hemlocks. In gaps, results were more confusing, with N mineralization actually higher under hemlock gaps than under sugar maple gaps, and nitrification rates approximately equal. Mladenoff’s study suggests that differences in nutrient cycling must be measured on the level of individual trees, not stands, which are too variable to allow detection of differences in nutrient cycling. Finzi et al. (1998b) supported Mladenoff’s results. Their measurements of the forest floor beneath individual hemlock and sugar maple trees (along with four other species) suggested that net N mineralization and nitrification rates were lower, though not significantly so, under hemlock than under sugar maple trees. Both papers suggest that sugar maple and hemlock litter have similar amounts of nitrogen, and so it is the speed of decay of litter that results in the differences in nutrient cycling beneath each canopy. Finally, Ferrari (1999) showed a direct correlation between litterfall lignin:N ratio and N mineralization and nitrification rates in small plots in Sylvania, supporting the conclusions of Mladenoff, Finzi, and others that hemlock litter is responsible for the slower nitrogen cycling under hemlock canopies. Conifer species such as hemlock have higher nitrogen use efficiency than hardwood species such as sugar maple, and so slower rates of nitrogen cycling could give hemlock seedlings a competitive advantage over sugar maple seedlings.

2. Lower pH and soil moisture than hardwood stands (Tubbs 1995, Finzi et al. 1998b)

Climate differences under hemlock canopies as opposed to hardwood canopies include a lower soil pH, drier soil, and cooler temperatures (Finzi et al. 1998b, Stearns 1951, Tubbs 1995). Hemlocks tend to establish on very mesic soils (Godman and Lancaster 1990, Tubbs 1995), yet the soil under hemlock canopies is drier than that under nearby hardwoods. Daubenmire (1930) compared evaporation from the soil surface beneath a hemlock and a beech-maple canopy in Indiana. He found no significant differences in evaporation under the two canopies, but did find that the top layer of soil was drier under hemlock than under beech-maple because: 1) the dense hemlock canopy blocked some precipitation from reaching the forest floor, and 2) hemlocks took up all of the available moisture from the soil surface, actually bringing soil moisture conditions below the wilting point for hemlock at several points during the summer. However, Pregitzer et al. (1983) found that soil moisture varied widely under hemlock stands across a slope in Michigan. Hemlocks were found on both a relatively dry upland site, and also at the most mesic site at the bottom of the slope. The differences in topography in this study were more important than any species-caused differences in forest floor moisture. In the field sites used in this study, I have hemlock forest floor conditions that range from very wet (perched water table with almost constant standing water) to very dry (virtually no understory plants at all, hemlock litter dry to the touch).

Unlike soil moisture and perhaps rates of N cycling, pH under hemlock canopies does appear to be universally low. Rogers (1980) surveyed hemlock stands on a transect from Wisconsin to Nova Scotia, and found that the average soil pH ranged from roughly 4.0 to 4.75 across this gradient (the lowest pH was in east central Ontario, and the highest on the shore of Lake Superior). No hemlock stand surveyed had a pH of higher than 5.45, and the minimum pH found was 3.25. Likewise, Daubenmire (1930) found pH ranges from 3.6 to 4.7 in his Indiana hemlock stands. This range did not overlap at all with beech-maple stands nearby, where the soil pH ranged from 5.3 to 7. Finzi et al. (1998b) determined in a study of pH beneath individual trees that this lowered pH was due to the effects of hemlock litter. The soil beneath hemlocks was significantly more acidic than that under sugar maple, white ash, and red maple, and slightly more acidic than beech and red oak soils. Soil pHs below 7.5 cm depth, however, did not significantly differ, indicating that the pH change was not an inherent difference in soil microsites, but rather caused by the vegetation. pH of hemlock logs averages 4.5 whether logs are found beneath hemlocks or beneath sugar maples (see Chapter 3), so hemlock wood, in addition to litter, may help to maintain this low soil pH. It is important to note that all three dominant seedling species in hemlock-hardwood forests (hemlock, yellow birch, and sugar maple) can germinate at pHs as low as 3.0 (Raynal et al. 1982), so this mechanism could affect seedling survival but most likely not germination. It is unclear whether or not lowered pH negatively impacts sugar maple seedling survival more than hemlock survival.

3. Dense shade cast by hemlock (Bourdeau and Laverick 1958)

In addition to altering the soil chemistry and climate beneath them, hemlock trees form an extremely dense canopy that causes deep shade in the understory and prevents even the most shade tolerant seedlings from surviving past the first growing season (Catovsky and Bazzaz 2000). Though species such as sugar maple readily germinate on the forest floor of hemlock stands, the dense shade (year-round) and low nutrient availability result in the death of virtually all seedlings before they can reach the canopy (Rogers 1978 and Ferrari 1993 *in* Davis et al. 1993, Frelich and Graumlich 1994). When disturbance increases the amount of light beneath a hemlock stand, however, reciprocal replacement is the rule rather than the exception. In mixed stands, sugar maples and other hardwoods are generally more likely to replace fallen hemlock trees than are hemlocks (Barden 1979, Frelich and Graumlich 1994). Sugar maples take over about one third of the small and medium sized gaps that form in old-growth hemlock stands (Dahir 1994). This suggests that dense shade is a critical component of stable hemlock patches, preventing the ascension of sugar maple to the canopy.

4. Clumped hemlock and birch seed dispersal near adult trees (Houle and Payette 1990, Rooney and Waller 1998)

Hemlock and especially birch seeds travel far enough to reach most parts of any stand with adult seed-producing trees (McEuen and Curran 2004), but seeds do not travel into adjacent stands. Houle and Payette (1990) found that although seeds of birch can travel considerable distances (mainly by blowing over the snow since these seeds are winter-dispersed), distribution of seeds is clumped near adult birch trees. Rooney and Waller (1998), Catovsky and Bazzaz (2000), and McEuen and Curran (2004) did not find evidence of clumping of hemlock seeds near adults or a positive correlation between hemlock basal area and seed abundance, but do speculate that seed rain would be an important limit of seedling distribution on the scale of individual hemlock and sugar maple patches (which range in size from 3 to 30 ha, Davis et al. 1998). Also, with the characteristically low viability (less than 25% for hemlock, Godman and Lancaster 1990) and high first-year mortality of hemlock and birch (Linteau 1948, Chapter 2), small differences in seed rain as distance from parent trees increase may still affect the number of established seedlings. This would result in the majority of hemlock and birch seedlings being found near adult hemlock and birch trees.

5. Susceptibility of hemlock and yellow birch seedlings to smothering by hardwood litter (Koroleff 1954, Tubbs 1978, Frelich et al. 1993)

Smothering of hemlock seedlings by litter is commonly assumed to be another reason that hemlock seedlings do not invade sugar maple patches (and since birch seedlings are similar in size if not more fragile, this mechanism also works for birch). Koroleff (1954) suggests that leaves directly smother (block light to) seedlings, while Frelich et al. (1993) propose a combination of smothering and drought, since leaf litter dries more quickly than underlying soil. In my study, areas with thick hardwood leaf litter almost never had established hemlock or birch seedlings, but it is possible that mortality attributed to smothering or drought damage is actually due to some other property of hardwood litter, or that the mechanism is different for hemlock and for birch seedlings. For example, Peterson and Facelli (1992) have suggested that hardwood litter blocks germination cues in birch. Regardless of the mechanism, sugar maple seedlings are less affected by leaf litter, since their radicles can penetrate leaf litter to reach mineral soil beneath and even first-year seedlings are large and tall enough to avoid being covered by hardwood litter.

Substrate limitations to hemlock and birch seedling establishment

The possible mechanisms listed above help to explain why hardwood species are unable to invade hemlock stands except in gaps, but they only partly explain why hemlocks do not successfully invade hardwood stands. Hemlock is the eastern United States' most shade tolerant conifer species, and arguably our most shade tolerant tree (Curtis 1959, Dahir 1994). Hemlocks can become established in as little as 5% of full sunlight, survive in a suppressed state for decades, and respond to release (increased growth with sudden increases in light availability) until they are at least 240 years old (Tubbs 1978, 1995). Hemlock is one of, if not the, only eastern tree species able to ascend to the canopy without the help of a treefall gap (Frelich and Graumlich 1994). Why, then, haven't hemlocks shown signs of any meaningful expansion (Frelich et al. 1993) into hardwood patches? And why are birches so closely associated with hemlock but not sugar maple? I hypothesize that the seedling germination and early establishment requirements of hemlock and birch limit them to substrates that are more common in hemlock/birch stands than in hardwood stands, preventing expansion into sugar maple-dominated stands.

Many authors have documented one part of this substrate limitation: the limitation of hemlock (Nelson 1997, Rooney and Waller 1998, Tobin 2001) and to a lesser extent birch (Stearns 1951, Coffman 1978, Reif 1992) to decaying wood. Because both hemlock and birch seedlings are drought intolerant and need consistently moist substrates to establish, decaying wood is an ideal substrate, maintaining high moisture contents even under drought conditions (Boddy 1983). However, while decaying wood is more abundant under hemlock than under mixed hemlock-hardwood canopies due to slower decay rates of conifers (Campbell and Gower 2000), decaying wood is still available under sugar maple canopies. The substrates to which hemlock and birch seedlings are limited must be available in hemlock stands but rare or unavailable in sugar maple stands. The substrate limitation hypothesis, then, can be further defined as the limitation of established hemlock and birch seedlings to hemlock and/or birch decaying wood. The first step in testing this hypothesis was to measure where on the forest floor hemlock and birch seedlings are found, in Chapter 2.

CHAPTER TWO

TSUGA, *BETULA*, AND *ACER* SEEDLING DISTRIBUTIONS ACROSS FOREST FLOOR SUBSTRATES IN UPPER MICHIGAN, USA I: PATTERNS OF SEEDLING DISTRIBUTION AND SURVIVAL

Abstract: We measured the abundance, survival, and age class distribution of tree seedlings of *Tsuga canadensis* (eastern hemlock), *Betula allegheniensis* (yellow birch), and *Acer saccharum* (sugar maple) on decaying wood of the same species and on soil at four field sites in Upper Michigan, USA to determine whether species of decaying wood differ in their ability to support seedlings that depend on wood as an establishment substrate. We also wondered, if wood species differ, what are the implications for forest structure in the primary hemlock-hardwood forest of Michigan? We hypothesized that hemlock wood supports higher hemlock and birch seedling abundances and survival rates than those on maple wood and soil. Birch and hemlock seedlings were highly dependent on decaying wood for seedling establishment whereas sugar maple showed the opposite pattern. Independent of seed rain, light, and log size, hemlock logs generally supported the highest abundances of first-year and established (>1 yr old) seedlings of birch and hemlock. Averaged over three sites, densities (seedlings/m^2) of established seedlings on hemlock:birch:sugar maple wood:soil were 0.42:0.21:0.08:0.01 for hemlock seedlings, 0.60:0.15:0.10:0.01 for birch seedlings and 0.09:0.03:0.04:0.98 for maple seedlings. Long-term seedling survival was also greater on hemlock wood, such that hemlock wood supported seedlings as old as 13 years while on maple wood seedlings > 3 years old were very rare. Despite this general pattern among sites, site differences in seedling density were highly significant and may be related to variation in water availability. We conclude that hemlock wood is the preferred substrate for hemlock and birch seedlings whereas

maple wood and soil are not. We also conclude that the limitation of hemlock and birch seedlings to hemlock decaying wood combined with the distribution of hemlock wood help explain 1) the close hemlock-birch association, 2) the maintenance of distinct, temporally stable hemlock and hardwood patches, and 3) the decline of hemlock in managed forests where mature hemlock trees are removed and hemlock wood is consequently scarce.

Introduction

Numerous studies have shown the importance of decaying wood as an establishment substrate for the seedlings of some tree species (Gray and Spies 1997, Cornett et al. 2001, Lee and Sturgess 2001, McGee 2001, Mori et al. 2004, Casperson and Saprunoff 2005). The association of these species with decaying wood, which is rare under all circumstances and varies in abundance spatially and with time since disturbance or stand establishment, may be a critical mechanism structuring forests. For example, diminished tree mortality and consequently lower decaying wood inputs following selective logging (Newberry 2001, Hura and Crow 2004) can affect future canopy composition by decreasing seedling recruitment for those species that favor decaying wood for establishment (Casperson and Saprunoff 2005). Despite the recognition of the importance of decaying wood in forest dynamics, wood is usually treated as a single category or categorized by decay class (Christy and Mack 1984, Takahashi et al. 2000, Mori et al. 2004), but almost never by species (Cornett et al. 2001). If there is species-specific variation in the suitability of decaying wood as a seedling establishment substrate, what are the implications for forest dynamics?

Cornett et al. (2001) showed that in northern Minnesota *Thuja occidentalis* wood was twice as likely as *Betula papyrifera* wood to be colonized by new *Thuja* germinants, but given that only new germinant populations were reported it is unknown if these patterns translate into longer term patterns for established seedlings. In the primary hemlock-hardwood forests of Upper Michigan we observed that decaying logs of eastern hemlock (*Tsuga canadensis* (L.) Carr.) seemed to support more tree seedlings than sugar maple (*Acer saccharum* Marsh.) logs, that seedlings were predominantly yellow birch (*Betula alleghениensis* Britton) and hemlock seedlings, and that these seedlings appeared to be rare on the forest floor. Furthermore, sugar maple seedlings appeared to be rare on logs. The hemlock-northern hardwood system may be ideal for testing for species differences in suitability of decaying wood because canopy tree distribution in these forests may depend on seedling establishment substrate preferences and the distribution of substrates.

Hemlock-dominated forest intermixed with sugar maple-dominated forests covered large areas of Upper Michigan and northern Wisconsin, USA until the late 1800s. These forests have declined markedly in area since harvesting began in the late 1800s. In Upper Michigan, more than 99% of mature hemlock-hardwood forest has been converted to other cover types (Noss and Peters 1995), and by 1993 hemlock occupied only 0.5% of the landscape (Mladenoff and Stearns 1993). Yellow birch, which is strongly spatially associated with hemlock (Frelich et al. 1993, Kotar et al. 1999), is also in decline (Woods 2000, Schwartz et al. 2005). The strong hemlock-birch association is puzzling, as hemlock is among the most shade tolerant trees in north America and birch is mid-tolerant. However, both birch and hemlock are small-seeded, drought-intolerant species (Eckstein 1980, Erdmann 1990, Godman and Lancaster 1990), and established seedlings of both have been found to be associated with decaying wood in primary forests (Reif 1992, Corinth 1995). Relic primary forests stands show a pronounced patch structure with hemlock-dominated patches (3- 30 ha, Davis et al. 1998) with high admixtures of yellow birch adjacent to sugar maple-dominated patches (Frelich et al. 1993). Pollen core studies indicate that these patch boundaries have changed little since their formation about 3,200 years ago (Davis et al. 1993), and several self-reinforcing mechanisms have been proposed to explain the long-term maintenance of patch structure. These mechanisms include the diminished light, water, and perhaps nitrogen levels beneath hemlocks which allow hemlock but not sugar maple seedlings to survive (Finzi et al. 1998a, Campbell and Gower 2000, Catovsky and Bazzaz 2000), and the abundance of hardwood leaf litter in sugar maple stands, which smothers young, small hemlocks but not the larger sugar maple germinants and seedlings (Koroleff 1954, Tubbs 1978, Frelich et al. 1993). While proposed mechanisms offer a partial explanation for the maintenance of patch structure, they do not explain why hemlock patches almost always contain a large basal area component of yellow birch, or why the presence of decaying wood in sugar maple-dominated stands does not result in the establishment of hemlock trees within sugar maple patches.

In this study we ask: are there differences in the suitability of wood species for seedling establishment, and if so, do these patterns help to explain the close spatial association of hemlock and birch and the stability of hemlock-dominated and sugar maple-dominated patches? We hypothesized that hemlock and birch seedlings are restricted to hemlock and birch wood for seedling establishment. To address this question, we identified decaying wood to species and measured seedling abundance, survival rates, and age distributions across decaying wood and soil at four primary forest sites in Upper Michigan. Our specific predictions were:

1. Independent of variation in light, seed rain, and log size, hemlock and birch seedlings are more abundant on hemlock and birch wood than on sugar maple wood and soil, and sugar maple seedlings are more abundant on soil than on wood.
2. Survival of hemlock and birch seedlings is greatest on hemlock and birch wood.
3. The greater abundance and survival of both hemlock and birch seedlings combined with the predicted greater quantity of decaying hemlock and birch wood in hemlock-dominated than in sugar maple-dominated stands partially explain the maintenance of the hemlock-hardwood patch structure and the hemlock-birch spatial association.

Materials and Methods

Between 2002 and 2005, we studied four primary hemlock-hardwood forests in Upper Michigan (Table 2.1). Three of these sites, the Porcupine Mountains Wilderness State Park, Sylvania Wilderness Area (Ottawa National Forest), and the Huron Mountain Club Reserve (private ownership), are characterized by a patchy distribution of forest types, with areas of hemlock/birch bordering hardwood forests dominated by sugar maple with basswood (*Tilia americana*) (Pastor and Broschart 1990). Stands contain minor components of balsam fir (*Abies balsamea*), red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), northern white cedar (*Thuja occidentalis*), and *Ostrya virginiana.* Field plots are located in areas that have been selectively logged only for white pine (*Pinus strobus*) in the late 1800s (Woods 1981, Simpson et al. 1990). The fourth site, in the state-owned Sand River area near Skandia, MI, is a patch of hemlock-dominated forest surrounded by areas that were selectively harvested for white pine, sugar maple, and birch. Unlike the other three sites, Sand River is poorly-drained, has been mainly cleared of birch seed sources, and has lower deer browse pressure (D. Wilson, MDNR, pers. comm.) This site is treated separately in the results section.

At each site, paired field plots (0.1 ha) were placed on either side of distinct hemlock/hardwood borders to allow comparison between hemlock (>55% basal area hemlock) and hardwood (10 - 35% basal area hemlock) stands which could differ in seed availability, environmental factors, and surface area and species composition of logs. There were no obvious topographic differences between the members of each pair, and paired plots were separated by 40 to 110 m. Sixteen field plots were located: seven within the Huron Mountain Club Reserve (one hemlock plot had no suitable mixed plot nearby), four each within Sylvania and the Porcupine Mountains, and one in Sand River (where no uncut areas of hardwoods existed).

Within each field plot, every log, stump, or downed branch > 10 cm in diameter was counted, and dimensions, decay stage, and wood species were recorded for each wood piece. Wood pieces are collectively referred to as logs for simplicity, while those representing main stems are referred to as boles. Logs in decay stage V (the most highly decayed stage, where wood is almost fully incorporated into surrounding soil; Pyle and Brown 1998, Graham and Cromack 1982) were not counted. Wood species of the 413 logs present in field plots by 2004 was determined by microscopic examination of thin slices of wood (40x to 200x, microscopes at the USDA Forest Products Laboratory, Madison, WI, see Chapter 4 for details), and 47 logs of species other than hemlock, birch, and sugar maple were excluded from analysis. Note that identification of wood in the field is not reliable for well-decayed logs; comparison of microscopic features on several wood cross-sections was required.

All tree seedlings (stems ≤ 30 cm in height in order to be comparable to Rooney and Waller 1998) growing on a log were counted, identified to species, and their height, diameter, age class (first-year seedlings or established), and substrate (bark, litter, moss, etc.) were recorded. For each log, an identical seedling survey was conducted on an equal surface area of soil 1 m away from and in the same orientation as the log. Soil plots were randomly placed on either side of a log. Large seedlings/saplings (> 30 cm tall but not in canopy) were noted when they occurred on either logs or soil, but individuals in this larger size class were rare or absent in most field plots and are not reported. We assumed, in order to calculate soil surface area, that stumps were flat and boles and branches were half-cylinders. Given that most boles were intermediate between flat surfaces and half-cylinders, this resulted in a conservative measure of seedling density for boles. In 2002 and 2003, sugar maple seedlings were often so abundant on soil that only a subsample of seedlings (every 10th or every 20th seedling) was measured. In 2004 each sugar maple seedling on soil was placed into an age class but other characteristics were not measured.

In late August 2002, after the high-mortality period of June and July when many first-year seedlings die of drought, 190 seedlings growing on hemlock (n = 18 logs), birch (17) and sugar maple (13) logs were marked with plastic toothpicks. Logs were chosen via stratified (by log species) random sampling from a list of logs of each species in each site. On each log, we started at one end and marked several seedlings of each available species, up to 10 seedlings in total without regard to seedling age. Seedling survival was recorded in summer 2003, 2004, and 2005.

We also collected established (older than one year) hemlock and birch seedlings from 88 logs in 2002 (see Chapter 3 for more detailed methods). For seedlings ≥ 2 mm in diameter immediately above the root collar, we counted growth rings using a 50x dissecting microscope. Second- and third-year seedlings < 2 mm in diameter were aged in the field by counting bud scars (field aging of hemlock is highly imprecise above three years of age). Because sugar maple logs only rarely support seedlings, in 2004 we collected and aged seedlings from 16 additional sugar maple logs with established hemlock or birch seedlings to ensure that our estimates of maximum seedling age on sugar maple logs were accurate. Sugar maple logs have therefore been considerably oversampled and were sampled over a considerably larger survey area than the other wood species.

Canopy photographs were taken approximately 30 cm directly above each log in field plots and all logs from which seedlings were sampled using a digital camera (Nikon Coolpix 995, set to grayscale) with a fisheye lens. All photos were analyzed using GLA software (Version 2.0, 1999, Institute of Ecosystem Studies) by a single technician. SideLook software (v. 1.1.01, 2005, M. Nobis, www.appleco.ch), which was developed in 2004, was used to automatically threshold a subset of 22 canopy photos for comparison. The gap light indices (canopy openness) of automatically and manually thresholded canopy photos were similar (matched pairs mean difference = 0.62%, s.e. 0.16, n = 22 pairs, p = 0.001; Pearson's correlation = 0.75).

