

Effects of nitrogen supply and wood species on *Tsuga canadensis* and *Betula alleghaniensis* seedling growth on decaying wood

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Abstract: Eastern hemlock (*Tsuga canadensis* (L.) Carrière) and yellow birch (*Betula alleghaniensis* Britt.) in primary Michigan forests depend on decaying wood for seedling-establishment sites, but seedling densities vary across wood species (hemlock, yellow birch, and sugar maple (*Acer saccharum* Marsh.)). We collected seedlings and wood from a natural field experiment and conducted a companion greenhouse experiment to determine whether seedling mass and nitrogen (N) content varied with wood species and whether they were related to wood inorganic N supply. Yellow birch seedlings were largest on hemlock wood in the field ($P = 0.003$) and greenhouse (but $P > 0.05$), while hemlock seedling mass did not vary across wood species. N concentration and N mineralization rate varied by species (N concentration: hemlock < yellow birch < maple; N mineralization rate: hemlock > yellow birch \approx maple), but neither seedling mass nor N content was significantly correlated with wood inorganic N supply. In the greenhouse, yellow birch seedlings responded to fertilization with N when growing on hemlock and maple but not yellow birch wood and appear to be limited by phosphorus when growing on yellow birch wood. We conclude that yellow birch seedling growth varies with wood species, and is limited by both N and phosphorus, while hemlock seedlings are unresponsive to variation in wood species during the first two growing seasons.

Résumé : Dans les forêts vierges du Michigan, la pruche du Canada (*Tsuga canadensis* (L.) Carrière) et le bouleau jaune (*Betula alleghaniensis* Britt.) dépendent du bois en décomposition pour l'établissement de leurs semis mais la densité des semis varie selon l'espèce de bois (pruche, bouleau jaune et érable à sucre (*Acer saccharum* Marsh.)). Nous avons collecté des semis et du bois dans le cadre d'une expérience sur le terrain et mené une expérience parallèle en serre pour déterminer si la masse et le contenu en azote (N) des semis variaient selon l'espèce de bois et s'ils étaient reliés à la disponibilité de l'azote inorganique dans le bois. Les semis de bouleau jaune étaient les plus gros sur le bois de pruche au champ ($P = 0,003$) et en serre (mais $P > 0,05$) alors que la masse des semis de pruche ne variait pas selon l'espèce de bois. La concentration de N et le taux de minéralisation de N variaient selon l'espèce (Concentration de N : pruche < bouleau jaune < érable, taux de minéralisation de N : pruche > bouleau jaune \approx érable), mais ni la masse des semis ni le contenu en N étaient significativement corrélés avec la disponibilité de N inorganique dans le bois. En serre, les semis de bouleau jaune réagissaient à la fertilisation azotée lorsqu'ils croissaient sur le bois d'érable ou de pruche mais pas sur le bois de bouleau jaune et leur croissance semblait limitée par le phosphore (P) lorsqu'ils croissaient sur le bois de bouleau jaune. Nous concluons que la croissance des semis de bouleau jaune varie selon l'espèce de bois et qu'elle est limitée par N et P tandis que les semis de pruche ne réagissent pas aux différences entre les espèces de bois pendant les deux premières saisons de croissance.

[Traduit par la Rédaction]

Introduction

In primary hemlock–hardwood forests of Upper Michigan, decaying wood is the main seedling-establishment substrate for *Tsuga canadensis* (L.) Carrière (eastern hemlock), and *Betula alleghaniensis* Britt. (yellow birch) (Stearns 1951; Reif 1992; Corinth 1995). Decaying wood (decaying

logs, stumps, or branches more than 10 cm in diameter) accounts for less than 10% of the forest-floor surface area in these forests, but supports most of the hemlock and yellow birch seedlings (Marx 2005). Stilt-rooted trees and linear groups of mature hemlock and yellow birch provide evidence that in the absence of fire or other catastrophic disturbances, seedlings that establish on decaying wood can survive and reach the canopy (Stearns 1951; Knechtel 1903, cited in Harmon et al. 1986; Reif 1992). Given the amount of time that both hemlock and yellow birch seedlings remain in logs before the seedlings are able to support their own weight or explore other substrates (>13 years; Marx 2005), decaying wood is likely important for long-term growth and survival of seedlings.