Seed rain was measured near 15 randomly selected logs within each of 12 plots (3 plots from which the surrounding area had been logged for hardwoods were excluded). Seed traps were constructed from 22 cm-diameter plastic pots (366 cm^2 surface area), lined with plastic weed cloth and with a piece of 1/2 inch wire mesh covering each trap about 1 inch below the top. Plastic canvas (6 squares per inch) was used in the bottom of traps to allow drainage but prevent entry of seed predators. Seed traps were placed alongside the midpoint of each log and seeds were collected from August 2003 to late May/early June 2004, with leaves cleared from trap surfaces in October 2003 at first snowfall. In 2004, contents of the remaining 137 undisturbed traps (of 180 placed) were dried at 65°C, and seeds were counted and a subsample was cut open to determine percentage of seed filled. Birch seeds, the most abundant type, were counted up to 200 seeds, with the remaining number of seeds estimated by weight. Note that seeds were collected in the year following a mast seed year for birch and sugar maple.

Our data are a combination of seedling density and count data, with individual logs treated as the experimental unit (except for analyses of survival and age). Factors examined include site, log species, stand type, and wood area. The large number of zero values obtained (as many as 97% of logs within a study site lacked seedlings), while biologically meaningful, made the data difficult to normalize by transformation. We used negative binomial regression (SAS 9.1.3, proc GLM, dist=nb, SAS Institute, Cary, NC) to analyze count data, but these data are presented as density (seedling count divided by log surface area) values in figures and tables. Our Sand River site contained only a single plot, so we were unable to perform statistics on this site. In addition, in certain years sample sizes of seedlings at the Huron Mountain field were too low to allow successful convergence of the maximum likelihood algorithm used by SAS when more than one variable was included in the regression model. When reliable statistical results could be obtained for this site, they are reported, otherwise data are reported without test statistics.

Results

Decaying wood distribution

Logs covered a larger percentage of the forest floor in hemlock (5.3% ± 0.71 s.e.,) than in mixed stands (4.3% ± 0.52, paired t-test of percentage of forest floor $p = 0.048$).

There was no difference in the average decay stage of each wood piece in the two stand types (mean = 2.9 and median = 3.0 for both, stages follow Graham and Cromack 1982). Hemlock logs comprised 35% of the log surface area in hemlock stands, birch 18%, and sugar maple 29%, with 18% of area made up by minor species (versus 27%, 18%, 48%, and 8% in mixed stands). Hemlock plus birch logs covered on average 2.8% (27.5 ± 7.3m^2) of the forest floor in hemlock stands versus 1.9% (18.6 ± 5.2 m^2) in mixed stands. At the Porcupine Mountains, but not at Sylvania or the Huron Mountains, hemlock logs had a greater average diameter than did sugar maple logs (one-way ANOVA, $p = 0.015$, hemlock = 32.1 cm, sugar maple = 22.7 cm). Surface area distribution of individual wood pieces did not vary significantly with species at any site (Figure 2.1).

General seedling distributions

Hemlock and birch seedling density were greater in hemlock-dominated than in sugar maple-dominated plots, but because this difference was due to a single mixed plot in the Porcupine Mountains, we pooled stand types for analyses of seedling abundance. Established hemlock and birch seedlings were several orders of magnitude more abundant on logs than on soils across field sites (Table 2.2). Virtually all soil plots (91%, 274 plots) lacked hemlock and birch seedlings in all three years, while 35% (111 logs) of logs supported at least one hemlock or birch seedling in at least one of the three years measured. Sugar maple seedling densities showed a pattern opposite that of hemlock and birch seedlings, with significantly greater seedling densities on soil than on logs. 42% of soil plots in 2003 and 75% of soil plots in 2004 (after a mast year in 2003) had at least one sugar maple seedling. In contrast, only 3% of logs in 2003 although 33% of logs in 2004 supported at least one sugar maple seedling.

At all sites, for first-year and established hemlock and birch seedlings, the number of seedlings on hemlock wood was greater than that on sugar maple wood, with the exception of established birch seedlings at the Huron Mountain Club (Table 2.2, Figure 2.2). Averaged over all sites except Sand River (see explanation below), densities (m^2) of established seedlings on hemlock:birch:maple:soil substrates were 0.42:0.21:0.08:0.01 for hemlock seedlings, 0.60:0.15:0.10:0.01 for birch seedlings and 0.09:0.03:0.04:0.98 for maple seedlings. Thus hemlock and birch seedlings were at least five times more abundant on hemlock wood than on sugar maple wood, and at least 42 times more abundant than on soil. In addition, although hemlock logs made up 33% of the number of logs, 34% of the logs in decay stages II through IV (classes most suitable for seedling establishment), and 36% of total wood surface area, they supported disproportionately large percentages of the total hemlock (50% to 67%) and birch (40% to 75%) seedlings on logs, depending on year. In contrast, birch (21% of surface area) and sugar maple (43%) logs supported proportions of seedlings equal to or below their proportion of log area.

The difference between the number of established seedlings on hemlock logs and the number of seedlings on sugar maple logs was significant at the Porcupine Mountains (seedling counts: log species effect test chi-square $p < 0.045$ in each year, for each seedling species; seedling presence averaged over several years: nominal logistic fit, Wald test $p = 0.0025$, Table 2.2), and borderline significant at Sylvania Wilderness (log species effect chi-square $p > 0.071$ in each year, for each seedling species).

Seedling distributions by site

Collectively, our results suggest that general patterns in abundance of seedlings on log species are similar across sites, although absolute seedling densities are affected by site factors including substrate moisture. There were significant site effects on seedling counts in all years (chi-square $p < 0.0001$ in each year for each seedling species). At the Huron Mountain Club, our driest site (based on data from a nearby weather station, Table 2.1) there was an almost complete lack of established hemlock and birch seedlings despite abundant first-year hemlock seedlings, with established seedlings on between 3 and 10% of logs, depending on the year and species compared. At Sylvania and the Porcupine Mountains, seedling numbers were higher than at the Huron Mountain Club and greater proportions of logs (9 to 37%) supported seedlings. Sand River was our only poorly drained site, and as such was also wettest, with greater soil moisture (79.1%, July 2003) than other sites (average 55.5%, see Chapter 3 for methods). Due to stand size and composition, Sand River was represented by only a single hemlock field plot, making statistical comparisons impossible, but there were patterns at this site that warrant reporting. Established hemlock seedling densities were by far the highest at this site, with densities on hemlock logs $7.82/m^2$ and soil $1.03/m^2$ compared to less than $0.40/m^2$ and $0.020/m^2$ at other sites on logs and soil, respectively. Compared to hemlock seedlings birch seedlings were relatively rare (e.g. on logs birch densities ranged from $1.16/m^2$ to $2.00/m^2$ depending on year), probably due to the removal of most nearby seed trees, but birch densities were still high compared to other field sites. High hemlock densities on logs and especially on soils at this site are likely due to the presence of continually wet soil, even in late summer, and illustrate that although logs are still important establishment sites in wet areas, seedling are less restricted to logs at wet sites than at dry sites. If we included Sand River as a site there were significant site effects on seedling counts in all years (chi-square $p < 0.0001$ for each seedling species in each year, $n = 4$). When Sand River was removed, the effect of site was still significant in some cases (chi-square $p = 0.0001$ for birch seedlings in 2004, $p = 0.042$ for hemlocks in 2003) but not in all ($p = 0.620$ for birches in 2002).

By directly comparing the number of seedlings on each log to the seedlings on its paired equal-area, nearby soil plot, we could remove site and other environmental effects and isolate the effect of log versus soil substrate on seedling abundance. Paired t-tests demonstrated the same patterns seen in the averaged log and soil seedling densities reported above. With three sites pooled, in 2002 the number of hemlock and birch seedlings on logs exceeded the number of seedlings on the same area of corresponding soil by 0.62 (hemlock) and 0.71 seedlings (birch, $n = 302$, both species paired t-test $p < 0.01$). Logs also had 9.29 *fewer* sugar maple seedlings than nearby soils in ($n = 302$, $p < 0.0001$). In 2004, differences between logs and soils were even larger due to a birch and sugar maple mast year in 2003; logs had 3.52 more birch seedlings than soil ($n = 311$, $p = 0.005$), and 30.45 fewer sugar maple seedlings ($n = 311$, $p < 0.0001$). To separate seedling presence/absence from abundance, we repeated these same paired t-tests using only pairs where at least one seedling was present (on the log, soil, or both). We obtained the same results in all cases (with p-values ≤ 0.003).

Environmental factors potentially affecting seedling abundance

Light is a critical resource limiting survival in forest understories, but light levels did not vary consistently among log species (Table 3.2, Chapter 3). Log surface area also did not vary among log species, and in most size classes hemlock logs supported the greatest number of hemlock and birch seedlings (Figure 2.3). Variation in seed rain is another factor that if confounded with log species could result in a false conclusion that log species are driving seedling abundance patterns. Although seed rain of hemlock and birch was greater in hemlock-dominated plots than in mixed plots, seed rain did not vary significantly among log species, with the exception that more hemlock seeds fell onto birch logs than sugar maple logs in mixed stands at the Porcupine Mountains (Table 3.2, Chapter 3). Because seed rain was only sampled near a subset of logs, the addition of seed rain to the tests of the effect of wood species on seedling abundance reported above halved our sample size. This prevented us from testing seed rain in hemlock versus mixed stands. With stand types pooled, wood species effects on seedling abundance were no longer significant with seed rain in the model for hemlock seedlings at the Porcupine Mountains, and the seed rain effect was significant (chi-square $p < 0.05$). However, when we tested the strength of the wood species effect alone in hemlock versus mixed plots (i.e. partially controlling for seed rain and wood abundance differences by controlling for overstory/seed source composition), the effect of wood species on seedling abundance was no less significant in mixed plots (where the average p value for wood species effect was 0.09, with two out of three cases < 0.05) than in hemlock plots (average $p = 0.15$, two out of three cases < 0.05) . While seed rain almost certainly affected first-year seedling abundance, wood species was an important factor determining seedling abundance even in mixed plots at the Porcupine Mountains, the only site with significant seed rain differences across wood species.

Seedling survival

Mortality across three years was high, with only 50 of the original 190 tagged seedlings surviving to 2005. Hemlock seedlings had the highest survival rates when growing on hemlock logs and the lowest rates when growing on sugar maple logs (Table 2.3). Birch seedling survival was significantly greater on hemlock logs than on sugar maple logs from 2002 to 2003, even when first-year seedlings (which had higher mortality rates than established seedlings) were excluded. After 2003, though, birch survival did not vary across wood species. We were unable to find an adequate sample size of sugar maple seedlings growing on logs, but did tag nine sugar maple seedlings, all but one of which were found growing on hemlock logs. Based on differences in sugar maple abundance in the year following a mast year, early sugar maple survival on logs appears to be low. After a mast seed year in 2003, sugar maple seedling density on logs at the Porcupine Mountains averaged $1.34/m^2 \pm 0.31$ (versus $0.045/m^2 \pm 0.026$ in 2003, paired t-test $p < 0.0001$), but only one third (median = 33%, n = 95; 17% of logs still supported sugar maples) of the established seedlings in 2004 survived the winter to be counted in a seedling census in 2005.

The age distribution of hemlock and birch seedlings on logs (Figure 2.4) is consistent with our 2002-2005 survival data. Both hemlocks and birches older than three years were rare on sugar maple logs, despite oversampling of this log species in 2004. Hemlock seedlings were as old as 13 years on hemlock and 12 on birch logs. Birch seedlings had a similar distribution. Sugar maple seedlings on all log species were very rare (Figure 2.4).

Discussion

Seedling distribution and survival

At all field sites, hemlock and birch seedlings were more abundant on logs than on soils whereas sugar maples were more abundant on soils than on logs. Hemlock logs support the highest seedling densities of both birch and hemlock at each field site (with the exception of established birches at the Huron Mountain Club). These results support our hypothesis that differences in the suitability of wood operate on the species level, with hemlock and birch logs more favorable for seedling establishment than sugar maple logs. In addition to numerous hemlock, birch, and sugar maple logs, our field plots also contained one to eleven *Thuja occidentalis* (cedar), *Abies balsamea* (balsam fir), *Ostrya virginiana*, *Tilia americana* (basswood), *Acer rubrum* (red maple), *Pinus strobus* (white pine), and *Quercus sp.* (oak) logs. Sample sizes of these minor species are too small to allow statistical comparisons, but in general hemlock and possibly cedar logs serve as establishment sites for large numbers of hemlock and birch seedlings, while balsam fir, another conifer, does not appear to support high seedling densities. Among the hardwoods, only birch commonly supports seedlings.

The restriction of hemlock and birch to logs is likely due, in part, to higher and more constant water content in logs and their ability to shed leaf litter (Christy and Mack 1984, Cornett et al. 2000), but the scarcity of sugar maple on logs (also noted by Tubbs 1995) is puzzling. Field observations suggest that seedlings germinating on logs become chlorotic (possibly N deficient, see Chapter 3) and die, often within the first growing season. The endomycorrhizal sugar maple seedlings (Klironomos 1995) are unable to join existing ectomycorrhizal (ECM) networks of hemlock and birch (Booth 2004) and to become colonized by ECM fungi already in wood (Kropp 1982b), which may result in the observed nutrient deficiency. Logs are one of the few sites on which young hemlock and birch can escape competition from the much larger and initially taller sugar maples, which carpet the soil around logs in mast years, even in hemlock stands.

Survival of tagged birch seedlings from 2002 to 2005 was uniformly low across log types, but hemlock survival was highest on hemlock logs overall and at each site except Sand River. The differences in early survival rate of hemlock but not of birch are unexpected since hemlock grows slowly in low light and can survive in the understory for well over 100 years (Dahir 1994). Our age distribution results are generally consistent with seedling survival results, but indicate that the oldest birch seedlings are found on hemlock logs. Long-term survival of birch seedlings, then, is highest on hemlock logs even though short-term survival (2002 to 2005) of young seedlings does not differ across log species. The lack of hemlock and birch seedlings older than four years on sugar maple logs is particularly striking. Despite oversampling, we found only a single 6-year-old birch and a single 6-year-old hemlock seedling on sugar maple logs.

Age distribution and seedling survival rates show the continued narrowing of the niche for successful hemlock and birch seedling establishment. First-year seedlings can germinate on substrates where established seedlings are almost never found, but quickly die, often due to drought (Linteau 1948, Friesner and Potzger 1932 in Friesner and Potzger 1944). First-year seedlings present in May and June were often dead by late August when we returned to collect wood samples. For the next two years, seedlings may survive on sugar maple logs. By the end of the third growing season, hemlock and birch seedlings are found almost exclusively on hemlock and birch logs. Under low light conditions, they will remain there for decades before ascension to the canopy is a possibility (Tubbs 1978, Dahir 1994). One important piece of data that is missing from this study is the distribution of saplings, which would confirm the restriction of seedling regeneration to hemlock and birch logs. Unfortunately, we found very few hemlock and birch seedlings taller than 30 cm. At Sand River, the only site at which we found hemlock saplings, all saplings were either on soil or on conifer (hemlock, balsam fir, white pine, or spruce) logs. Birch saplings were found on both hemlock and birch logs at the Porcupine Mountains and Sand River sites.

Possible mechanisms explaining these species-level differences in seedling abundance are beyond the scope of this paper, and are addressed in Chapter 3. However, we have shown that light levels and seed rain rarely vary across wood species and are therefore not likely to be the cause of variation in seedling abundance. Seed rain was abundant and varied widely across and within our field sites, only varied with wood species in a single case whether stand types were pooled (Chapter 3) or as analyzed separately here, and the effect of wood species was important even in the single site and stand type at which seed rain differences across wood species were found. Given the differences in short-term survival of seedlings across wood species, it seems unlikely that the effects of light and seed rain on first-year seedling abundance (Chapter 3) were important in determining established seedling abundance beyond the second or third year.

Ecological and management implications

Despite variation across field sites, collectively our results indicate that the species-level differences in seedling density and survival on decaying wood may help maintain the boundaries of adjacent hemlock and sugar maple-dominated patches (Figure 2.5). The greater abundance of hemlock wood in hemlock stands (which is not surprising) may maintain patch boundaries, since hemlock wood, like hemlock litter, favors hemlock seedlings over sugar maple. Even in hemlock stands, hemlock wood is rare (covers < 3%) and likely limits seedling establishment. We have shown that hemlock and birch seedlings are both more abundant and attain a greater maximum age on hemlock and birch logs than on sugar maple logs. There is, then, a larger and older seedling bank in areas that have numerous hemlock and birch logs (hemlock stands) than in those with fewer logs of these species (mixed hemlock-hardwood stands). Recruits from the sapling bank are quite possibly the only hemlocks that have a chance of reaching the canopy in between catastrophic disturbances; hemlock sapling that ascend to the canopy in single-treefall gaps can be quite old (average is 149 years (Dahir 1994)). The differences in the survival rate of hemlocks on different log species (Figure 2.5) suggest that even small changes in the availability of microsites on which hemlock seedlings can survive their first few decades have a direct bearing on the number of these older saplings in a stand. Our field plots contained at least 10% hemlock basal area and contained hemlock logs, yet hemlock saplings were very rare. In a sugar maple stand without hemlock logs, saplings would likely be absent, preventing hemlock and birch from invading until a fire or other disturbance removed hardwood litter and allowed regeneration from seed.

Our seedling distribution results also suggest an explanation for the close spatial association of hemlock and birch stems (Figure 2.6). Hemlock is almost always found in stands containing a large basal area component of birch (Brown and Curtis 1952, McIntosh 1972, Rogers 1978). In fact, the spatial association between individual hemlock and birch trees is stronger than that of any other tree species association found in forests of the Great Lakes region (Kotar et al. 1999, Rogers 1980). The apparent restriction of both hemlock and birch seedlings greater than four years old to hemlock or birch logs, and the positive correlation between hemlock and birch seedling densities on each log (averaged across years, 2004 excluded for birch, $r = 0.50$, $p < 0.0003$ at the Porcupine Mountains) explain this pattern. Seedlings of hemlock and birch often become established on the same log, and can apparently coexist until it decays, as evidenced by pairs of stilt-rooted hemlock and birch trees with tangled roots (Figure 2.6). Booth (2004) has found that hemlock and birch share mycorrhizal networks, offering one explanation for the ability of the two species to co-occur in such close proximity even after reaching the canopy. Birch occurs in a number of forest types, but appears to form this association only with hemlock, further suggesting that it is hemlock wood that maintains the hemlock-birch association.

The focus of this study is on differences in the suitability of three wood species for seedling establishment, but an equally interesting result is the almost complete lack of established hemlock seedlings at the Huron Mountain and Sylvania field sites. Rooney and Waller (1998) also noted in their survey of hemlock stands that many stands had no existing hemlock regeneration, and that the proportion of stands without seedlings varied by year. Graham (1941) hypothesized that it was not rare, in Upper Michigan, to have several decades of poor regeneration in which few or no hemlock seedlings become established, followed by a mast seed year and wet conditions that allowed abundant regeneration. Our results suggest that at the Huron Mountain site, not only did very few hemlock seedlings establish between 2002 and 2005, but in all of our field plots except for the Sand River plot, few hemlock seedlings that established in the several decades before we began our study survived long enough to grow between 30 cm and canopy height. At the same time, at least (we only surveyed each field site once during the middle of the growing season, making this a conservative count) 44 hemlock seedlings germinated on logs (655 m^2 total area) in 2002, 230 seedlings in 2003, and 173 seedlings in 2004, so seed or germination limitation alone are not entirely responsible for the lack of seedling establishment. Instead, there appears to be high mortality of first-year seedlings before and/or during their first overwinter period, whether due to frost, pathogens (although O'Hanlon-Manners and Kotanen 2004 suggest that at least for seeds, logs provide a refuge from fungal pathogens), lack of sufficient storage reserves to continue growth the next summer, or browsing by deer in the short period between snowmelt and hardwood seedling leafout. This high mortality continues over the next several years, as indicated in Table 2.3, and likely increases again as seedlings reach a height where they are browsed by deer. Slight differences in the availability of hemlock wood, given this high mortality, can translate into large differences in the number of hemlock and birch seedlings and saplings.

The restriction of hemlock and birch seedlings to decaying wood, and specifically to hemlock wood which covers less than 3% of the forest floor, is one reason that established seedlings are usually rare or absent in second-growth forests. Tyrrell and Crow (1994a) estimate that hemlock-hardwood forests take 400 years to reach peak coverage of decaying wood, and in forests managed by selection silvicultural systems decaying wood coverage likely never peaks as trees are harvested rather than left to die. Even in unmanaged old-growth forests, wood of all species pooled covers at most 10% of the forest floor in these eastern forests (Corinth 1995, this study), and only an average of about 5% in our sites. Given the lack of decaying wood in young secondary and selection harvested forests, management for natural regeneration of hemlock and birch (if planting of seedlings and saplings is not practical) should include methods to increase the amount of logs (even scattering of wood pieces as small as $0.029m^2$ (43x43in) supported seedlings). Seeding of existing logs may also be helpful. We seeded logs with hemlock, birch, and sugar maple seeds in 2003, but very few seeds germinated and thus further trials are necessary. At least in moderately wet forests such as those found in the Porcupine Mountains, our results indicate that survival and establishment of seedlings will be better on hemlock or birch logs than on sugar maple logs. Forest management guidelines in Michigan and Wisconsin include leaving some snags (dead standing trees) or trees of low economic value standing to become decaying wood in the future and for wildlife habitat (Martin and Lorimer 1996, Neumann and Peterson 2001), but do not yet specify which species should be left. Sugar maple logs support few young hemlock and birch seedlings and no older seedlings, and log species must be considered in efforts to understand and increase hemlock and birch regeneration.

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Table 2.1. Locations and characteristics of field sites. Weather data were obtained from NOAA COOP weather stations and are the sum of 2003 monthly averages: Marquette weather station (46°33'N / 87°23'W) for the Huron Mountains, Marquette Wso Airport (46°32'N / 87°33'W) for Sand River, Ontonagon (46:50N/89:12W) for the Porcupine Mountains, and the Lac Vieux Desert, WI (46:07N/89:07W) station for Sylvania. Ecological sections follow Albert 1995. ATM = *Acer-Tsuga-Maianthemum*, ATD = *Acer-Tsuga-Dryopteris*, and TMC = *Tsuga-Maianthemum-Coptis* (Kotar et al. 1988).

Site	Latitude and longitude (UTM coordinates)	Summer precipitation (inches) (May through September)	Ecological section and subsection /Habitat type	Growing season (days with min. temp. >= 32F)
Huron Mountain	46:52 N 087:51W	13.02 inches	IX.2 Michigamme Highland/ATM and ATD	209
Porcupine Mountains	46:42-8 N 089:41-:58W	16.53	IX.8 Lake Superior Lake Plain and IX.6.1 Gogebic-Penokee Iron Range/ATM and ATD	180
Sylvania Wilderness	46:12-3 N 089:14W	17.72	IX.3.2 Winegar Moraine/ATM and ATD	Not recorded at station.
Sand River	46:26N 087:11W	16.58	VII.3 Dickinson/TMC	178

Table 2.2. Density (seedlings/m^2 with s.e. in parentheses) of hemlock and birch seedlings on different forest floor substrates. Established seedlings are older than one year, first-years refer only to seedlings in their first growing season. Hemlock densities are averaged over 2002-2004, while birch and sugar maple densities exclude a mast year in 2003 (2003 is excluded for first-year seedlings, 2004 for established seedlings). n = 302 logs and soils in 2002, 308 in 2003, and 312 in 2004.

Site	Substrate	Hemlock density (first-year)	Hemlock density (established)	Birch density (first-year)	Birch density (established)	Maple density (first-year)	Maple density (established)
Huron Mountain	Hemlock logs	1.08 (0.41)	0.19 (0.08)	0.07 (0.04)	0.13 (0.08)	0.39 (0.28)	0.02 (0.02)
	Birch logs	0.47 (0.17)	0.07 (0.04)	0.15 (0.10)	0.01 (0.01)	0.20 (0.09)	0.02 (0.02)
	Maple logs	0.22 (0.05)	0.05 (0.04)	0.12 (0.09)	0.14 (0.14)	0.15 (0.06)	0(0)
	All logs	0.58 (0.15)	0.11 (0.03)	0.11 (0.05)	0.11 (0.06)	0.22 (0.09)	0.01 (0.01)
	All soil	0.14 (0.04)	0.01 (0.00)	0.04 (0.02)	0 (0)	1.89 (0.24)	2.44 (0.50)
Porcupine Mountains	Hemlock logs	0.50 (0.18)	0.70 (0.21)	5.33 (2.47)	1.22 (0.53)	0.15 (0.08)	0.09 (0.03)
	Birch logs	0.41 (0.17)	0.41 (0.18)	1.88 (0.66)	0.16 (0.09)	0 (0)	0.05 (0.05)
	Maple logs	0.06 (0.06)	0.02 (0.02)	0.33 (0.24)	0.02 (0.01)	0.01 (0.01)	0 (0)
	All logs	0.35 (0.10)	0.43 (0.11)	3.06 (1.19)	0.62 (0.26)	0.07 (0.03)	0.05 (0.02)
	All soil	0.12 (0.04)	0.01 (0.00)	0.19 (0.06)	0.01 (0.00)	0.18 (0.04)	2.63 (0.52)
Sylvania Wilderness	Hemlock logs	0.52 (0.45)	0.76 (0.68)	4.89 (3.24)	0.44 (0.35)	0.23 (0.18)	0.17 (0.17)
	Birch logs	0.29 (0.13)	0.27 (0.15)	0.45 (0.16)	0.28 (0.26)	0.12 (0.06)	0.03 (0.03)
	Maple logs	0.08 (0.05)	0.36 (0.10)	0.75 (0.31)	0.14 (0.08)	0.37 (0.23)	0.11 (0.06)
	All logs	0.22 (0.09)	0.41 (0.14)	1.41 (0.62)	0.24 (0.10)	0.24 (0.12)	0.10 (0.05)
	All soil	0.01 (0.01)	0.02 (0.02)	0 (0.02)	0.01 (0.00)	0.88 (0.15)	4.74 (0.76)

Table 2.3. Percent survival of birch and hemlock seedlings on different log species. 2003 represents survival from late summer 2002 to mid summer 2003. 2004 represents survival to the third, and 2005 survival to the fourth, growing season. For each column (not row), percent survivals with different letters were significantly different (Fisher's exact test, individual contrasts between species, $p < 0.05$). n = 96 hemlock and 85 birch seedlings, sugar maple seedlings not shown.

	Birch survival			Hemlock survival		
	2003	2004	2005	2003	2004	2005
Hemlock wood	62.7% a	20.9% a	11.6% a	90.3% a	67.7% a	55.2% a
Yellow birch wood	56.5% a	26.1% a	13.0% a	66.7% b	46.2% a	35.9% ab
Sugar maple wood	26.3% b	15.8% a	10.5% a	65.4% b	46.2% a	28.0% b

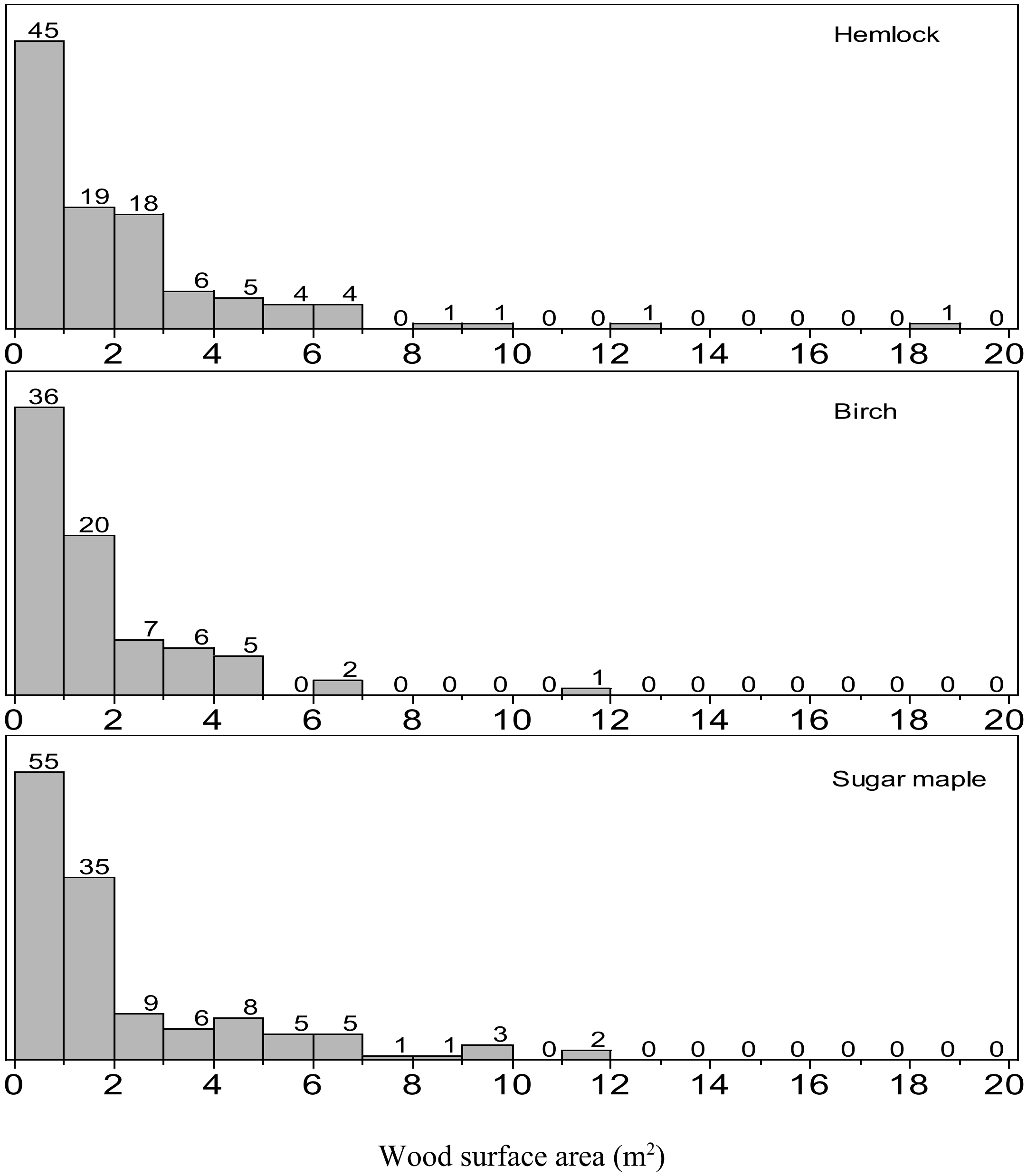

Figure 2.1. Distribution of surface area of logs. All sites are pooled, n = 318 logs total.

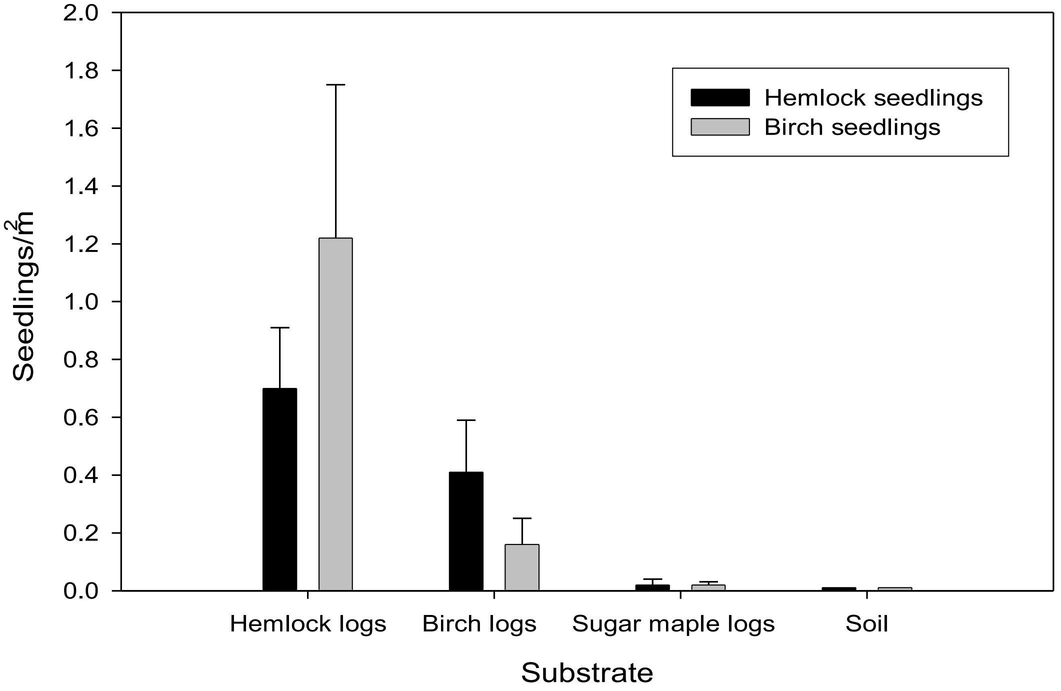

Figure 2.2. Hemlock and birch seedling densities across substrates at the Porcupine Mountains. Densities are means + 1 s.e. of established (older than one year) seedlings, averaged across all years for hemlock and excluding the year following a mast year (2004) for birch. n = 101 logs and 101 soils. Other sites show different densities but similar patterns across substrates, as indicated in Table 2.2.

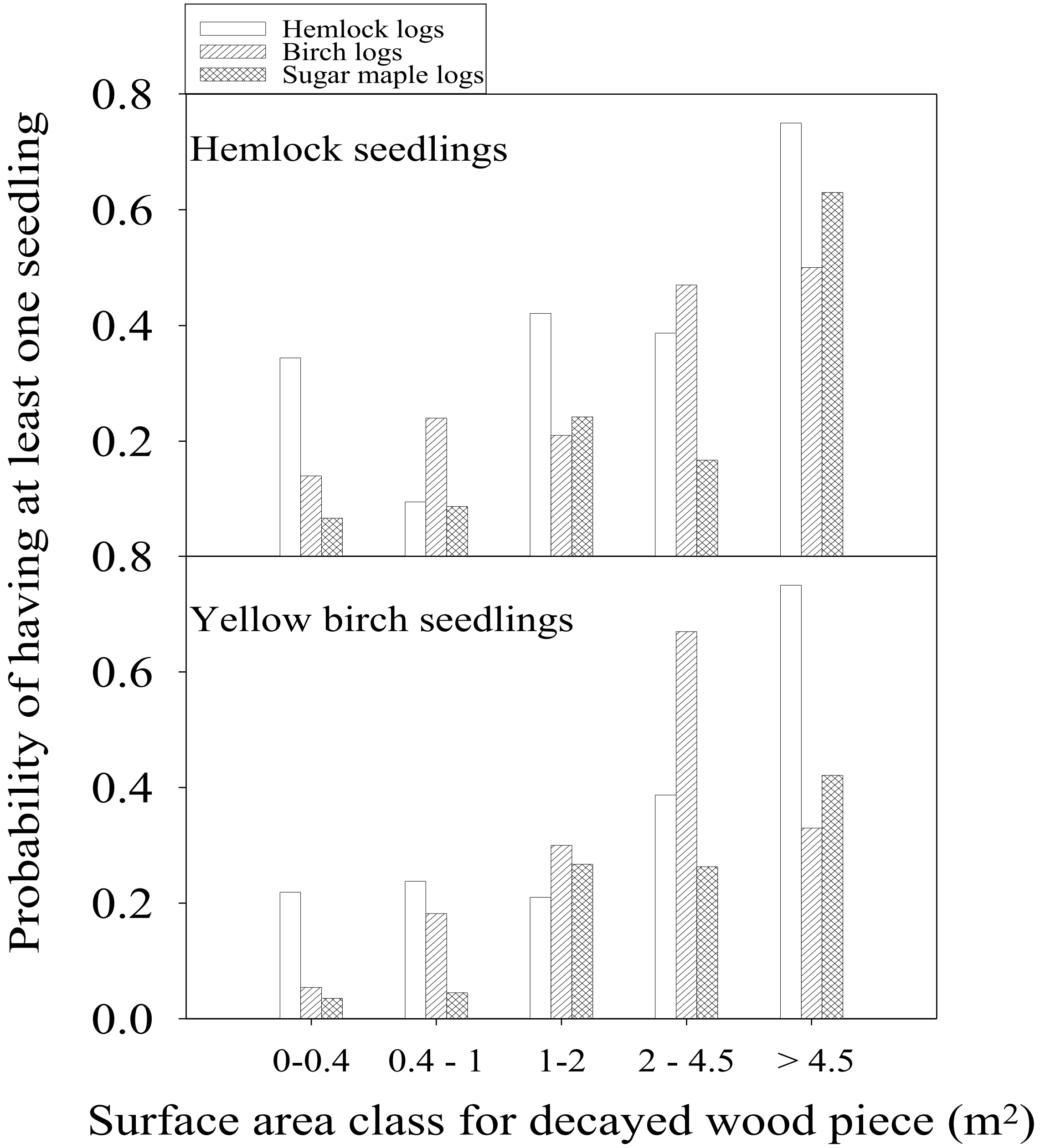

Figure 2.3. Probability of seedling presence (in one or more years, 2002-2004) on logs, by log surface area and species. n = 296 logs present for all three years; Sand River excluded, minimum of 6 logs of each species in each surface area class.

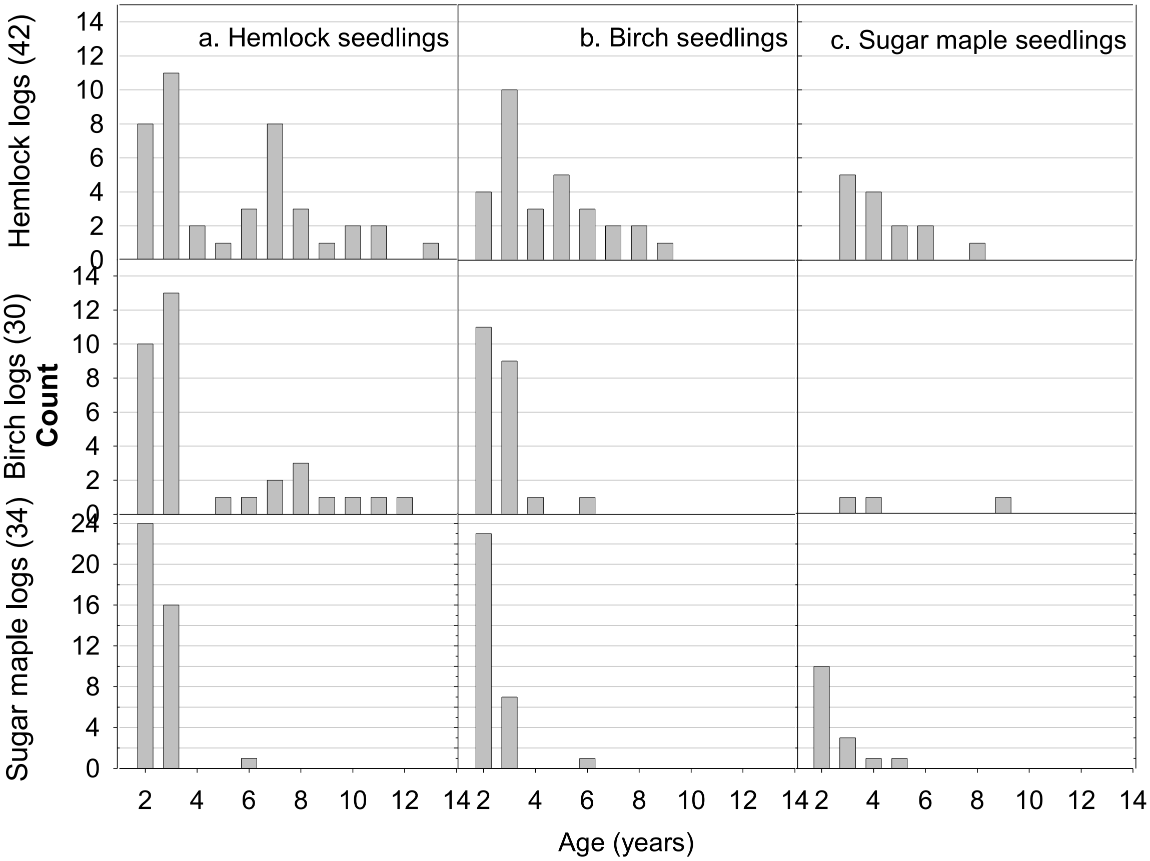

Figure 2.4. Age distribution of hemlock, yellow birch, and sugar maple seedlings on different log species. Log sample sizes are listed after each Y axis label. When comparing across log species, note the different scale for sugar maple logs due to oversampling of this species. n = 117 hemlock, 83 birch, and 32 sugar maple seedlings.

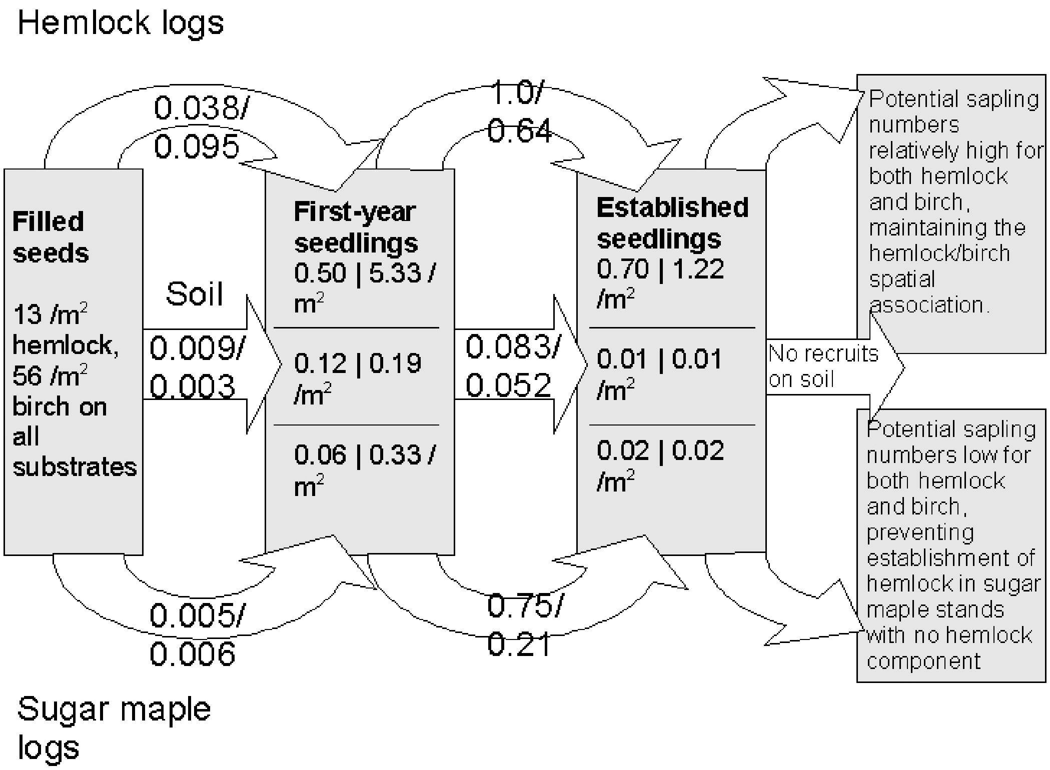

Figure 2.5. Estimated probabilities of survival of seeds and seedlings on hemlock logs, sugar maple logs, and soil at the Porcupine Mountains field site. Probabilities of survival for hemlock seeds or seedlings are listed first, followed by the probability of birch survival. All probabilities were generated by dividing the density of seedlings in an age class by the density of seedlings/seeds in the previous age class, except for probabilities of survival from first-year to establishment on logs. These probabilities are based on survival of tagged seedlings.