Not all decaying wood supports seedling growth (Christy and Mack 1984; Takahashi et al. 2000). Barely decayed wood (stage I; Goder 1961) supports few seedlings com-

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pared with wood in more advanced decay stages. Wood species also vary, and hemlock and yellow birch wood support higher densities and survival rates of seedlings than does *Acer saccharum* Marsh. (sugar maple) wood, even within the same 0.1 ha area or when factors such as light, seed rain, and field site are treated as covariates (Marx 2005). This suggests that seedling densities vary because of the characteristics of the wood species themselves, and that studies of resource availability on the scale of individual pieces of decaying wood (e.g., Cornett et al. 1997) may be helpful in explaining variation in seedling abundance. Water, light availability, and nitrogen (N) content may vary with wood species and are all potential limiting resources for growth and survival of seedlings in the understory of northern temperate forests (light, Pacala et al. 1993; N, Walters and Reich 1997; water, Caspersen and Kobe 2001).

As many as 88% of hemlock and 74% of yellow birch seedlings die in the first year, mostly as a result of water stress (Patzger and Friesner 1932, cited in Friesner and Patzger 1944; Linteau 1948). Thus, for these small-seeded species, high water availability is critically important and may explain why seedlings are much more abundant on decaying wood than on soil. Decaying wood is usually the wettest substrate on the forest floor (Cornett et al. 1997) and dries out slowly even under full sun (Boddy 1983), providing a site for establishment (defined here as survival to the second growing season) of hemlock and yellow birch seedlings in an otherwise inhospitable environment. However, while the high water-holding capacity of decaying wood largely explains the differences in seedling density between wood and soil, water content has not been shown to vary among species of decaying wood in the field (Cornett et al. 1997; Marx 2005). In the primary hemlock–hardwood forests we studied, median water content in May ranged from 77% to 80% of wet mass across three wood species in 2004, yet, on average, yellow birch in a greenhouse drought-tolerance experiment did not wilt until wood reached 25% water.

In the forests studied here, where single- and multiple-treefall gaps are the most frequent form of disturbance (Frelich and Graumlich 1994), light levels vary widely across the forest floor and are, on average, low (Baldocchi and Collineau 1994). Furthermore, light availability could be confounded with wood species, since the slower decay of hemlock wood in comparison with yellow birch and sugar maple wood (Arthur et al. 1993; Tyrrell and Crow 1994) and the tendency of light availability to decrease with gap age (Dirzo et al. 1992) may result in lower average light levels above hemlock logs. In other words, if gaps close at the same rate but hemlock logs remain on the forest floor longer than hardwood logs, it may be more common to find hemlock logs beneath already closed or nearly closed gaps than to find hardwood logs beneath closed gaps. Light may limit or colimit seedling growth and needs to be considered as a covariate in any study of the effect of wood species on field-grown seedlings. The range of light levels in this field study (2%–15% canopy openness) is well within the tolerance limits of hemlock seedlings, which can survive in less than 1.8% of full sunlight (Bourdeau and Laverick 1958; Hadley 2000). Yellow birch seedlings require higher light levels than hemlock (Erdmann 1990; Kobe et al. 1995) to survive, and

are more likely to show increases in growth with increasing light (Tripler et al. 2002).

The main focus of this study is on the differences in inorganic N concentration [N] and N mineralization rates (N_{\min}) among logs of various species and the relationship between wood N supply and seedling growth and N content. N is often regarded as the most limiting nutrient in northern temperate forests (Cole and Rapp 1981), although evidence of N-limited seedling growth in forest understories is mixed (Walters and Reich 1997; Tripler et al. 2002). In a study of understory hemlock seedlings, Catovsky and Bazzaz (2002) found that N fertilization of seedlings increased survival but caused only slight increases in growth after 1 year. Hemlock saplings did not increase in height or radial growth after being fertilized with N (Tripler et al. 2002). Yellow birch seedlings, on the other hand, respond to N fertilization with increased growth within several months when grown under high-light conditions (Canavera 1978; DeHayes et al. 1980; high light conditions only, Tripler et al. 2002). Yellow birch seedlings respond more favorably to NH_4^+ addition than to NO_3^- addition under low light conditions (Margolis and Vézina 1988), yet as with hemlock seedlings, there is little evidence of N limitation of yellow birch in low light understory conditions (Tripler et al. 2002).