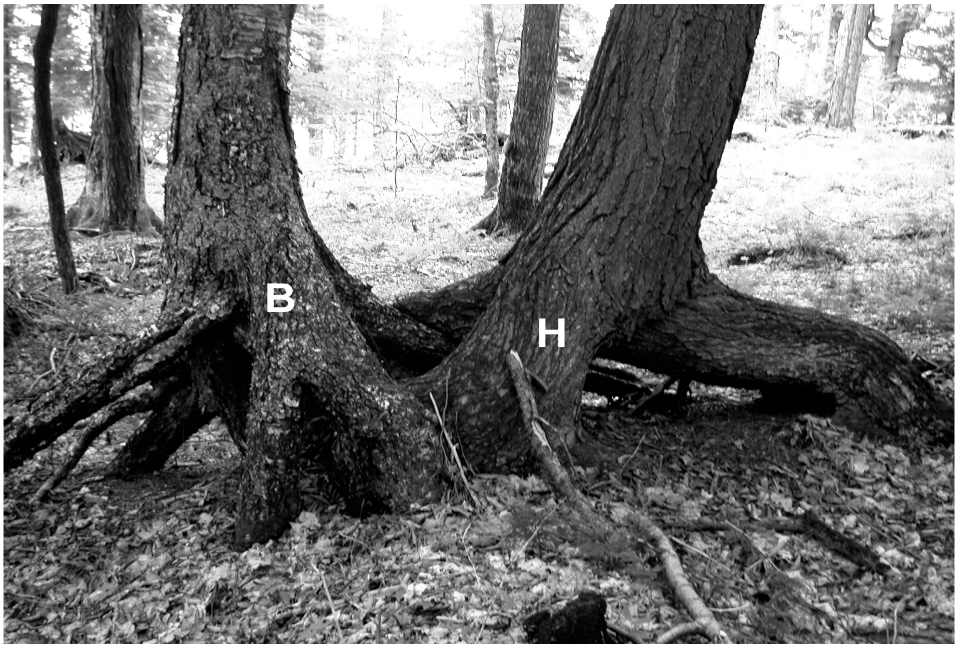

Figure 2.6. Paired hemlock and birch canopy trees. The birch tree is labeled with a B, the hemlock tree with an H. Photo was taken at Sylvania Wilderness Area, near Devil's Head Lake.

CHAPTER THREE

TSUGA, *BETULA*, AND *ACER* SEEDLING DISTRIBUTIONS ACROSS FOREST FLOOR SUBSTRATES IN UPPER MICHIGAN, USA II: MECHANISMS UNDERLYING SEEDLING DISTRIBUTION

Abstract: Eastern hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghenies*is) seedlings in primary Upper Michigan hemlock-hardwood forests are limited to decaying wood for establishment. In an earlier study, we demonstrated that seedling densities and survival are greater on hemlock wood than on birch or sugar maple wood. Here, using a natural experiment at three field sites and a greenhouse experiment, we quantified intrinsic wood chemical, physical and decay characteristics among three species of decayed wood and related them to seedling abundance, survival and growth. Water and light availability did not vary among decayed wood species. Instead, higher hemlock and birch seedling survival on hemlock than sugar maple wood may have been associated with the lower pH, more balanced nitrogen and phosphorus supply, greater likelihood of seedling mycorrhizal infection, greater moss coverage, tendency to decay by brown-rot fungi, and longer residence time in decay classes favorable for seedling establishment of hemlock wood. These endogenous factors acted independently of exogenous factors such as light availability and stand type, and suggest that other species of wood with similar characteristics may be important for seedling establishment in hemlock-hardwood forests and in other systems.

Introduction

In an earlier study we demonstrated that the abundance and survival of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and yellow birch (*Betula alleghaniensis* Britton) seedlings in primary hemlock-northern hardwood forests differ among establishment substrates in the following order; hemlock wood > birch wood > sugar maple wood and soil (Chapter 2). We also found that these patterns were independent of the exogenous factors seed rain, light availability, and decaying wood piece size, suggesting that variation in endogenous species specific-characteristics were responsible.

There is little information on species differences in decaying wood characteristics of possible relevance to tree seedling survival and growth. However, efforts directed at explaining the greater abundance of hemlock and birch seedlings on wood, in general, than on undisturbed soil might offer some insight on what some of these factors might be. Compared to soil, wood has greater water content (Boddy 1983, Tubbs 1995), less leaf litter (Harmon 1989, but see Simard et al. 2003), attainment of germination temperatures earlier in the spring (Godman and Lancaster 1990), fewer fungal pathogens (Zhong and van der Kamp 1999, O'Hanlon-Manners and Kotanen 2004), and reduced densities of sugar maple (*Acer saccharum* Marsh.) seedlings (Tubbs 1995, Chapter 2). Of these, the high water content of wood and its relative lack of hardwood leaf litter (which can kill seedlings by smothering them, blocking germination cues, or drying out quickly; Koroleff 1954, Peterson and Facelli 1992, Corinth 1995) are two of the best-studied explanations in hemlock-hardwood forests (Godman and Lancaster 1990, Frelich et al. 1993). Abundant hemlock and birch regeneration on soil after litter-clearing disturbances such as fire or mechanical scarification is indirect evidence for the importance of litter shedding by logs to seedling establishment (Maissurow 1941, Peterson and Facelli 1992, Strong 1995, Simard et al. 2003). Log species could vary in litter shedding if surface characteristics differ, and western conifer species do vary in these respects (Harmon 1989). Wood that is effective at shedding leaf litter, however, also tends to shed seeds (Harmon 1989), so a thin layer of litter might be a more favorable surface for seedling germination than bare wood or bark. Soil beneath hemlock canopies is usually dry and often below the wilting point of most seedlings and herbs (Daubenmire 1930, but see Pregitzer et al. 1983). Decaying wood, on the other hand, is usually the wettest substrate on the forest floor (Cornett et al. 1997) and dries out slowly even under full sun (Boddy 1983), factors which might be particularly important for small-seeded, drought-intolerant seedling species such as hemlock and yellow birch (Friesner and Potzger 1936, Linteau 1948, Erdmann 1990, Godman and Lancaster 1990). In the one study we are aware of that compared decaying wood water content among species, water content did not differ between *Betula papyrifera* and *Thuja occidentalis* wood in the field (Cornett et al. 1997).

Wood species are known to differ in wood chemistry (Arthur et al. 1993), decay rates (Arthur et al. 1993, Tyrrell and Crow 1994a), and predominant decay fungi (Zabel and Morrell 1992), all of which are likely interrelated and have implications for factors associated with tree seedling establishment. Differences in decay rates could affect nutrient cycling (see below) and the residence time that wood is available as a substrate for seedling establishment. Shorter residence time would reduce the chance of seeds encountering a log and becoming established, and also may result in logs decaying out from underneath slow-growing, light-limited saplings before those saplings are able to physically support themselves. Seedlings as old as 13 (hemlock) and 9 years (birch) can be less than 30 cm tall when growing beneath a closed forest canopy, with correspondingly slow root growth (Marx, unpublished data). In general, hardwood logs are thought to decay more quickly than conifer logs (Arthur et al. 1993), but comparative field data are scarce (Chapter 2). Furthermore, most seedlings are found on decay stages II through IV (middle decay stages, Takahashi et al. 2000), so the residence time of these decay stages is particularly important.

Log species could differ in their abilities to provide mineral nutrients to tree seedlings. These differences could be associated with interrelated differences in wood chemistry, decay organisms, decay rates, and associated biota (e.g. mycorrhizae), but these linkages are largely speculative and unexplored. Of all the macro- and micronutrients, nitrogen (N) is often regarded as the most limiting nutrient in northern temperate forests, (Cole and Rapp 1981), though evidence of N-limited seedling growth and/or survival in understories is scarce and equivocal (Walters and Reich 1997, Catovsky and Bazzaz 2002), perhaps because light is very low and most limiting in these habitats. Furthermore, it is not known if seedlings should be expected to be predominantly N-limited on decaying wood as nutrient cycling in decaying wood is little studied. Studies to date suggest that mineral N concentrations and mineralization rates in (or under) decaying wood are similar to those for forest floor (Takahashi et al. 2000, Spears et al. 2003). Species comparisons of total N content have indicated that hardwood wood initially contains more N than conifer wood (Arthur et al. 1993), but the amount of N changes with decay stage (Holub et al. 2001) and is highly variable. Spears et al. (2003) found few differences not only in mineral N concentrations but also for organic N and a broad range of cations in solutions collected with lysimeters beneath the decaying wood of four conifer species. Arthur et al. (1999) found that total calcium and magnesium concentration on a mass basis were lower in birch than in sugar maple wood. Given what little attention has been paid to species specific differences in wood chemistry related to plant nutrition, generalizations cannot be made. Conceivably, specific limiting nutrients in decaying wood could differ from forest floor layers, and also among species of decaying wood.

If there are differences in nutrient availability to seedlings among log species, they could be mediated, in part, by differences in pH. Phosphorus and zinc, for example, are more available on organic substrates at pHs well below neutral (Smith 1989). Another possibility is that species may vary in their biotic communities in ways that affect plant nutrient availability but which can not be measured as solute concentrations or mineralization rates. For example, uptake of N and especially of phosphorus is increased by ectomycorrhizal infection (Kytoviita and Arnebrant 2000, Perez-Moreno and Read 2000). Mycorrhizae are not necessary for, but do increase the rate of, uptake of amino acids, an organic N source for tree seedlings (Perez-Moreno and Read 2000, Persson and Nasholm 2001). Mycorrhizae are likely to be a requirement for long-term survival of eastern hemlock seedlings given the advantage they provide for nutrient acquisition and given the obligate mycorrhizal nature of the closely related western hemlock (Christy et al. 1982). Furthermore, the logs of western conifers serve as refuges for mycorrhizal fungi and serve as inocula for western hemlock seedlings (Harvey et al. 1976, Kropp 1982c), although it is not known if western hardwood species (e.g. *Alnus rubra* Bong.) can serve the same purpose. In our study system, it is possible that, like western conifers, eastern hemlock wood provides mycorrhizal inocula for eastern hemlock and yellow birch seedlings (both ectomycorrhizal species) and it is possible that it does this to a greater degree than does sugar maple wood.

Wood decaying fungi fall into three general classes, brown rots, white rots and soft rots. Soft rots are associated primarily with angiosperm wood, typically attack only the outer layer of wood early in decay (Goodell et al. 2003) and are numerically relatively unimportant as wood decomposers compared to brown and white rots, thus they are not examined further here. White- and brown-rotted wood have different textures and patterns of decay, and although a single log may have sections decayed by both types of fungi, in general deciduous species are attacked by white rots and conifers by brown rots (Zabel and Morrell 1992). Brown rot fungi primarily digest cellulose and hemicellulose, altering but not consuming most of the lignin in the wood and resulting in wood with characteristic cubical breaks (Goodell et al. 2003). White rot fungi can digest lignin as well, and cause decaying wood to break apart in soft strings. White rots depolymerize wood components and then immediately digest the products, while brown rot fungi initially depolymerize wood more rapidly than they are able to consume it (Zabel and Morrell 1992). To our knowledge nothing is known about the implications of these differences for nutrient availability to tree seedlings, but brown rot fungal decay could result in excess, unconsumed nutrients that are then potentially available to seedling roots.

In summary, fragmentary evidence suggests that several decayed wood characteristics could vary among species, and in ways that could influence their quality as tree seedling establishment substrates. Studies specifically addressing this topic are lacking. In an earlier study of hemlock-hardwood forests, we found large and parallel differences in hemlock and yellow birch seedling abundance among hemlock, birch, and sugar maple wood substrates. Moreover, differences in seedling populations among decaying wood species were independent of exogenous factors including seed rain, light and wood piece size, suggesting that species-specific variation in endogenous decaying wood characteristics were responsible. Our objectives in this study were to: 1) quantify and compare intrinsic characteristics of hemlock, birch, and sugar maple wood that are potentially associated with hemlock and birch seedling establishment, and 2) where possible, relate wood characteristics to differences in seedling abundance, growth, and survival across wood species while controlling for exogenous factors. We accomplished this with complementary field and greenhouse experiments. From field-collected data and samples we measured the exogenous environmental factors canopy openness, seed rain, habitat type, and hemlock basal area, and the intrinsic wood characteristics decaying wood chemistry (pH, water content, and nutrient concentrations and mineralization rates), wood decay characteristics (fungal rot type, wood residence time), wood surface physical characteristics (bark, litter, and moss cover), and seedling mycorrhizal inoculation. A companion greenhouse experiment examined differences in growth rates, nutrition, survival and mycorrhizal infection for birch and hemlock seedlings growing on decaying wood of hemlock, birch, and maple. For field data, we examined the effect of intrinsic wood characteristics on seedling abundance using regression models that included exogenous factors in models as covariates with seedling abundance as a response variable.

Methods

Field site descriptions

For this study we used sites in three primary hemlock-hardwood forests in Upper Michigan (Huron Mountain Club, Porcupine Mountains, and Sylvania Wilderness) between 2002 and 2005 (see Chapter 2 for locations and field plot selection methods). Field plots (0.1 ha, 1.5 ha total area) were located in these sites in hemlock-dominated patches (> 55% basal area hemlock) and in adjacent mixed hardwood patches (10 - 35% basal area hemlock).

Habitat types of each plot were determined using a habitat classification system developed for northern Wisconsin (Kotar et al. 1988) but considered appropriate for Upper Michigan (J. Kotar, pers. comm., 2003). Soil moisture had been measured in each plot prior to habitat typing, but differences in average soil moisture were small and did not correspond to differences in indicator species presence or abundance. Plots were either ATM (*Acer-Tsuga-Maianthemum*, a dry-mesic to mesic, moderately nutrient-rich habitat type often dominated in our plots by *Maianthemum* and ferns), ATD (*Acer-Tsuga-Dryopteris*, a more mesic and more nutrient-rich type than ATM with greater fern cover), or ATM-ATD/ATD-ATM habitat types.

Field sampling

Censuses of decaying wood and tree seedlings were carried out in each field plot. All decaying wood > 10 cm in diameter in decay stages I-IV (stages follow Graham and Cromack 1982) in each plot was counted, identified to species, and measured. We identified wood to species by microscopic examination (70x to 400x, microscopes at the USDA Forest Products Laboratory in Madison, WI) of thin wood slices of each sample mounted on slides. Wood was categorized as being attacked by brown rot (solid cubical or rectangular chunks of dark brown wood on most of the surface) or white rot (predominantly wet, soft, stringy fibers of wood) fungi (Goodell et al. 2003). Coverage of bark, moss-covered bark, moss, litter, and bare wood was recorded by categorizing the substrate found under clear 2 inch by 2 inch square quadrats placed across the diameter of each log every 1.5 m. Due to our method of scoring moss-covered bark (moss with visible ridges, patchy moss cover with bark visible in bare spots) this category is most likely equivalent to a thin moss layer, and will be referred to as thin moss. Every tree seedling (defined as less than 30 cm in height, which encompassed nearly all individuals and which was comparable to Rooney et al. (2000)) growing on wood was also counted and identified to species, and seedling counts on each wood piece were analyzed with negative binomial regression models described below. More detailed seedling survey methods can be found in Chapter 2.

In August 2002, we collected wood and 2-year-old hemlock and birch seedlings to be destructively sampled for analyses of wood N supply rate and seedling mass and N content. This necessitated sampling outside of our field plots since plots were being used to monitor seedling abundance and survival from 2002-2005. We walked around the outside of four field plots from each field site, described in Chapter 2, starting 10 m outside of the plot border and continuing in additional circuits at 10 m increments. The decay stage of every log, stump, or downed branch (with diameter > 10 cm) visible in each circuit was checked until reaching a sample size of 10 conifer and 10 hardwood logs, all decay stage III (soft sapwood, usually little bark cover) or decay stage IV (soft throughout, usually no bark cover, branch stubs easily pulled free, Graham and Cromack 1982) for each plot. We collected samples from a total of 260 logs (chosen such that half of the logs had hemlock or birch seedlings) and collected the top 10 cm of soil from beside 78 of these logs (6 near each plot, randomly selected) after removing intact leaves from the surface. From each piece of log that had hemlock or birch seedlings growing on it in the field, we collected one, or two if available, established seedling(s) of each species for measurement of mass and N content. Entire seedlings were collected from as close to the log midpoint (to avoid log edge effects) as possible. Only two-year-old seedlings were used in this study.

In July 2004 we collected additional seedlings from Sylvania Wilderness and the Porcupine Mountains for mass and N content measurements. Up to 4 two-year-old hemlock and 4 two-year-old birch seedlings were collected from each of the 41 logs sampled. Unlike in 2002, sugar maple logs were oversampled because seedlings on sugar maple logs are so rare. This necessitated canvassing a large area around field plots to obtain an adequate sample size of seedlings on sugar maple logs.

Analysis of field samples

N characteristics: Soil, wood, and seedling samples were transported on ice to Michigan State University and stored in a 4ºC cold room. In 2002, wood and soil samples were stored for 1 to 10 days before extraction for inorganic N (NO_3^- and NH_4^+). In 2004, wood and soil samples were extracted within 48 hours. For each sample, we determined gravimetric moisture content by drying an approximately 10 g sample at 105°C. In 2002, two subsamples (23 to 27g fresh weight) of each log or soil sample were used for a laboratory potential N mineralization measurement (modified from Powers 1980). Subsamples were placed in a 125-mL plastic specimen cup, and the volume was determined using the mL scale of the cup. An initial sample of each piece of decayed wood or soil core was immediately extracted with 50 mL of 0.5M K_2SO_4 solution, while final samples were incubated at room temperature (23-24°C) for 28 days before extraction. Extracts were analyzed for inorganic N colorimetrically with an autoanalyzer (OI Flow Solution IV, OI Analytical, College Station, TX), with NO_3^--N determined by the cadmium reduction method, and NH_4^+-N with the phenol-hypochlorite method (Page et al. 1982). Refrigerated extracts that could not be analyzed within one month were frozen until analysis. In 2004, wood samples were extracted with 50 mL of 2M KCl instead of K_2SO_4. Net mineralization rates (Nmin) were calculated as the difference between initial and final inorganic N amounts. We chose to express both initial N concentrations ([N]) and Nmin on a volume basis (ug N (mL wood)$^{-1}$ or ug N (mL wood)$^{-1}$ (day)$^{-1}$) because seedling roots exploit a given volume of wood or soil and because soil is denser than wood, making comparisons on a mass basis misleading.

Field-collected seedlings were kept on ice until processed in the laboratory. 2002 field seedlings were examined with a dissecting microscope (10x to 70x) for evidence of ectomycorrhizae. 2004 field seedlings were scanned immediately upon return to the laboratory as high-resolution digital images which were later examined for evidence of ectomycorrhizae. Colored felty mantles on roots or root tips that were orange or yellow were considered evidence of mycorrhizae, and because seedlings were for the most part only 2 years old, white, smooth, non-mycorrhizal bare root systems were easily distinguishable. In both years, seedlings were then dried for at least 48 hours in a 65 ºC drying oven. Seedlings were ground to powder using a mortar and pestle, and analyzed individually for N concentration by the Dumas combustion method on a CN analyzer (Carlo Erba, Milan, Italy). Hemlock and birch seedlings were pooled by individual log for all statistical analyses.

Water content and pH: Water content of 239 logs in August 2002, 172 logs in late June/early July 2003, and 127 logs in late May 2004 was measured gravimetrically as the difference between field weight (samples collected > 24 hrs after last rainfall) and oven-dried (at least 3 days at 105°C) weight of wood samples, divided by field weight. Logs measured in 2002 were selected from outside field plots as described above in *Field sampling*, while logs in 2003 were randomly selected from within plots at all field sites, and logs in 2004 from within plots at the Porcupine Mountains and Sylvania Wilderness. pH of 63 logs randomly selected from those collected in 2002, for which no data on seedling abundance exists, was also measured. Unlike soil, once decayed wood is dried it cannot easily be re-wetted, so we modified a standard soils procedure (Klute 1986) and measured pH of fresh wood. For each sample a mass of wet wood equivalent to 3 g of dried wood, calculated using the water content of each wood piece determined on a subsample, was placed in a sample cup and deionized water (pH ~ 5.5) was added to bring the total volume to 60 mLs. This was done to account for differences in density among wood samples, and ensured a 20:1 ratio of water to dry wood for all samples, leaving sufficient water to immerse the pH probe. Samples were shaken for 1 hour and allowed to settle. pH was read 6 minutes after immersing the probe.

Exogenous factors: light and seed rain

Canopy photographs were taken between May and August approximately 30 cm directly above each log in field plots and any log from which seedlings were collected in 2002. Photos were taken using a digital camera (Nikon Coolpix 995, set to grayscale) with a fisheye lens. All photos were analyzed using GLA software (Version 2.0, 1999, Institute of Ecosystem Studies, Millbrook, NY) by a single technician. SideLook software (v. 1.1.01, 2005, M. Nobis www.appleco.ch), which was developed in 2004, was used to automatically threshold a subset of 22 canopy photos for comparison. The gap light indices (canopy openness) of automatically and manually thresholded canopy photos were similar (matched pairs mean difference = 0.62%, s.e. 0.16, n = 22 pairs, p = 0.001; Pearson's correlation = 0.75).

Seed rain was measured near 15 randomly selected logs within each of 12 seedling census plots, four at each site (3 plots in the Huron Mountain Club from which the surrounding area had been logged for hardwoods were excluded). Seed traps were constructed from 22 cm-diameter (380 cm^2 surface area) 2-gallon plastic pots, lined with plastic weed cloth and with a piece of 1/2 inch wire mesh covering each trap about 1 inch below the top. Plastic canvas (6 squares per inch) was used in the bottom of traps to allow drainage but prevent entry of seed predators. Seed traps were placed alongside the midpoint of each log and seeds were collected from August 2003 to late May/early June 2004, with leaves cleared from trap surfaces in October 2003 at first snowfall. In 2004, contents of the remaining 138 undisturbed traps were dried at 65°C, and seeds were counted and a subsample was cut open to determine percentage of seed filled. Birch seeds, the most abundant type, were counted up to 200 seeds, with the remaining number of seeds estimated by weight. Note that seeds were collected in the year following a mast seed year for birch and sugar maple.

Greenhouse experiment

We carried out a 115-day (mid-July through early November) experiment at the Michigan State University Plant Science Greenhouses to compare mass and N content of hemlock and birch seedlings grown on hemlock, birch, and sugar maple wood. Both birch and hemlock seedlings were planted on all three wood types in a full factorial design. In late May 2004, stage III and IV wood was collected from 20 logs each of yellow birch, hemlock, and maple logs in Sylvania Wilderness and the Porcupine Mountains. [N] of each sample was measured in the laboratory as described in the *Analysis of Field Samples* section above. From each wood sample, a 180 mL subsample was placed into each of two pots (wood was embedded in moist perlite), one for hemlock seeds and one for birch seeds. For 10 of the logs per species, two additional subsamples (one for birch and one for hemlock seedlings) were used for a fertilizer treatment, and one additional subsample was used for a seedling drought tolerance experiment using only birch seedlings. Birch was used because birch leaves visibly wilt while in previous experiments with spruce needles remained turgid even after seedlings had died, and because birch roots grew quickly enough to have penetrated nearly the entire volume of the wood pieces on which they were grown at harvest. The drought tolerance experiment pots were set up using the same methods as the main experiment, except that after three months birch seedlings were no longer watered and were instead monitored until they wilted. When all birches within a pot had wilted, the wood on which they were growing was collected and weighed for determination of water content.

Eastern hemlock seeds (Ontario source, Ontario Tree Seed, Angus, ON) and yellow birch seeds (Michigan source, USFS Toumey Nursery, Watersmeet, MI) were stratified in perlite and wet sand at 4ºC for two months before being placed on trays of wet perlite in the greenhouse in early July. One week later, after birch seeds had germinated and most hemlock seeds had cracked seed coats but did not have visible radicles, nine seeds of either birch or hemlock were pushed into the surface of the wood in each pot. Wood was saturated every day to ensure that seeds in the top layer of wood did not dry out. Birch seedlings quickly developed cotyledons, and were thinned to four seedlings per pot. Hemlock seedlings grew vertically and lost their seed coats before expanding their first leaves almost three weeks after birch seedlings, and were not thinned. Throughout the experiment, seedlings were shaded with aluminum (Aluminet, Polysack USA, San Diego, CA) 70% shade cloth. Seedlings were grown under natural light conditions in July and August and supplemented with standard greenhouse lighting (16 hours per day) above the shade cloth for the remainder of the experiment. Temperatures in the greenhouse ranged from 21 to 35ºC.

For the first month of the experiment, seedlings were watered to excess with groundwater which contained some inorganic N. After this establishment period, filters were added to remove inorganic N and seedlings were watered to excess with deionized water containing negligible nitrate (< 0.1 mg/L NO_3-N) and no measurable ammonium every second day. Also after one month, Scotts Proturf 38-0-0 Poly-S was applied to pots in the fertilizer treatment at 200 kg N per hectare (0.3188 g per pot). Surprisingly, this application of N quickly killed approximately half of the fertilized seedlings (with no detectable pathogen presence, MSU Diagnostics Lab). Seedlings that survived the first week after fertilization tended to survive to the end of the experiment.

After 115 days, all surviving seedlings were harvested, cleaned, and refrigerated. Seedling root systems were systematically visually scanned under a dissecting scope (10x - 70x) within 36 hours of harvest for evidence of mycorrhizal infection. Seedlings were then dried at 65ºC, weighed individually, pooled by pot, and ground by mortar and pestle or with a steel ball pulverizer into a fine powder. N content of ground seedlings was analyzed as described above for field seedlings. The remaining dried seedling powder from a subset of birch seedlings (individual seedlings were pooled from each of 7 randomly selected hemlock, 6 birch, and 7 sugar maple wood samples) was analyzed for boron, calcium, copper, iron, potassium, phosphorus, magnesium, manganese, and zinc concentration (ppm). Samples were microwave digested at 205°C for 30 minutes (MARS 5, CEM Corporation, Matthews NC) with 1 part hydrogen peroxide, 1 part nitric acid, and 2 parts deionized water. Digested samples were diluted 1:1 with deionized water and analyzed with a direct current plasma atomic emission spectrometer (SMI III, Spectrametrics, Inc., Andover, MA). Hemlock seedlings did not show variation in size in the greenhouse and so were not analyzed for nutrients besides N.

Log residence time

Tyrrell and Crow (1994a) have already estimated residence time for hemlock logs at sites similar to ours. To estimate residence time of birch and sugar maple logs, 38 birch and 46 sugar maple logs were located in the Porcupine Mountains and Huron Mountain Club Reserve. We also sampled six hemlock logs to compare age estimates to those determined by Tyrrell and Crow. Logs showing evidence of having spent time as standing dead trees (bracket fungi growing perpendicular to the ground, extensive woodpecker holes, early decay stage logs with no visible remnants of the crown) were not selected. All logs used were clearly identifiable as decay stage II (only sapwood soft, branches remain), III (most or all bark lost, except in the case of birch, branch stubs remaining, and soft sapwood with a hard inner core), or IV (soft throughout, branches and most branch stubs absent; stages follow Graham and Cromack 1982), could be identified to species in the field by using a hand lens to examine wood characteristics, and were associated with at least two obvious release trees. Release trees were defined as trees that had responded to the gap created by the death of a canopy tree (now a sample log) with increased growth. Release trees used were either small-diameter trees growing beside the stump end of each log, or, more rarely, small trees whose branches had grown laterally directly over the stump end of the log. Most trees that showed a clear release were hemlocks (63%) or sugar maples (22%). Each release tree was cored at breast height (16-inch 4.3 mm-diameter increment borer), and cores were dried in paper straws, mounted on wood blocks and sanded (150 through 600 grit sandpaper). Date of release for each tree was determined by measuring the width of each annual ring (Velmex Unislide with QC1100 measuring system, Velmex, Inc., Bloomfield, NY) and comparing the uniformly weighted moving average ring widths for both release trees of a given log in JMP (JMPIn 5.1, 2004, SAS Institute, Cary, NC) using a modification of the Lorimer and Frelich

(1989) method. If both trees showed a release (at least one 7-year average of ring widths greater than 2 standard deviations above the mean 7-year ring width) within 10 years of each other, the release dates of the most recent simultaneous release were averaged and the log was assumed to have fallen in that averaged year. These were conservative criteria and resulted in a low sample size, and may have slightly underestimated dates of release since only logs where both trees had responded to release with a large increase in ring width at the same time were included. A second set of release dates was determined by subjectively scoring each tree separately using 5-year moving averages and counting the most recent release even if it was just under 2 standard deviations above the mean for trees with consistently thin growth rings but a clear peak in width. We included release dates if one or both trees for a given log showed a release. Ages of stage III logs were not included in figures or analyses since their age range spanned parts of decay stages II and IV and yielded no additional information about the total stage II-IV residence time of logs.

Data analysis

We tested the effects of various exogenous factors and wood characteristics on seedling abundance and determined which of these factors vary with wood species. Seedling abundance data from logs in field sites were analyzed as seedling counts rather than as densities based on the high number of logs with zero seedlings or extremely small seedling and seed rain counts. A zero count is equal to a zero density, which is problematic because a relatively high proportion of small logs have no seedlings at all, and the remainder have very high variance in seedling densities due to multiplication of few seedlings many times over to generate densities per square meter. Zero-inflated count data are resistant to transformation and we first tested various non-parametric statistical methods (analyzing presence/absence and logs supporting seedlings separately, negative binomial nonlinear regressions, placing logs into abundance classes before analysis) as methods of screening the effects of environmental and wood characteristics. We ultimately used parametric tests (t-tests, ANOVAs, and single linear regressions) to screen individual factors measured on logs both inside and outside of field plots, and nonparametric tests to build explanatory models of seedling abundance on logs in field plots. Exogenous and endogenous factors compared across wood species were, with the exception of nitrogen mineralization rates, normally distributed or could be transformed and so ANOVA tests were appropriate.

Using single linear regression models, we related 12 factors that might affect seedling abundance to seedling abundance measured in the field: light, seed rain (for first-year seedlings), wood water content, decay stage, rot type, wood species, % bark, % thin moss, % litter, log surface area, first-year seedling history, and established seedling history. Data were divided by site because, despite strong generality in trends among sites, site effects were still significant for most factors, including seedling abundance. (Chapter 2). This exploratory analysis allowed us to generate a percent of the variation in seedling abundance that was explained by each individual factor. In addition, we used multiple linear regression to explore candidate best-fit multiple regression models of seedling abundance. Linear regression screening of factors gave easily interpretable and potentially biologically relevant information, as well as our only measure of overall fit of candidate multiple regression models, but was used for exploratory purposes only.

Greenhouse data were analyzed using a combination of correlations, t-tests, and linear regressions to determine the relationships between wood nutrient content, fertilization, and mycorrhizal colonization and seedling growth and N content. With the exception of nitrogen mineralization (Nmin) rates of wood, greenhouse data were successfully logarithm-transformed. Because Nmin rates were resistant to transformation, they were analyzed using non-parametric tests and Nmin and [N] data are presented in Figure 3.3 as medians rather than as means.

In order to generate best-fit multiple regression models of factors influencing seedling abundance, we used negative binomial regression in SAS (proc genmod, dist=nb option). Negative binomial modeling is the appropriate technique to use with the overdispersed, zero-inflated seedling counts in our study. Each starting model included seedling history (the number of established seedlings on the log in the previous year), and then we added each additional factor in the order: seed rain (for first-year seedlings only), log size, light, log species, rot type, decay stage, % bark, % litter, % moss. For established seedlings, we also added first-year seedlings from the previous year and determined which additional factors were significant with both seedling history and first-year seedlings in the model, but we did not include first-years in final models because often no other factors were important with both established and first-year seedling history in the model. The addition of second-order interactions that contained categorical variables to models caused the model algorithm to fail to converge. This was not purely a sample size problem, as in field sites and years where the distribution of seedling abundance data was not similar in shape to a negative binomial distribution (e.g. when most data were zero values with several high outliers), even interactions containing only numerical variables resulted in a lack of convergence. Consequently, not all second-order interactions and no higher-order interaction terms are presented in our best-fit models.

Akaike information criteria (AICc) were used to compare model fits, and AICs were corrected for our relatively small sample size. AICc corrects for overfitting of models, and in several cases models containing only seedling history (our starting models) had the lowest AICc. We did not, however, include these seedling history-only models as candidate best-fit models but rather continued to add factors because models with additional factors had similar AICc values and those additional factors were significant even with seedling history in the model. As we added each factor to the candidate best-fit model, factors remained if they were significant (chi-square p-value < 0.05), and replaced existing factors when the new model AICc was > old model AICc + 2. Given the close agreement between negative binomial regression and standard multiple regression, as well as between models selected by comparing log-likelihoods and those comparing AICc, we suspect that all of the modeling techniques we used are sensitive to the few logs with high abundances of seedlings. We are more confident that the factors identified by these techniques are important in determining seedling abundance than in the p-values assigned to each individual factor.

Results

Exogenous factors: habitat type, seed rain, and light

Percentage of filled seeds was low at all field sites, ranging from 9% to 20% for hemlock, 5% to 32% for birch, and 18 to 24% for sugar maple across sites, and did not vary systematically across log species or stand type, thus viable seeds were considered to scale with total seeds counted and will not be discussed further. Seeds of hemlock and birch were well dispersed and abundant, with 131 of 138 seed traps (22-cm diameter) containing at least one hemlock and at least one birch seed. Seed rain density did not vary among log species with the exception of hemlock seeds in mixed plots at the Porcupine Mountains, where traps alongside birch logs received significantly greater numbers of seeds than those alongside sugar maple logs (ANOVA, effect of log species on hemlock seeds/m^2, p = 0.034, Table 3.2). Stand type differences in seed rain are discussed further in Chapter 2, and in this study although seed rain varied widely within each log species it was positively related to the number of hemlock and birch germinants. However, seed rain density explained little variation in first-year birch or hemlock seedling abundance in most cases (maximum $R^2 = 0.18$), nor did the size of each log (maximum $R^2 = 0.15$). When seed rain falling into each trap was multiplied by the size of each log to generate an estimate of total seed rain on each log, seed rain explained 8 to 58% of variation in first-year hemlock seedling abundance (0 - 4% of birch seedling abundance).

Basal area of hemlock affected seedling abundance (see Chapter 2), while neither hemlock nor birch seedling numbers varied with habitat type in the Huron Mountain or the Sylvania Wilderness sites. Hemlock abundances were significantly greater on logs in the less mesic ATM plots than in the more mesic ATD plots at the Porcupine Mountains in 2002 and 2003 (t-test, p = 0.010 to 0.031, n = 100, data not shown), but not 2004, and hemlock, birch, and sugar maple logs were equally likely to be found in each habitat type at this site.

Canopy openness (a surrogate for light) varied from 2 to 17% across logs from all sites, but 70% of the values were < 6%. Canopy photos cannot accurately detect small differences in light availability below this point (Machado and Reich 1990), and thus the small (~ 0.70%) differences in canopy openness above sugar maple logs as opposed to birch and hemlock logs at the Porcupine Mountains and Sylvania are not biologically meaningful. While sites varied in light availability, with values higher at the Huron Mountain site, mean values were similar among log species at each site (Table 3.2). Light was rarely a significant predictor of first-year or established hemlock and birch seedling abundance, explaining at most 5% of the variation in seedling abundance in a single-factor regression.

Endogenous factors: Water content, decay, and wood surface characteristics

Field water content did not vary with wood species at most sites (Figure 3.1) and was only about 10% lower than field capacity measured for 16 samples of hemlock and sugar maple wood in the laboratory (data not shown). Sugar maple logs had greater water content than both hemlock and birch logs (student's t-test, $p < 0.03$, mean difference = 9% for both species) at the Huron Mountains in 2002, while in 2003 sugar maple logs were *drier* than birch logs at Sylvania Wilderness (student's t-test, $p = 0.03$, mean difference = 7%), suggesting that sugar maple water contents may fluctuate more than those of other species. However, in a greenhouse drought tolerance study of birch seedlings planted on hemlock, birch, and sugar maple wood, there was no difference across log species in the number of days birches survived without water or the water contents at which they wilted. Birches wilted at wood water contents between 16 and 50% (mean 24.5% ± 1.4 s.e., $n = 30$, Figure 3.1), and we encountered only six out of 452 logs measured over 2002-2004 in the field that had less than 50% water. Water is always available in the lumen of wood (and therefore available to seedlings) that is at greater than 30% water content (P. Kamdem, pers. comm. 2005). Water content was not significantly and positively related to seedling abundance in most sites at most years, with the exception of first-year hemlock seedlings in 2003 at the Huron Mountain Club ($R^2 = 0.16$, $p < 0.001$, $n = 85$).

We examined wood decay rate from the perspective of the length of time wood can serve as a substrate for seedling establishment (usually decay stage II - IV, Takahashi et al. 2000, Mori et al. 2004, Chapter 2) and hereafter call time spent in these decay stages residence time. The residence time for hemlock logs has already been determined in two of our study sites by Tyrrell and Crow (1994a) and their estimates matched our estimates based on a small sample of six hemlock logs (Figure 3.2). The range of ages of logs in decay stage II-IV (maximum possible residence time) was 2 to 57 years for hemlock, 6 to 45 years for birch, and 10 to 30 years for sugar maple, based on our conservative estimates (Figure 3.2). Average surface area of the three log species does not vary in field plots (ANOVA, $p = 0.48$). However, average hemlock log diameter was greatest in both field plots (mean = 28.2 cm, birch = 24.5, maple = 23.9, includes boles, stumps, and branches, ANOVA $p = 0.054$) and the boles aged by coring release trees (mean 57.5 cm, birch = 44.0 cm, maple = 43.2 cm, ANOVA $p = 0.008$). These differences may partially explain the slower decay rate of hemlock logs, since larger-diameter logs might be expected to decay more slowly than smaller logs.

Hemlock logs are more likely than birch or sugar maple logs to be brown-rotted rather than white rotted (Table 3.2; chi-square analysis, likelihood ratio $p < 0.005$ at each site), and the Huron Mountains site has the most brown-rotted logs. Within each wood species, brown-rotted logs did not have significantly different numbers of seedlings than white-rotted logs. Rot type explained significant variation in seedling abundance at the Huron Mountain Club when it was the sole factor in a regression ($R^2 = 0.05$ to 0.14 across seedling species and years, all p-values < 0.05) and appears in several of the negative binomial multiple regression models detailed below (Table 3.1).

Wood species varied consistently across sites in the proportion of their surface area that was covered by thick and thin moss cover, bark, and litter but differences were significant (one-way ANOVA $p < 0.05$) only at the Porcupine Mountains. Hemlock logs had the least bark coverage, the most litter, and the most combined thick and thin moss cover. Hemlocks appeared to accumulate moss cover over time, as decay stages I - III had the greatest percent cover of thin moss, while stage IV had the least percent cover of thin moss and the greatest of thick moss. Birches had the greatest percent bark cover at all sites ($p = 0.008$ at Porcupine Mountains), due to their pattern of retaining an almost intact ring of bark around a highly decayed bole, while sugar maple logs did not have any differences in surface area cover that were consistent across all sites. Thin moss cover explained significant but small amounts of variation in abundance of first-year birch and hemlock seedlings at the Porcupine Mountains and Sylvania sites ($R^2 = 0.05$ to 0.15 across species and years), and appears in one of the explanatory models below (Table 3.1).

Endogenous factors: Wood chemistry and mycorrhizae

pH of hemlock logs was low, and significantly different from that of both birch and sugar maple logs (ANOVA $p < 0.0001$, n=63, Table 3.2). pH was related to log species and not the environment of each log, as evidenced by different pHs found on logs and adjacent soils and the lack of site or stand type effects on pH (data not shown). Soil pH, which ranged from 3.9 to 5.7, was affected by site (ANOVA $p = 0.017$, n= 31).

Mineral N characteristics of wood varied significantly across species (N min 2002 Wilcoxon/Kruskal-Wallis chi-square $p = 0.023$, [N] 2002 ANOVA $p = 0.004$, [N] 2004 ANOVA $p = 0.001$), and was always lower in wood than in soil (Figure 3.3). [N] and Nmin were inversely ranked across species, with the highest Nmin and lowest [N] in hemlock logs, and vice versa for sugar maple logs (Figure 3.3). In all log species, NH_4^+ dominated [N], with NO_3^- negligible in 2002 and approximately 30% of [N] in 2004, regardless of log species (Marx, data not shown). Within each individual log, Nmin was positively correlated with [N] measured at the start of the laboratory incubation (Pearson's $r = 0.346$, $p < 0.001$). It is important to note that because 2002 and 2004 [N] were measured at different times of the growing season (late May for 2004, late August for 2002), were extracted with two different salt solutions, and 2002 samples spent as long as 10 days in cold storage, these two measures are not directly comparable. 2002 values were higher than 2004 values, perhaps due to these methodological differences, but rankings across species were the same in 2002 and 2004.

Seedling mycorrhizal infection status of seedlings also varied with wood species. Mycorrhizae, which may increase uptake of N and P, were rarely found on two-year-old seedlings collected from the field. Only 2 out of 45 (4%) 2-year-old seedlings in 2002 and 8 out of 186 (4%) seedlings in 2004 were infected with all log species pooled. Mycorrhizae were more abundant on older seedlings collected from the field in 2002, with 12% of birch seedlings and 10% of hemlock seedlings on hemlock logs infected, and 0% of birches and 3% of hemlocks on birch logs infected (n = 50 birch and 88 hemlock seedlings older than 2 years). There were almost no older seedlings on maple logs (Chapter 2). In the greenhouse, rates of infection were higher than in the field for first-year birch seedlings, with 20.3% of seedlings infected (n = 237 unfertilized seedlings) but similar for hemlock seedlings (4.9%, n = 263). Hemlock and birch logs supported greater percentages of mycorrhizal birch seedlings (25% on each wood species) than did sugar maple logs (11%), while similar proportions of hemlock seedlings (3-7%, 13 out of 263 total) were infected across wood species.

Seedling nutrient concentrations and growth

In the field and greenhouse we used seedling growth and nutrient concentrations as bioassays of differences in nutrient availability among log species. In both the field and the greenhouse (unfertilized treatment) seedling birch seedling mass was greater on hemlock logs than sugar maple logs (field: t-test $p = 0.003$, greenhouse: t-test $p = 0.092$,

Figure 3.4). Hemlock seedling mass did not significantly differ across wood species in the greenhouse or the field (ANOVA p-values > 0.1, Figure 3.4). Despite differences in birch seedling mass and in wood N characteristics across species, there was no correlation between either [N] or Nmin with birch seedling N content or mass, in either the field or the greenhouse (N content: Pearson's correlation always < |0.431|, p > 0.189; seedling mass: < |0.519|, p > 0.124).

In the greenhouse, both N-fertilization and mycorrhizal colonization increased the mass of seedlings under some circumstances. Fertilized birch seedlings growing on hemlock and sugar maple logs in the greenhouse were three to four times as large as their unfertilized counterparts growing on different pieces of the same log (paired t-test n = 10 pairs, p = 0.0004, Figure 3.6c, Figure 3.7). Fertilized seedlings on these two wood types also had increased N contents (fertilized = 0.224 g, unfertilized = 0.065 g , n = 9 pairs, p = 0.0001). However, birch seedlings growing on birch logs did not respond to fertilization with increased mass or N content (mass:p = 0.706; N content: p = 0.151, n = 8 pairs, Figure 3.7). Despite statistical significance across wood species, hemlock seedlings did not respond to fertilization with a biologically meaningful increase in mass (median fertilized = 0.011 g, unfert. = 0.010 g, paired t-test with all species pooled, n = 14, p = 0.03), and differences for individual wood species were not significant. Hemlock seedlings had higher N contents when fertilized (fertilized = 0.025 g, unfert. = 0.017 g, n = 14, p = 0.004). The median mass of mycorrhizal seedlings was greater than that of non-mycorrhizal seedlings for both hemlock (t-test log-transformed data p < 0.0001, Figure 3.5) and birch (p = 0.023, Figure 3.6a and b, Figure 3.5).

In order to determine why fertilization affected seedlings on some wood types but not others, we compared micro- and macronutrient concentrations in a subset of our greenhouse-grown birch seedlings (Table 3.4). For several elements (copper and iron), a strong negative correlation between seedling concentration of each element and seedling mass combined with very high seedling concentrations indicated that seedlings had not yet diluted their seed reserves of these elements via growth by the time we ended our greenhouse experiment. Only seedling zinc differed significantly with wood species (Table 3.4), but showed no significant correlation between seedling mass and nutrient concentration. Although P concentration in birch seedlings did not vary significantly among log species, it explained a high percentage of variation in seedling mass, especially when birch logs were excluded from the analysis ($R^2 = 0.46$, $n = 11$, $p = 0.009$, Table 3.4). In addition, mean N:P ratios were smaller on hemlock (11.4) and sugar maple (13.9) logs than on birch logs (17.5, mean across species = 14.1, ANOVA $p = 0.031$), the log species on which seedlings also had the lowest mean P concentration. Seedling mass decreased as N:P ratio increased (Figure 3.8) and when all log species were pooled N:P ratio explained more variation in birch seedling mass than P alone ($R^2 = 0.35$, $n = 16$, $p = 0.009$).