Several authors have measured plant-available N (NO_3^- , NH_4^+ , and amino acids) in or beneath decaying wood from a single species, but at present it is difficult to draw conclusions regarding variation in plant-available N among species. Comparisons across existing studies are difficult to make, owing to wide variability in N content and [N] in wood and the lack of a standard method for measuring N in wood (Harmon et al. 1986). Yavitt and Fahey (1985) reported that NO_3^- and NH_4^+ concentrations in interstitial water of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) boles were below the limits of detection, though total N (mainly organic N) was approximately 1.97 mg/L. Takahashi et al. (2000) measured inorganic N in a water extract from logs that were most likely *Abies* spp. and *Picea* spp. from an old-growth forest in Japan, and found higher concentrations of NH_4^+ (0.87–1.26 mg/L) than NO_3^- (0.12–0.24 mg/L). Net N_{\min} in field incubations of Douglas-fir wood in Oregon averaged 0.2 g/m² during the winter and 0.65 g/m² during the summer (Hart 1999). In the one study that compared several species of wood using uniform methods, Spears et al. (2003) found few differences, not only in mineral N concentrations but also in organic N concentrations, and a broad range of cations in water solutions collected beneath the decaying wood of four conifer species. We note below that in our study, different measures of inorganic N availability and measurement of N in the field versus laboratory incubations yielded conflicting results. This illustrates the difficulty of comparing studies in which different methods were used to measure wood N and supports the need for studies that compare N availability in several wood species under uniform conditions.

It is possible that N is not the primary limiting nutrient for seedling growth, and that other macronutrients or micronutrients may limit or colimit seedling growth. Information is even less available about other nutrients in wood than about N, but Holub et al. (2001) found that in conifer wood, N and phosphorus (P) showed parallel increases in later decay

stages. Takahashi et al. (2000) determined that phosphate was more abundant than nitrate in water extracts from conifer wood in Japan. Arthur et al. (1999) found that calcium and magnesium concentrations on a mass basis were lower in yellow birch than in sugar maple wood, suggesting that wood species may vary in their ability to supply nutrients to plants. Seedling access to these nutrients and to N may be affected by mycorrhizae. The young hemlock seedlings studied here did not often show mycorrhizal colonization, but older seedlings were more likely to be colonized (Marx 2005), and mycorrhizal colonization is required for long-term growth and survival of the closely related western hemlock (Christy et al. 1982). Mycorrhizae are generally thought to provide tree seedlings with more N and P, and perhaps more forms of N, than they would be able to access on their own (Kytoviita and Arnebrant 2000; Booth 2004). Mycorrhizae increase the ability of seedling roots to forage and may increase uptake of P even more than that of N (Perez-Moreno and Read 2000).

Objectives

We analyzed hemlock and yellow birch seedlings and decaying wood samples (hemlock, yellow birch, and sugar maple) from an observational field study in Upper Michigan and conducted a 4-month greenhouse study to test the hypothesis that variation in N availability in decaying wood within and across species would explain variation in hemlock and yellow birch seedling mass and N content. Concentrations and rates of production of inorganic N were measured in decaying wood and adjacent soil, while mass, N and other nutrient contents, mycorrhizal status, and response to fertilization were determined for seedlings grown on the three different wood species. Light was treated as a covariate for field-grown seedlings. Based on a prior observation that seedling survival was greatest on hemlock wood in our field study (Marx 2005), we made three predictions: (1) independently of light, both hemlock and yellow birch seedlings would be largest on hemlock wood, followed by yellow birch wood, and smallest on sugar maple wood, (2) hemlock wood has a greater [N] and N_{\min} than sugar maple wood, and (3) seedling mass and N content are positively correlated with wood inorganic N supply, and more strongly correlated with availability of wood N than with that of any other nutrient.

Materials and methods

Field sampling

We examined relationships between log species in terms of N availability, seedling growth, and light availability using canopy photographs and log, soil, and seedling samples collected from four sites in Michigan's Upper Peninsula. The Porcupine Mountains Wilderness State Park, the Sylvania Wilderness Area (Ottawa National Forest), the Huron Mountain Club (private owner), and the Sand River area (state-owned land near Skandia) are primary hemlock-hardwood forests that have been harvested only by selective cutting of *Pinus strobus* L. (eastern white pine) in the late 1800s. Dominant tree species at all sites are hemlock, yellow birch, and sugar maple. Stands contain minor components of *Abies*

balsamea (L.) Mill. (balsam fir), *Acer rubrum* L. (red maple), *Thuja occidentalis* L. (eastern white cedar), *Ostrya virginiana* (Mill.) K. Koch. (ironwood), and *Tilia americana* L. (basswood). The Porcupine Mountains, Sylvania, and Huron Mountain sites are characterized by a patchy distribution of primary forest types, with admixtures of hemlock and yellow birch bordering sugar-maple-dominated northern hardwood stands (Pastor and Broschart 1990; Simpson et al. 1990; Frelich et al. 1993). The Sand River site is a patch of hemlock-dominated forest and is poorly drained, unlike the other three sites. Field studies beyond those detailed in this paper were carried out at these sites between 2002 and 2004, and readers are referred to Marx (2005) for additional methods relating to basal-area measurement, site and climate data, and abundance and survival of seedlings.