Explanatory models of seedling abundance

We developed multiple regression models of hemlock and birch seedling abundance to test explanatory factors that were measured in the field for the entire set of logs (and thus excluding nutrient supply, water content, and pH). Because field sites differed in seedling abundance likely, in part, due to unmeasured exogenous climate factors, models were developed using seedlings from the Porcupine Mountains site, which had the greatest sample size of seedlings. First-year seedling abundance in 2004 was best explained by the seeds falling on (seed rain in 2003 x log size for hemlock, seed rain for birch), sticking to (% thin moss cover), and for hemlock, receiving enough light on a given log (Table 3.1, Figure 3.9). For established seedling models of both hemlock and birch, most of the variation ($R^2 = 0.77$ to 97) was explained by the number of established hemlock seedlings in the previous year (seedling history), which is not surprising (Table 3.1). However, even with these factors in the model, several additional factors explained part of the remaining variation. For hemlock and birch seedlings in 2003, log size and rot type explained significant additional variation in hemlock seedling abundance, and rot type effects were especially strong (Table 3.1). Furthermore, when log species was added to models, overall model fit was lower and species effects were weaker than those of rot type. 2004 models for established seedlings differed in some ways. Like 2003 models, log size was significant in many cases, but it often added significant explanatory power through its interactions with seedling history. In addition, rot type was not as important as wood species for birch seedlings and neither factor was important for hemlock. For birch, 2003 was a mast seedling germination year such that established seedlings in 2004 were dominated by this young cohort. The lack of a strong association between birch seedling abundance and rot type in this year could occur if rot type were more important for long than for short term survival.

Not all factors influencing hemlock and birch establishment could be tested. For example, the effect of pathogens and the date at which wood species reach the optimal germination temperature of hemlock and birch are not examined here. Factors such as these may be responsible for the lack of seedlings on the majority of logs (69 to 88% of logs at the Porcupine Mountains), since none of the factors measured here could be used to correctly predict which logs had either first-year or established birch or hemlock seedlings present. Our most accurate discriminant analysis, for first-year hemlock seedling presence, still misclassified half of the logs with first-year seedlings as logs that did not have seedlings. However, on those logs that do support seedlings, we found that for both hemlock and birch seedlings, rot type, log size, seed rain and moss cover (for first-year seedlings), and survival of the previous years' established seedlings explain the majority of variation in seedling abundance.

Discussion

In a previous study (Chapter 2), we identified hemlock wood as a better substrate for hemlock and birch seedling establishment than birch wood or sugar maple wood, and increased survival rate as one of the mechanisms explaining this difference. In this study, over half of the variation in established hemlock seedling abundance was explained by the established seedlings present in the previous year (seedling history), a finding similar to that of Rooney et al. (2000). Established birch seedling distributions were also largely driven by long-term seedling survival. However, even with seedling history as well as light, log size, and seed rain in negative binomial regression models, several endogenous wood characteristics explained significant additional variation. Of the variables we could test in field wood samples, greater thin moss cover and brown rot fungi, which are both more abundant on hemlock logs, were associated with greater numbers of seedlings. For birch seedlings in the greenhouse, seedling mass and N content were both greatest on hemlock logs, indicating that the endogenous factors identified here were associated not only with hemlock and birch seedling abundance and survival but also with short-term growth and nutrient uptake increases. Collectively, our results indicate that several characteristics of hemlock wood may have contributed to increased seedling abundance, survival rate, and growth on this wood type: 1) Greater nutrient availability (lowest pH, greatest seedling growth rate and N content), 2) a greater percent of wood surface area covered by moss, and 3) a more favorable pattern of decay (greater tendency to be brown-rotted and longer residence time on the forest floor).

Wood and seedling nutrient supply

Hemlock logs have a much lower pH (~ 4) than either birch or sugar maple logs. The pH of the litter layer in hemlock stands in northern Michigan and Wisconsin is similar to that found in hemlock wood (Rogers 1980). However, the basal area of hemlock, birch, and sugar maple in the area surrounding each log had no effect on pH, and pH of wood and nearby soil were different, suggesting that unlike soil (Finzi et al. 1998b), hemlock logs maintain their internal pH regardless of environmental conditions around them. The near-neutral pHs found on sugar maple logs are less favorable for hemlock than the lower pHs found on hemlock logs, as several nutrients are less available at these higher pHs including phosphorus (which drops off sharply at pH 7.5 in organic soils), nitrogen, potassium, manganese, and zinc (Smith 1989).

Because nutrients were measured in a subset of seedlings, logs, and soil, and could therefore not be included in best-fit models, we can only speculate as to the importance of nutrient supply in determining seedling abundance in comparison to the other endogenous factors tested with regression models. Our greenhouse results suggest that nutrient differences are important even within the first one or two growing seasons, and the response of birch seedlings growing on hemlock or sugar maple logs to N-only fertilizer (Figure 3.7) indicates that N must be at least partially limiting on these wood types. %N in unfertilized seedlings was lower than that found in *Betula verrucosa* seedlings at optimal relative growth rates (Ingestad 1971) and was increased by fertilization. This would suggest that N is important for seedling growth and therefore plays a role in determining seedling abundance. However, taken as a whole, our results also strongly suggest that N is not the sole limiting nutrient for seedling growth on wood.

Although growth, survival, and abundance of seedlings were all greatest on hemlock logs (Figure 3.4, Chapter 2), neither N concentration ([N]) nor N mineralization rate (Nmin) were significantly correlated with birch or hemlock seedling N content or biomass, whether wood species were pooled or tested separately. Several other studies have also found a lack of correlation between N supply and hemlock or birch seedling growth (Crabtree and Bazzaz 1993, Finzi and Canham 2000), and some have found that N supply influences survival though not growth (Sivaramakrishnan and Berlyn 1999, Catovsky and Bazzaz 2002). In our study, [N] was lowest on hemlock logs while Nmin was highest. Both measures are potential indicators of N available to plants, and both measures also ignore some parts of the N cycle (Binkley and Hart 1989). [N] is affected by vegetation density and uptake, and thus likely a more accurate measure of N availability for individual seedlings (Walters et al., in press., but see Grenon et al. 2005), which is the scale in which we were interested in this study. Decaying hemlock logs contain more roots than sugar maple logs (Marx, pers. obs.), and greater root uptake could account for lower [N] despite higher Nmin in hemlock logs (Figure 3.3). Note that differences in N supply were only significant when we used the full set of wood samples collected from 2002 or 2004 (as in Figure 3.3), and not significant when we examined only wood samples from logs that supported 2-year-old seedlings (as in Figure 3.4). This was due to high variability in wood N supply in the smaller subset, and may have contributed to the lack of correlation between wood N supply and seedling characteristics. We did, however, find strong evidence for co-limitation of seedling growth on wood by N and phosphorus (P) supply. Three lines of evidence suggest that hemlock logs supply an optimal balance of nutrients to seedlings:

First, birch seedlings grown on hemlock logs for just four months were significantly larger than those grown on sugar maple logs. The measurable differences in growth in such a short period of time with exogenous factors held constant suggest that nutrients may be very important for short-term growth and survival, and given the length of time both hemlock and birch seedling roots remain in logs before the seedlings are able to support their own weight or explore other substrate, likely important for long-term growth and survival as well.

Second, mycorrhizal birches and hemlocks in the greenhouse were significantly larger than their non-mycorrhizal counterparts (Figure 3.6a and b, Figure 3.5). Access to both N and P is improved by mycorrhizae (Perez-Moreno and Read 2000), and both our greenhouse and field results suggest that seedlings growing on sugar maple logs (sugar maple is endomycorrhizal; Klironomos 1995) may have a lower chance of becoming colonized by ectomycorrhizae, possibly due to differences in ectomycorrhizal fungal communities across wood species that parallel those in wood fungal communities (Kropp 1982b), or to a lack of tree roots that would provide a source of mycorrhizal inoculum (Dickie and Reich 2005) in sugar maple logs. In the field, older seedlings were more likely to be mycorrhizal than 2-year-old seedlings, suggesting a survival advantage conferred by mycorrhizal inoculation. One caveat in interpreting these results is that seedlings may be infected with mycorrhizae because they are larger and have a greater rooting volume, rather than larger because they are infected with mycorrhizae.

A third reason that birch seedlings, if not both birch and hemlock, grow largest and survive best on hemlock logs may be that hemlock logs supply low but sufficient levels of both N and P, resulting in seedlings with the most balanced N:P ratio (11.4), similar to the ratio of 12.5 suggested for optimal growth with minimal nutrition (Ericsson and Ingestad 1988). On birch logs, birch seedlings had %P values lower than those required for optimal relative growth rate in *Betula pendula* (Ericsson and Ingestad 1988) and high N:P ratios. Seedlings on this wood type also did not respond to N-fertilization, suggesting that they were most limited by P. Thus, N:P explained only 13% of variation in seedling mass on this wood type. On hemlock and sugar maple logs, N:P explained 54 and 42%, respectively, of variation in seedling mass, suggesting that in addition to N, P limits growth on these species. Sufficient nitrogen and phosphorus availability in hemlock wood, whether mediated by pH, type of decay fungi, or mycorrhizal colonization, increased the growth (and, in the field, potentially the survival) of hemlock and birch seedlings under greenhouse conditions.

Wood surface characteristics

The importance of percent cover of thin moss in explaining both first-year hemlock and birch seedling abundance is not surprising, but its association with hemlock wood is novel. Several authors have reported a correlation of moss with seedling densities or germination in the past. Goder (1961) reported that moss cover and hemlock seedling density were positively correlated on decay stage II and III wood. In Oregon, moss-covered wood surfaces retain more western hemlock seeds than some bark-covered or bare surfaces (Harmon 1989), and this is likely true for eastern hemlock seeds in Michigan. Although for the most part thin moss and total moss cover were interchangeable, thin moss was a more reliable predictor of seedling abundance than the two moss types combined. This may be because very thick layers of moss reduce germination of seeds (Harmon and Franklin 1989) or prevent seedling roots from accessing nutrients and water below the moss mat. When thin and thick moss cover were combined, hemlock logs had a greater average percent cover of moss than did hardwood logs (Table 3.2), which may again contribute to their greater numbers of first-year hemlock seedlings and higher birch and hemlock seedling survival rates. Litter cover was also greater on hemlock logs, and litter is apparently not as harmful to seedlings on logs as it is to those on soil. 21% of established hemlock and birch seedlings in 2003 were growing on litter, which covered 20% of log surface area. As with moss, depth of the litter layer may be important (Peterson and Facelli 1992). Most logs had a thin surface covering of hemlock needles and small pieces of hardwood leaves, rather than the thick litter layer found on nearby areas of the forest floor.

Wood decay

Existing studies have estimated the decay rates of hemlock (Tyrrell and Crow 1994a), birch, and sugar maple (yellow birch and maple spp.: Arthur et al. 1993), but this is the first study to measure residence time of all three species using the same method and in the same field sites. The longer residence time of hemlock logs may benefit saplings by providing a sturdy substrate that supports sapling weight for at least a median of 54 rather than 21-24 years. Also, if well-decayed wood provides moisture and nutrients to saplings even after it no longer supports their weight, which seems likely given the horizontal habit of sapling and tree roots along and within logs, then hemlock logs should support a greater proportion of hemlock and birch saplings than do hardwood species. They may also support more of the hemlock saplings that capture gaps to ascend to the canopy, since such saplings are an average of 149 years old (Dahir 1994).

In addition to spending more years on the ground, hemlock logs tend to be decayed by brown-rot fungi rather than by white-rot fungi or both types. Rot type was one of the most consistently important factors in our models, sometimes remaining significant even when both seedling history and first-year seedlings were in the model. When log species and then rot type were entered into negative binomial regression models, log species explained additional variation only in a single model. There are several reasons that brown-rotted (hemlock) wood may be so favorable for seedlings. One possibility is that brown-rotted wood remains structurally sound and provides a good rooting medium for seedlings. A second possibility is that because brown-rot fungus decays wood at a faster rate than it can consume the products, at least initially, seedlings on brown-rotted wood have greater access to nutrients than seedling grown on white-rotted wood where decay products are immediately consumed (Goodell et al. 2003). A third possibility is that both decay fungi and seedlings respond to some other aspect of hemlock wood, such as availability of micronutrients or wood pH, and that brown-rot fungi and seedlings are most abundant under the same conditions.

Exogenous factors

Exogenous factors varied across field sites and may have explained large-scale variation in seedling abundance, but they rarely varied across species and were not usually important in determining seedling abundance (Chapter 2) or mass. Although water is important for the survival of both hemlock and birch seedlings, and may have explained why average seedling density was greatest at our wettest field site, wood water content does not vary across wood species (Figure 3.1). In addition, water content is far higher, even in summer, than that which causes birch seedlings to wilt in the greenhouse (Figure 3.1). Attempts to obtain a water loss curve from wood by using a pressure plate apparatus, which would be a more conclusive test of differences in water availability than water content, failed. This is likely because wood has at least three separate curves (water loss from vessels, pores, and between intact wood pieces, and possibly also sapwood versus hardwood) that would be treated as a single curve by this technique (D. Fredlund, pers. comm., 2004). Light and seed rain were important in determining the numbers of first-year seedlings, but like water content, they rarely varied across wood species and most likely do not drive patterns of established seedling density (Chapter 2, Table 3.3).

Ecological and management implications

The importance of hemlock wood for hemlock and birch seedling establishment (Chapter 2) partly explains the stability of hemlock- and sugar maple-dominated patches in primary hemlock-hardwood forests (Davis et al. 1995) and also why hemlock forests have not recovered after most were logged in the 1800s (Noss and Peters 1995). Our results here show that, compared to sugar maple wood, the greater quality of decaying hemlock wood as a seedling establishment substrate is associated with features of the wood itself and not the microenvironment in which it is found. Likewise, we've shown that sugar maple logs do not have the characteristics favored by hemlock and birch seedlings regardless of where such logs are found. Thus hemlock and birch are unlikely to establish in closed-canopy sugar maple forests unless decaying hemlock wood is available as a substrate, and tend to either remain in hemlock-dominated stands where decaying hemlock wood is more abundant or enter stands by germinating on mineral soil after severe disturbance (Tubbs 1969, Erdmann 1990, Peterson 2000). Sugar maple seedlings, on the other hand, are unable to use hemlock logs as seedling establishment sites, and seedlings that germinate on logs become chlorotic and often die within the first several months (Figure 3.10). Sugar maple seedlings may be N-limited on wood; 2-year-old sugar maples growing on logs have lower N contents than sugar maples growing on adjacent soil (paired t-test, n = 9 pairs, p = 0.065, Figure 3.10). Hemlock wood therefore has the additional advantage for hemlock and birch seedlings of being relatively clear of sugar maple seedlings.

For areas where increasing or maintaining hemlock basal area is a management goal, retention of hemlock decaying wood in particular is important. An attempt to seed logs in the field in 2003 failed due to either lack of seed germination or early mortality of germinants, but even first-year hemlock and birch seedlings are more abundant on hemlock logs in our field sites (Chapter 2). It seems likely, given our identification of brown-rot fungi, moss, pH, nutrient concentrations, and long residence time as wood characteristics that influence seedling establishment, that other conifer wood species such as cedar and white pine can also support hemlock and birch seedlings. Both white pine logs and cedar logs were observed with seedlings in our field sites (Marx, pers. obs.), though they were too rare to examine statistically, and like hemlock, cedar also tends to decay via brown-rot fungi, develop moss cover, and remain in the later decay stages for long periods of time.

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Table 3.1. Best-fit explanatory models of numbers of seedlings occurring on each log at the Porcupine Mountains. Chi-square and p-values are given for each significant factor in the model. Akaike information criteria (AICc) were used to select each best-fit model. Not all second-order interactions (and no higher-order interactions) were tested since many interactions, especially those containing categorical variables such as rot type, resulted in models that did not converge.

Year	**Response**	**Model**					
2003	**Hemlock established seedlings**	seedling history	log size	rot type			
	Chi-square p-value (pr > χ^2)	31.25 <0.0001	5.38 0.0203	21.60 <0.0001			
		seedling history		rot type	first-year history		
	Chi-square p-value (pr > χ^2)	47.32 <0.0001		19.99 0.0002	7.03 0.008		
2003	**Birch established seedlings**	seedling history	log size	rot type		light	
	Chi-square p-value (pr > χ^2)	21.38 <0.0001	8.13 0.004	19.65 0.0002		6.44 0.0111	
2004	**Hemlock established seedlings**	seedling history	log size				seedling history x log size
	Chi-square p-value (pr > χ^2)	21.60 <0.0001	17.64 <0.0001				9.21 0.0024
2004	**Birch established seedlings**	seedling history	log size	wood species			Seedling history x log size
	Chi-square p-value (pr > χ^2)	14.39 0.0001	17.33 <0.0001	9.75 0.0076			8.16 0.0043
2004	**Hemlock first-year seedlings**	seed rain*size			light	% thin moss	
	Chi-square p-value (pr > χ^2)	12.12 0.0005			8.58 0.0034	8.02 0.0046	
2004	**Birch first-year seedlings**	seed rain per trap				% thin moss	Seed rain x thin moss
	Chi-square p-value (pr > χ^2)	1.02 0.312				4.06 0.044	11.14 0.0008

Table 3.2. pH, seed rain, canopy openness, fungal rot type, and water content of hemlock, birch, and sugar maple logs. Means are presented with 1 s.e. in parentheses. Means followed by the same letter are not significantly different (student's t-tests, all possible contrasts, alpha = 0.05). Data from all sites were pooled for factors not significantly affected by field site. N = 63 logs for pH; 138 logs with seed traps; 314 logs for canopy openness (manual threshold); 271 logs for fungal rot type, and 318 logs for moss cover.

	Hemlock	**Birch**	**Sugar maple**
pH	4.2 (0.08) a	5.2 (0.30) b	6.7 (0.29) c
Hemlock seeds/m^2 Hemlock | Mixed stands			
Huron Mts.	1,494(395)a | 1,592(690)a	1,622(549)a | 349(143)a	2,366(373)a | 155(34)a
Porcupine Mts.	2,068(495)a | 383(140)ab	3,382(582)a | 2,375(1,446)a	1,283(336)a | 230(48)b
Sylvania	421(88)a | 711(399)a	583(323)a | 662(479)a	658(242)a | 452(119)a
Birch seeds/m^2			
Huron Mts.	8,110(1,462)a | 963(526)a	8,246(1,424)a| 1,289 (579)a	3,963(849)a| 1,386(310)a
Porcupine Mts.	2,555(697)a | 8,215(3,099)a	2,720(603)a | 11,743 (5,033)a	395(78)a | 2,797(2,670)a
Sylvania	3,963(849)a | 1,386(310)a	1,404(387)a | 1,013 (203)a	1,451(490)a| 470(71)a
Sugar maple seeds/m^2	118(26)a | 316(65)a	55(13)a | 255(61)a	171(30)a | 162(28)a
Canopy openness			
Huron Mts.	7.05% (0.50)a	7.10% (0.57)a	8.38% (0.42)a
Porcupine Mts.	4.05% (0.09)a	4.18% (0.16)a	3.48% (0.14)b
Sylvania	3.22% (0.17)a	3.16% (0.10)a	3.84% (0.18)b
% of logs brown-rotted			
Huron Mts. (118)	74.4%	20.0%	10.2%
Porcupine Mts. (82)	58.5%	16.6%	4.3%
Sylvania (71)	23.1%	4.5%	0%
% total moss cover			
Huron Mts.	23.7% (4.46)a	15.9% (4.01)a	15.7% (2.90)a
Porcupine Mts.	48.9% (4.84)a	28.3% (6.96)b	25.6% (5.49)b
Sylvania	35.8% (8.07)a	20.7% (5.67)a	27.3% (4.11)a

Table 3.3. Effects of log species and light on seedling mass and N content. Values are p-values from two-way ANOVA effect tests. Data were logarithm-transformed before analysis. In all cases, the interaction between logs species and canopy openness was not significant ($p > 0.250$) and the term was removed from the ANOVA.

Seedling species	Response	Effect of log species	Effect of canopy openness
Betula, field 2002 n = 17 logs	Mass	0.204	0.162
	N content	0.035	0.749
Betula, field 2004 n = 33	Mass	0.013	0.364
	N content	0.011	0.734
Betula, greenhouse n = 60	Mass	0.064	--------
	N content	0.817	--------
Tsuga, field 2002 n = 22	Mass	0.921	0.049
	N content	0.735	0.210
Tsuga, field 2004 n = 26	Mass	0.734	0.081
	N content	0.673	0.027
Tsuga, greenhouse n = 59	Mass	0.104	--------
	N content	0.220	--------

Table 3.4. Macronutrient percent of plant dry mass (g/g, Ca, N, P, K) and micronutrient concentrations (ppm, **or mg element/kg dry plant material(Incorrect units corrected 06/06.):** B, Cu, Fe, Mg, Mn, Zn) in whole birch seedlings grown on three species of wood in the greenhouse. Each value represents the mean nutrient concentration of composite samples (4 entire birch seedlings from a single pot make up each sample, N = 5 to 7 for each wood species), with 1 s.e. in parentheses. The ratio of macronutrients to one another (N is set to 100) in *Betula verrucosa* seedlings at optimum nutrition (Ingestad 1971), and the % dry mass that would be expected in our data given these ratios and a %N (setpoint for the ratios) of 1.60 are provided for comparison. * = Pearson's correlation between nutrient concentration and birch mass is significant, alpha = 0.05.

	Hemlock wood	**Birch wood**	**Sugar maple wood**	***Betula verrucosa* ratios / Expected % dry mass**	Correlation with birch mass (species pooled)
% dry mass of:					
Calcium	1.35 (0.04)a	1.45 (0.11)a	1.55 (0.10)a	7 / 0.11	-0.254
Nitrogen	1.44 (0.12)a	1.60 (0.16)a	1.72 (0.16)a	100 = 1.60	-0.327
Phosphorus	0.12 (0.01)a	0.09 (0.01)a	0.13 (0.02)a	13 / 0.21	0.539*
Potassium	0.47 (0.04)a	0.53 (0.10)a	0.64 (0.10)a	65 / 1.04	-0.551*
ppm of:					
Boron	0.12 (0.01)a	0.13 (0.01)a	0.12 (0.01)a		0.190
Copper	0.06 (0.01)a	0.06 (0.01)a	0.05 (0.01)a		-0.723*
Iron	0.78 (0.11)a	1.00 (0.24)a	0.80 (0.16)a		-0.922*
Magnesium	13.23 (0.79)a	13.47 (0.81)a	12.38 (0.43)a		-0.350
Manganese	1.84 (0.65)a	1.11 (0.28)a	0.78 (0.35)a		0.280
Zinc	0.47 (0.08)a	0.89 (0.11)b	0.39 (0.06)a		-0.058

Corrected below

Errors corrected June 2006 during revisions for CJFR article. Correct values are:

ppm of:				
Boron	48.36 (4.09)a	52.24 (7.08)a	50.59 (3.10)a	0.190
Copper	22.26 (2.68)a	24.16 (2.81)a	18.31 (2.34)a	-0.723*
Iron	310.10 (43.35)a	314.65 (63.54)a	279.78 (61.78)a	-0.922*
Magnesium	5277.79 (321.01)a	5532.80 (337.00)a	4995.01 (151.90)a	-0.350
Manganese	729.71 (256.51)a	357.54 (98.06)a	316.89 (169.92)a	0.280
Zinc	187.92 (31.57)a	360.42 (54.41)b	136.98 (21.44)a	-0.058

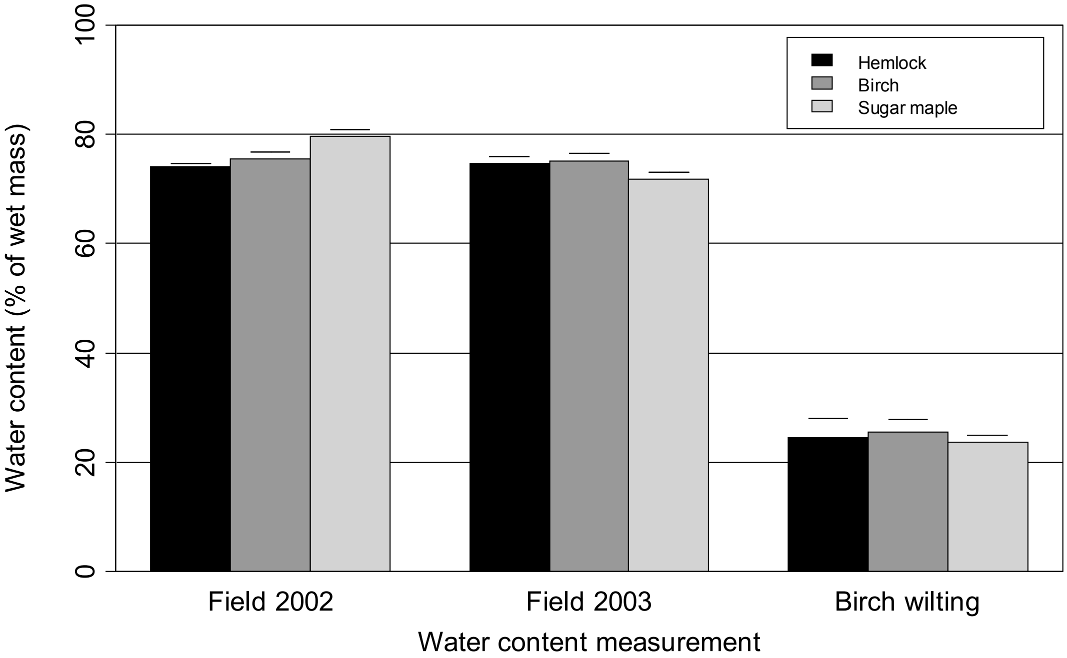

Figure 3.1. Field water content of wood pieces in 2002 and 2003 and water content of wood measured at the point at which birch seedlings planted on each wood piece wilted in the greenhouse. Means are presented with error bars representing 1 s.e. Field 2002 n = 239 logs, field 2003 n = 172 logs, greenhouse birch n = 30 pots

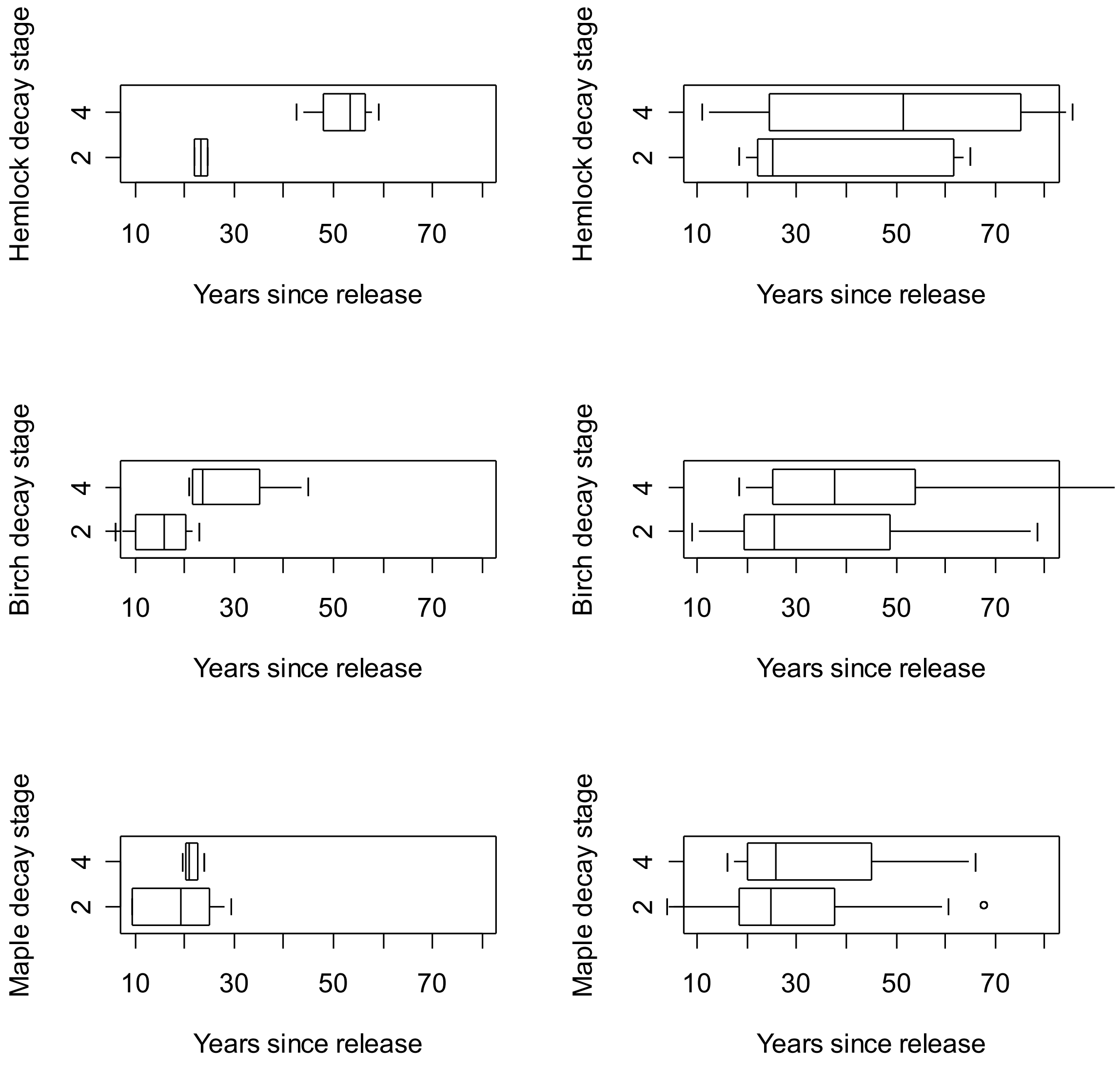

Figure 3.2a and b. Ages of hemlock, birch, and sugar maple logs in decay stages II and IV. a. (left) Conservative objective criteria for determining release. Release dates are the average of two trees per log. n = 5 hemlock, 8 birch, and 9 maple logs. b. (right) Subjective criteria for determining release. Release dates are averaged when both trees for a single log showed a release, but included even if from a single tree. n = 10 hemlock, 26 birch, and 28 maple logs. Outer limits of each box represent the 25th and 75th percentile, while whiskers extend to 1.5 x the interquartile range.

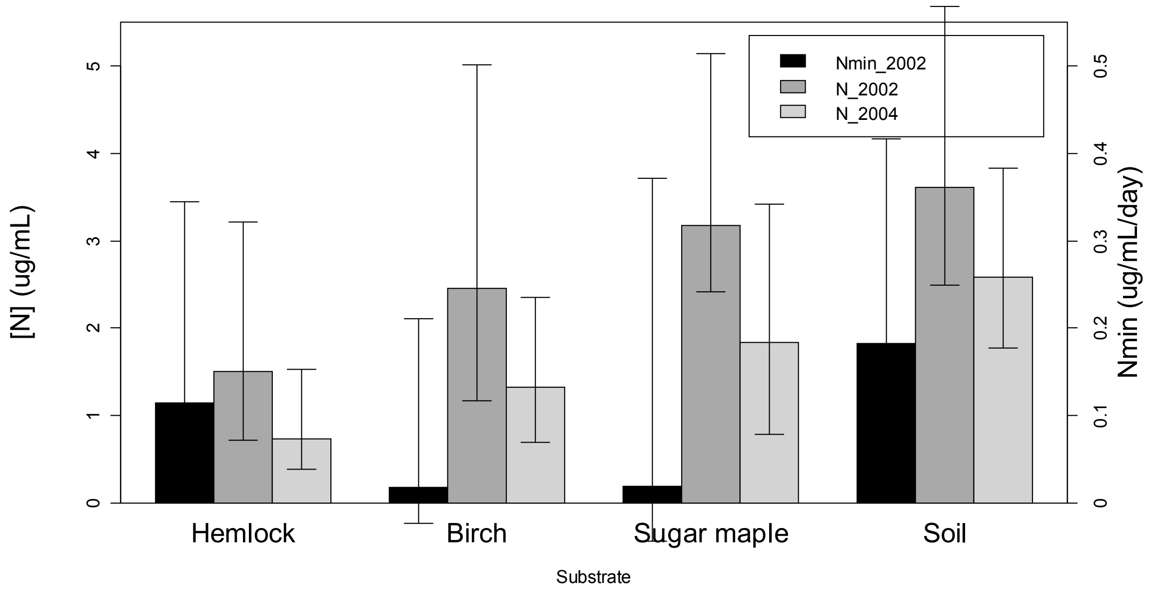

Figure 3.3. Median rates of N mineralization (Nmin) and inorganic N concentrations ([N]) in wood in 2002 and 2004. Nmin is plotted on the secondary Y axis. Bars represent medians, error bars represent the 25th and 75th percentiles. ANOVA tests performed on logarithm-transformed data indicated that the [N] of hemlock logs was lower than that of both birch and sugar maple logs in 2002, and lower than that of sugar maple logs in 2004. n = 128 wood samples in 2002 and 129 in 2004. Note that this is a larger sample than the subset from which 2-year-old seedlings were collected and used to test seedling/N supply relationships.

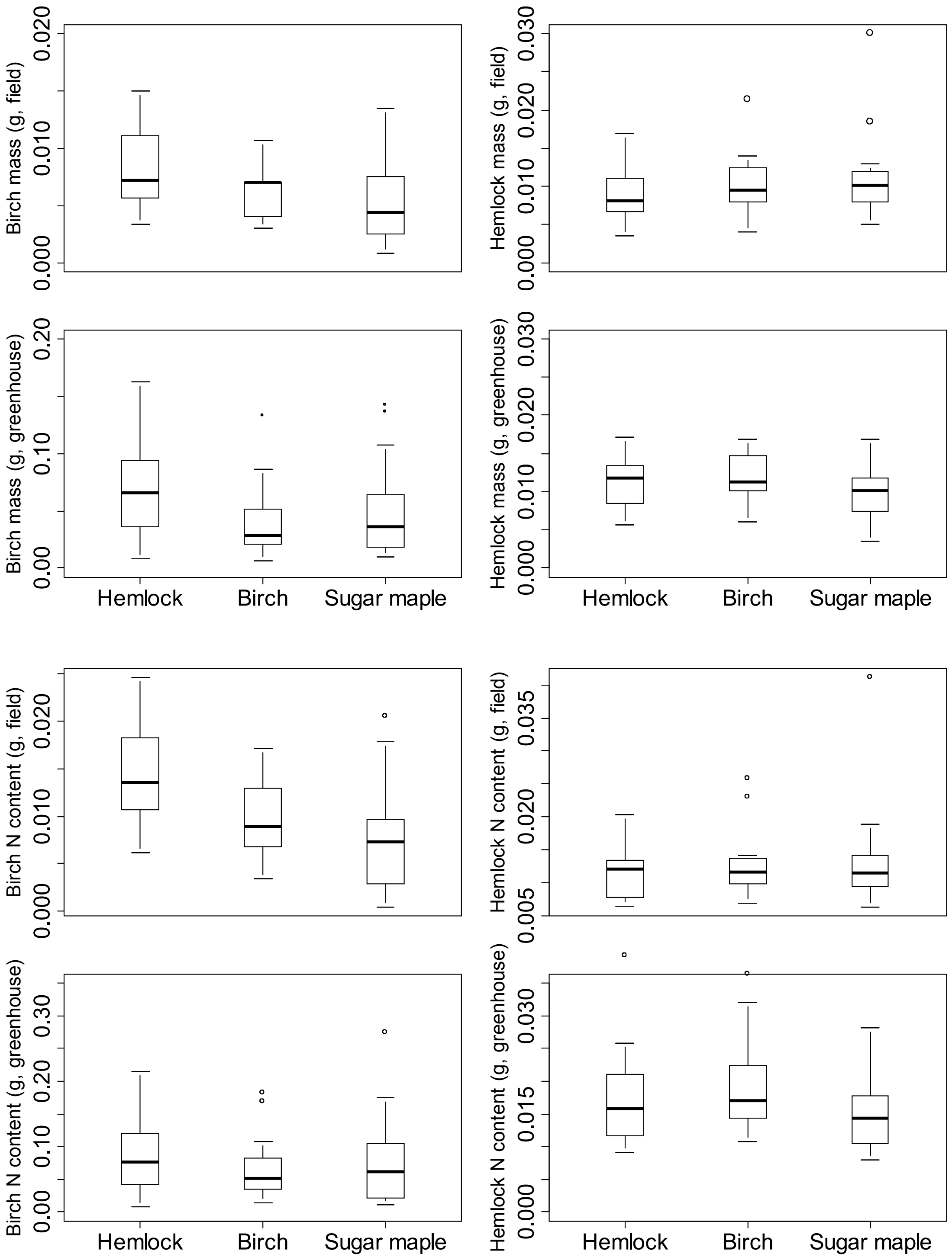

Figure 3.4. a. Median seedling mass, and b. Median N content, of birch and hemlock seedlings growing on three different wood species. n = Birch: 50 logs with birch seedlings in the field and 60 in the greenhouse; Hemlock: 48 and 59.

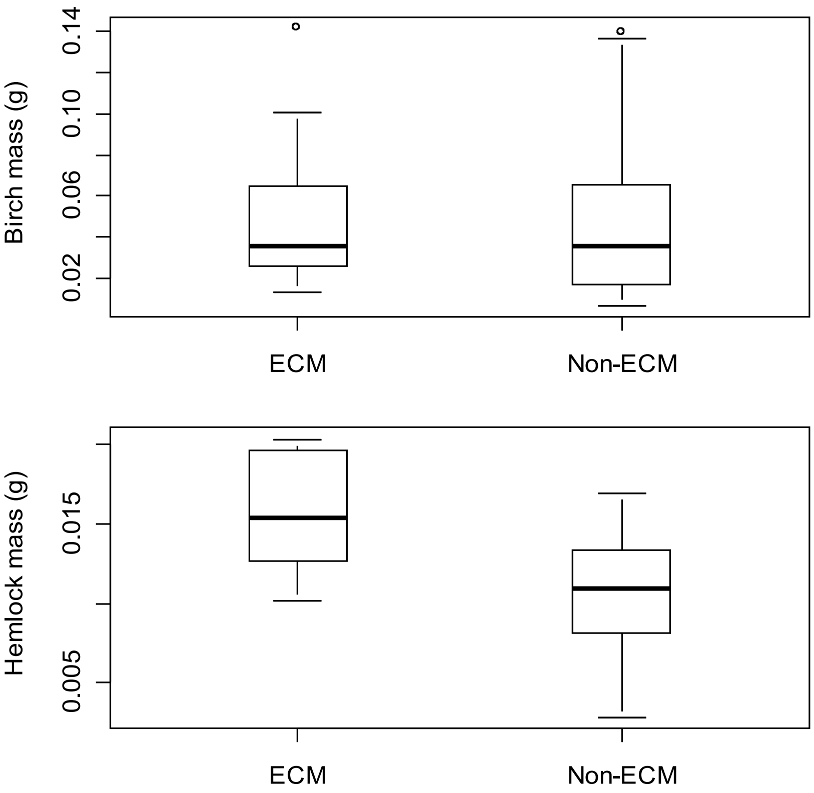

Figure 3.5. Mass of mycorrhizal and non-mycorrhizal greenhouse seedings. n = 233 birch and 258 hemlock seedlings. Only unfertilized seedlings are shown.

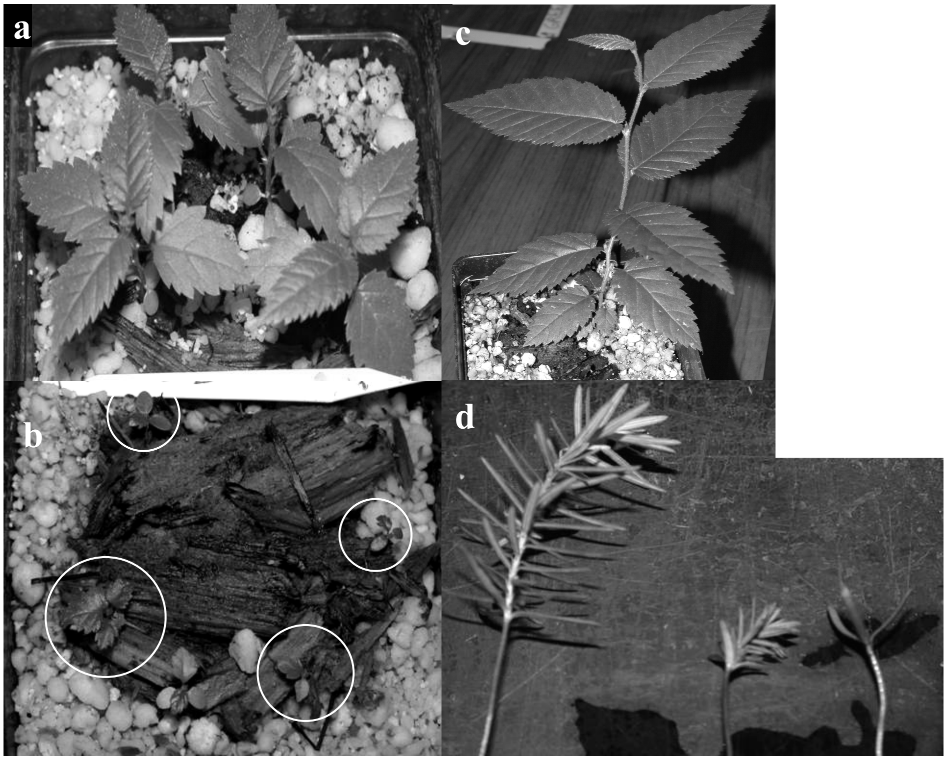

Figure 3.6. Greenhouse seedlings showed great variability in size. a. Mycorrhizal birches growing on a hemlock log. b. Non-mycorrhizal birches on a birch log. c. Fertilized birch. d. Non-mycorrhizal hemlocks on a single sugar maple log.

Figure 3.10. First-year sugar maple seedlings growing on a log and on nearby soil. The seedlings on the log (to the right of the dotted line) show signs of nutrient deficiency, unlike the first-year sugar maples on soil beside them.

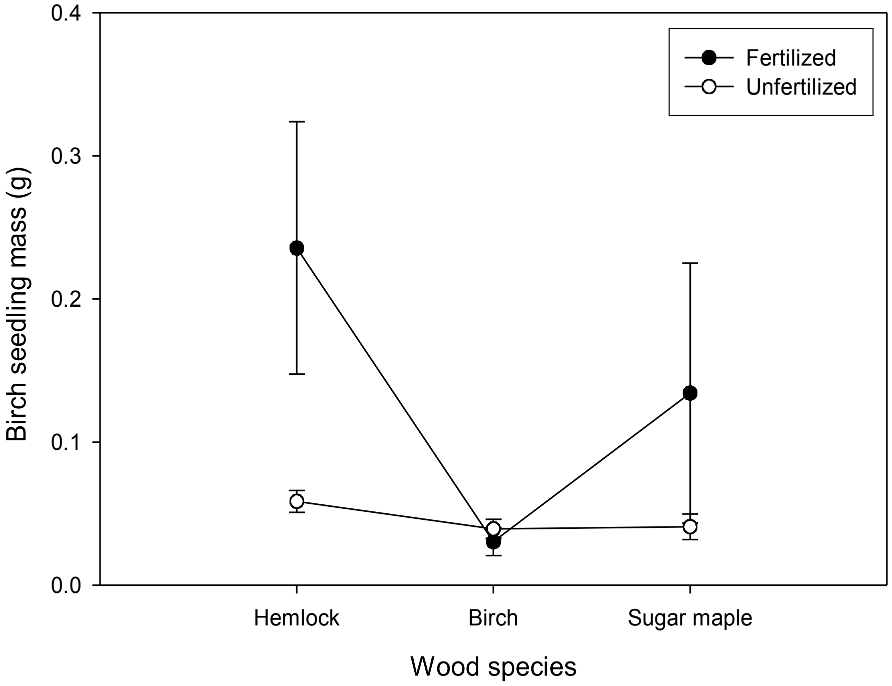

Figure 3.7. Response of birch seedlings to fertilization with N when grown on different wood species. Symbols represent mean values of birch seedling mass, pooled by pot. Error bars represent 1 s.e. n = 18 (6 hemlock, 8 birch, and 4 sugar maple) fertilized and 60 unfertilized pots (20 of each species).

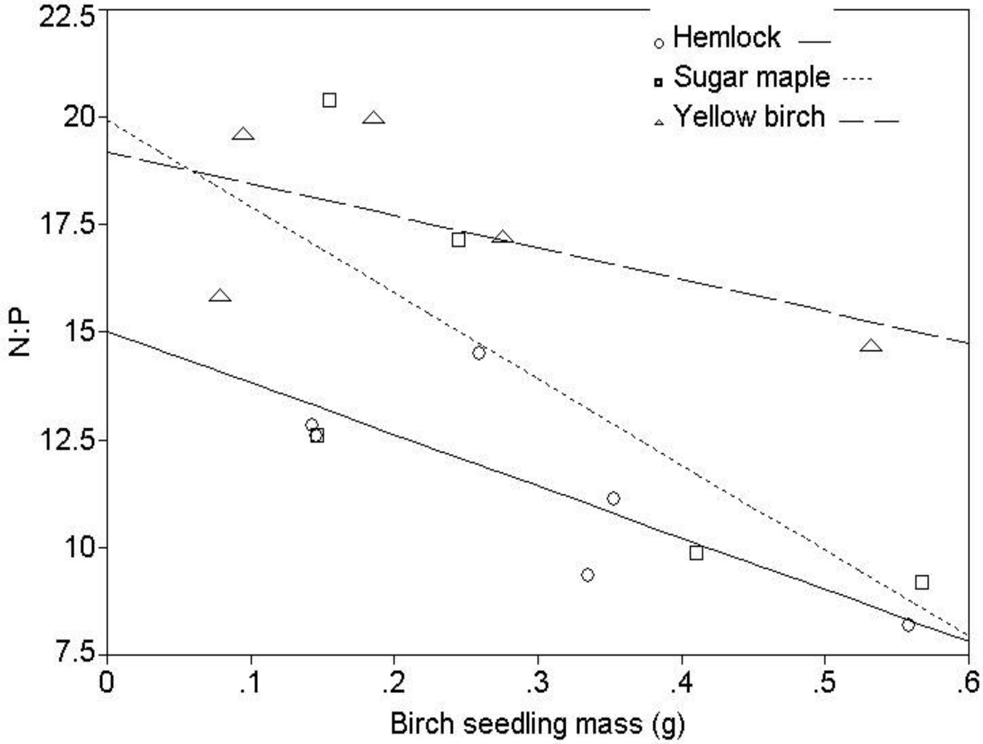

Figure 3.8. Relationship between birch seedling N:P and mass (pooled mass of four birch seedlings grown on the same piece of wood). n = 16.

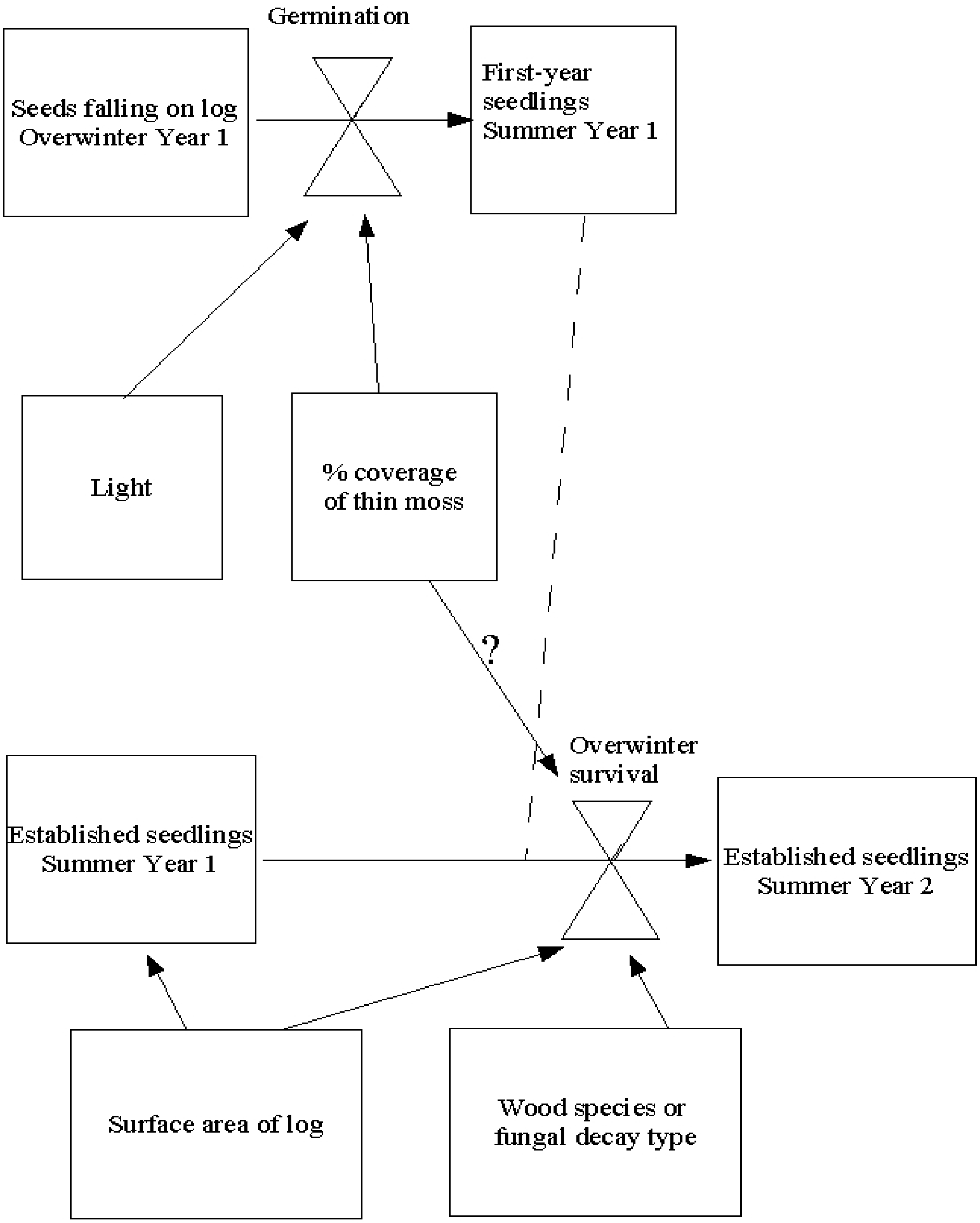

Figure 3.9. Conceptual diagram of factors influencing first-year and established seedling survival on decaying wood. Factors significant in best-fit models are indicated with solid lines. The dashed line indicates a factor that could not be tested with our data.

CHAPTER FOUR
ADDITIONAL METHODS

Identification of decaying wood to species

Wood samples from field plots were in many cases highly decayed (late stage IV). I was able to identify even these pieces to species using methods taught to me by Alex Wiedenhoeft at the US Forest Service Forest Products Laboratory in Madison, WI. I selected the least-decayed piece of wood I could find on each log as an ID sample. Samples were transported from the field to the lab in sealed ziploc bags, because it is critically important that decaying wood samples *never* be allowed to dry out. A dried sample, unless it can be re-wetted which is not always possible, will not yield usable slices for species identification. In the lab, I used GEM surgical-grade razor blades to cut wet samples of wood into the thinnest slices possible, being careful to get a good radial, tangential, and transverse section from each piece. Sections were mounted in a 1:1 mixture of ethanol and glycerine by putting sections in a small amount of solution on a microscope slide, adding a cover slip, and then boiling slides on a hot plate at medium to high heat until all of the ethanol and the water inside each wood section had boiled off. Too high heat caused sections to move out from under the cover slip when the solution boils and bubbles vigorously, and too low heat may not get rid of all of the water and replace all of the air spaces in the wood with glycerine solution. A well-prepared slide looks clean under the microscope; leftover air bubbles remaining from not enough boiling time were easily visible. I used clear nail polish painted around the outside edge of each cover slip to seal the slides, after which they could be stored vertically in a slide box and should last many years without drying out. I found that I usually needed magnification of at least 200x to see the finer characteristics of wood slides. *Abies* and *Tsuga* are often indistinguishable from one another even at that magnification, and I used a high quality microscope at as high as 400x at the Forest Products Laboratory to separate these species. The problem is not one of making the features large enough to see, it is more of resolution and depth of field, which is why a well-maintained and perfectly aligned microscope is essential for identification of these two species.

Key to wood species found in Upper Michigan hemlock forests

This key covers the following species: *Tsuga canadensis, Abies balsamea, Picea glauca, Thuja occidentalis, Pinus strobus, Acer saccharum, Acer rubrum, Betula spp.* (it is not possible to distinguish between *B. papyrifera* and *allegheniensis* with wood alone), *Tilia americana, Ostrya virginiana*. Note that many of the characteristics listed here were those I found most useful in identifying wood, and this is not a complete list.

Not included in the key, but present in my field sites, are:

Fraxinus and *Quercus*, both of which are ring porous and so will be immediately distinguishable from the hardwoods listed above.

1. Does the wood have pores (cross-section or transverse section)?

Yes: *Acer*, *Betula*, *Tilia*, or *Ostrya* SEE hardwood table.

No: *Tsuga*, *Abies*, *Picea*, T*huja*, or *Pinus* SEE conifer table.

2. Can’t tell from cross-section? Are there visible vessels or perforation plates on the radial section?

Yes: Hardwood.

No: Conifer.

Table 4.1. Characteristics of hardwood wood for species identification

Species	Perforation plate	Spiral thickenings	Intervessel pit size	Ray size
Acer rubrum	simple	+	NA	1-5 seriate
Acer saccharum	simple	+	NA	1-3 and 5-8 seriate
Betula	scalariform (many bars)	-	tiny	1-5
Tilia	simple	+	small	tall, laterally compressed, 3-4 seriate
Ostrya	simple and scalariform (few bars – reverse footprint)	+?	small, alternate, some books say medium to large in size	1-3 seriate

Acer saccharum: Usually obvious from the cross section alone, since it is often possible to pick out very thick rays and thinner rays in the same field of view. Rays in tangential section are, again, clearly of two different sizes. Spiral thickenings usually visible even in rather poorly done radial sections.

Acer rubrum: More often identified by default than by any particular distinguishing characteristic. Very easy to confuse with Ostrya or sometimes even Tilia, so be sure you have three good sections to work with and are able to see all of the identifying characteristics.

Betula: Perforation plates give this one away since none of the other species have scalariform plates with so many bars (a striped appearance rather than just a few bars here and there). Also, the tiny inter-vessel pitting is usually easy to see in the radial section. Cross section shows rays larger than pores, and cross section looks very different from maple but somewhat similar to Tilia and Ostrya. Often having bark samples makes actually doing microscope IDs unnecessary for birch.

Tilia: In a fairly intact samples, the rays give this one away. Rays look like they have been compressed sideways, with ray cells taller than they are wide. At first glance rays just look “wrong”. Be sure to check other characteristics as well (such as looking for very prominent spiral thickenings?), though, since stressed wood can sometimes look like basswood, and every once in a while there is a basswood that does not have extremely compressed rays. This is easy to confuse with red maple if you’re not careful.

Ostrya: Like red maple, usually identified by default. The perforation plates are a definite give-away, but are often very difficult to see. The scalariform plates with few bars will sometimes only have a single bar, creating a shape that almost looks like a reverse footprint – instead of a large ball of foot section and small (think men’s shoes) heel, keep the footprint as the same shape but have a line going halfway across the ball of foot section, making a small toe part and a large heel. The cross section sometimes has pores in multiples, looking a little different than maple.

Fraxinus and *Quercus* are ring porous, and oaks have HUGE rays, easily visible with a hand-lens or even with the unaided eye.

Table 4.2. Characteristics of conifer wood for species identification.

Resin canals YES			
	Epithelium	Cross-field pitting	Ray tracheids
Picea	thick walled	piceoid	+
Pinus (whites)	thin walled	fenestriform (looks completely different from piceoid and taxodeoid)	+
Resin canals NO			
	Ray parenchyma end walls	Cross-field pitting	Ray tracheids
Tsuga	nodular	piceoid	+
Abies	nodular	taxodioid	-
Thuja	smooth	taxodioid	-

Picea: Looks like *Tsuga* but with resin canals.

Pinus: This one is fairly easy. Resin canals are fairly large, and the fenestriform pitting looks different than any of the other species. Rays will appear to have large squarish windows in them. Pine will often also be different in its decay pattern, since I have found most of my pine samples as charred stumps or as a hollow stump with one or two pieces of virtually intact wood attached.

Thuja: Sometimes this will be easy since you can smell cedar. Again, decay characteristics *may* help, but be careful: some cedar no longer looks stringy and is mushier than you would expect. Cedar has no resin canals, and has very clearly smooth ray parenchyma end walls. It tends, in my samples, to have a "neater" appearance than other woods, in that the rays will be very clear, and your sections will look suspiciously good. I have mis-identified cedar as hemlock in the past. If you really, truly, can't see any nodular end-walls, don't invent them.

Tsuga and *Abies*: These two are very difficult to tell apart when decayed. Think of the hem-fir wood grade. If it's that hard to tell the *intact* woods apart…

Tsuga has piceoid pits rather than taxodioid. Without a good microscope, piceoid pits often just appear smaller than taxodioid. With a better one you will notice that the taxodioid pits have sort of football-shaped openings while piceoid pits are narrower. *Tsuga* also has biseriate bordered pitting. This means that as you look at the fibers, you will see lines of two pits going down each fiber, as opposed to *Abies* with just one line of pits. BUT be careful that you are not actually looking at two uniseriate, but overlapping, fibers. *Tsuga* does have ray tracheids. These are on the outside of each set of ray parenchyma, and the walls between them look different than the ray parenchyma end walls. The ray parenchyma end walls have a lot of invaginations on them, while tracheid end walls will often look like a line of Xs, one on top of the other. Hoadley (1990) has a great picture of this. Ray tracheids in *Tsuga* can be transparent and "scrappy" looking, with wavy edges. Finally, in the radial section, you'll see that *Tsuga* has strap-like extensions of the torus on the bordered pits. This is only apparent with a very high-powered microscope.

Abies, meanwhile, does not have ray tracheids. Look carefully, at a large section, to make sure you're not just missing them. *Abies* also often has nodular side walls to its ray parenchyma cells, not just nodular end walls. So all walls of the cell have invaginations, not just the end walls. *Abies* lacks biseriate bordered pitting and torus extensions. The most important section by far for this and for *Tsuga* will be the radial section, so put a lot of these on the slide so you can try to be sure to get a good section. It's also important that these sections be thin. Often I am only able to use the very edges of a section to see some of the more difficult characteristics. Again, if you can use bark to help you, do so. Extremely thick, reddish bark is probably not *Abies*. And very thin, fibrous bark is probably not *Tsuga* unless it came off of a branch.

Wood decay fungi classification

Wood may be decayed by a number of organisms, including white rot fungi, brown rot fungi, and soft rots. In my initial survey of decaying wood, I listed whether wood was white-rotted or brown-rotted. This was based on a visual identification of wood characteristics. Brown-rotted wood was light to dark brown in color, and decayed as discrete chunks, usually cubes or rectangles of wood. Brown-rotted wood often snapped cleanly along vertical or horizontal breaks when it was pulled from the rest of the log. White-rotted wood was distinguished by two sets of characteristics. White-rotted wood was sometimes saturated with water and a mass of long soft strings. It was possible, in highly decayed wood, to reach into a log and pull out a handful of these strings, which would compress when squeezed, unlike brown-rotted wood. White-rotted wood also sometimes looked very dry and was solid to the touch. The top surface of the wood was occasionally black, but unlike charcoal did not leave black streaks on hands or other surfaces. In this "dry" form of white rot, the wood under this hard surface showed the characteristic form of white rot with wet strings throughout.

Several logs were brown-rotted on one end and white-rotted on the other, and early decay stage logs often did not yet show signs of either fungal type. Soft rots, stains, and bacterial decay were not recorded in the field, although stains were occasionally present on sugar maple and oak logs found in field plots, turning the wood a blueish green color. Soft rots may have been present in my field sites. These fungi degrade the outside layers of wood, and often decay wood also simultaneously attacked by white rot fungi (Goodell et al. 2003). It is possible that some of the early decay stage logs I classified as not yet being attacked by fungi were in fact being attacked by soft rots, since soft rots attack the outside layers of wood but leave it relatively hard and intact.

CHAPTER FIVE
CONCLUSIONS

In Chapter 2, I demonstrated the restriction of established hemlock and birch seedlings to decaying wood and in particular to hemlock and birch wood. First-year seedlings are found on a broad range of substrates, and though rare are even found on soil. By the fourth growing season, however, hemlock and birch are found almost exclusively on hemlock and birch wood. Hemlock wood is a better substrate than birch wood in most cases, especially for survival of hemlock seedlings. This may help maintain the distribution of adult hemlock, birch, and sugar maple seedlings and the close spatial association between hemlock and birch seedlings, saplings, and canopy trees. The tendency of hemlock and birch seedlings to grow on wood is not enough to explain the species association at either the stand level or the individual tree level. Their restriction to hemlock wood, however, makes this an almost complete explanation. The one remaining question is why paired hemlock and birch trees are the same diameter. One reason may be that they grew at the same rate, possibly sharing nutrients with adult trees or each other through the same mycorrhizal network. This could be tested by coring tree pairs and comparing their growth rings. Likewise, the restriction of hemlock and birch seedlings to wood types more abundant in hemlock-dominated than in sugar maple-dominated stands fills a gap in the existing explanations for maintenance of the hemlock/hardwood patch structure.

Explanations for the suitability of hemlock wood for seedling establishment were explored in Chapter 3. Although some results are preliminary and will need further study, hemlock wood: 1) remains in the decay stages that support the greatest numbers of seedlings for a longer period of time than birch or sugar maple wood, 2) has a more favorable pattern of decay, usually developing a layer of moss over brown-rotted wood, 3) provides a balance of nitrogen and phosphorus, in addition to providing sufficient phosphorus for seedling growth, 4) has a low pH, which may be related to its tendency to be attacked by brown rot and its ability to provide phosphorus to seedlings. Although the seedlings I studied were rarely mycorrhizal, there are several results in these chapters that suggest that hemlock may be better able to provide mycorrhizal inoculum to seedlings than sugar maple wood, and possibly birch wood. Mycorrhizae may also be one of the reasons that sugar maple seedlings have such poor survival on wood.

In the introduction to this dissertation, I contrasted how easily hemlock seedlings could be killed with the stability of stands of adult hemlocks. *Adelges tsugae*, hemlock woolly adelgid, has destroyed many of the hemlock forests in New England and along the east coast, and seems likely to kill both adults and young seedlings and saplings of hemlock since it prefers new growth. Barring a major advance in control of the adelgid, it will likely reach Michigan's hemlock forests at some point in the next decade, and the old-growth systems studied here will lose a large proportion of their hemlock trees. The results presented here suggest that leaving dead and downed hemlock trees in place will be helpful in eventual restoration efforts, assuming that they don't provide a refuge for adelgid. Additional research into the use of yellow birch as “placeholders” for hemlock would be of interest, since birch logs can support at least young hemlock seedlings, and birch and hemlock can coexist in close proximity. Any approach will need to exclude white-tail deer or greatly reduce deer densities. Hemlock restoration efforts would be an interesting test of some of the ideas about hemlock and birch regeneration and the interdependence of hemlock and birch presented here.

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SUBSTRATE LIMITATIONS TO *TSUGA CANADENSIS* AND *BETULA ALLEGHENIENSIS* SEEDLING ESTABLISHMENT

By

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ABSTRACT

SUBSTRATE LIMITATIONS TO *TSUGA CANADENSIS* AND *BETULA ALLEGHENIENSIS* SEEDLING ESTABLISHMENT

By

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In this dissertation, I provide evidence that the distribution of hemlock (*Tsuga canadensis*), yellow birch (*Betula allegheniensis*), and sugar maple (*Acer saccharum*) decaying wood maintains two patterns of tree distribution in Upper Michigan: the eastern hemlock-northern hardwood patch structure and the hemlock/yellow birch spatial association. Patches (3-30 ha) of hemlock with scattered yellow birch have remained hemlock-dominated and the same size for over 3000 years, even when adjacent to patches of northern hardwood forest usually dominated by sugar maple. Across both patch types, hemlock are most closely spatially associated with yellow birch, an association that makes little sense from a life history perspective, since yellow birch is a gap-phase hardwood and hemlock is a late-successional often slow-growing conifer. However, both hemlock and yellow birch seedlings are most abundant on wood and, I demonstrate here, in particular on hemlock wood. I show that hemlock wood is the most favorable substrate for hemlock and yellow birch seedling establishment (seedling density = 0.42 hemlocks /m^2, 0.60 birches /m^2), followed by yellow birch wood (0.21, 0.15), and that sugar maple wood (0.08, 0.10) and undisturbed soil (0.01, 0.01) are less suitable and support few to no hemlock and yellow birch seedlings older than three years. Sugar maple seedlings, in contrast, do not establish on any species of decaying wood (sugar maple seedling density = 0.03 to 0.09 /m^2 across wood species). Hemlock and yellow birch wood are rare everywhere, but are most abundant in hemlock patches where they cover 2.8% of the forest floor, reinforcing the hemlock-northern hardwood patch structure and the spatial association between hemlock and yellow birch.

I combine field studies of seedling demographics, wood distribution, seed rain, and decaying wood properties in three field sites in Upper Michigan, USA with greenhouse studies of seedling growth, ectomycorrhizal colonization, and nutrient content to determine why hemlock wood and to a lesser extent yellow birch wood support higher densities of hemlock and yellow birch seedlings than either sugar maple wood or soil. Hemlock logs are more favorable for hemlock and yellow birch seedling establishment for several reasons, among them lower pH, sufficient nitrogen and phosphorus supply, a tendency to decay more slowly than hardwood logs and to be attacked by brown rot rather than white rot decay fungi, and a tendency to lose bark cover and develop moss cover. A greater ability to provide ectomycorrhizal inoculum to seedlings and the relative absence of sugar maple seedlings on hemlock logs may also contribute to the higher survival rates of hemlock and birch seedlings. The full text of this dissertation is available free of charge until at least 2010 at www.lauramarx.net.