Field samples were collected in 2002 and 2004. In August 2002, we collected wood and 2-year-old hemlock and yellow birch seedlings from all four field sites to be destructively sampled for analyses of wood N characteristics and seedling mass and N content. We centered our sampling areas on 0.1 ha field plots reserved for complementary studies (Marx 2005). We walked around the outside of 13 different plots, starting 10 m outside the plot border and continuing in additional circuits at 10 m increments. The decay stage of every log, stump, or downed branch (diameter >10 cm) visible in each circuit was checked until we obtained a sample 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). We collected samples from a total of 260 logs (chosen to ensure that half had hemlock or yellow birch seedlings and half had no seedlings) and used a trowel to collect a sample of the top 10 cm of soil from beside 78 of these logs (6 near each of 13 field plots in randomly selected locations). Soil was collected after intact leaves were removed from the surface and was generally sandy loam to loamy mineral soil, including parts of the A and E horizons. From each log that had hemlock or yellow birch seedlings growing on it, we collected one, or two if available, established seedling(s) of each species for measuring mass and N content. Entire seedlings (roots, stem, and leaves) were collected as close as possible to the log midpoint, to avoid log-edge effects. We used only 2-year-old seedlings in this study because this age class was most abundant and could be collected from all three wood species.

In late May 2004 we collected additional wood and soil samples from the Sylvania Wilderness and Porcupine Mountains sites. Wood samples were later used for our greenhouse experiment. We also collected seedlings from these two field sites in July 2004 to obtain a larger sample of seedlings, sampling sugar maple logs from a much wider area than other log species to ensure collection of an adequate sample of seedlings on sugar maple logs. Up to four 2-year-old hemlock and four 2-year-old yellow birch seedlings were collected from each of the 41 logs sampled in 2004.

Analysis of field samples

Soil and wood samples were transported on ice to Michigan State University and stored in a 4 °C cold room. In 2002, samples were stored for 1–10 days before extraction

for inorganic N (NO_3^- and NH_4^+). In 2004, samples were extracted within 48 h. For each sample, we determined gravimetric moisture content by drying an approximately 10 g sample at 105 °C. In 2002, two subsamples (23–27 g fresh mass) of each log or soil sample were used for a laboratory measurement of potential N mineralization (modified from Powers 1980). Subsamples were placed in a 125 mL plastic specimen cup and the volume was determined using the millilitre scale of the cup. An initial sample of each piece of decayed wood or soil core was immediately extracted with 50 mL of 0.5 mol/L K_2SO_4 solution, while final samples were incubated at room temperature for 28 days before extraction. Extracts were analyzed for inorganic N colorimetrically with an autoanalyzer (OI Flow Solution IV, OI Analytical, College Station, Texas), with NO_3^- -N determined by the cadmium reduction method and NH_4^+ -N with the phenol hypochlorite method (Page et al. 1982). In 2002, refrigerated extracts that could not be analyzed within 1 month were frozen until analysis. In 2004, wood samples were extracted with 50 mL of 2 mol/L KCl instead of K_2SO_4 because of faster run times and less clogging of the autoanalyzer system with this method. Net N_{min} was calculated as the difference between initial and final amounts of inorganic N. We chose to express both N_{min} and initial [N] on a volume basis ($\mu\text{g N}\cdot\text{mL wood}^{-1}\cdot\text{day}^{-1}$) 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.

We measured the pH of 63 logs randomly selected from the pool of conifer and hardwood logs collected in 2002 and from soil beside 34 of these logs. Unlike soil, once decayed wood is dried it cannot easily be rewetted, so we modified a standard soils procedure (Klute 1986) and measured the 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 mL. This was done to account for variation 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 h and allowed to settle before the pH was measured. Calculation of pH means as well as statistics was performed using concentrations of H^+ ions that have been back-transformed into values on the pH scale for presentation.

Field-collected seedlings were kept on ice until processed in the laboratory. Seedlings collected in the field in 2002 were examined with a dissecting microscope (10–70 \times) for evidence of ectomycorrhizae. Seedlings collected in the field in 2004 were scanned as high-resolution digital images, which were later examined for evidence of ectomycorrhizae. Seedlings were then dried for at least 48 h in a 65 °C drying oven. Seedlings were ground to powder with a mortar and pestle and analyzed individually for [N] by the Dumas combustion method on a CN analyzer (Carlo Erba, Milan, Italy). Seedling N was expressed as whole-plant N content ([N] \times seedling mass).

Canopy photographs

Canopy photographs were taken approximately 30 cm directly above each seedling collected in 2002 and 2004, using

a digital camera (Nikon Coolpix 995, set to grayscale photographs) with a fisheye lens. If two seedlings were less than 0.5 m apart, one picture was taken of both seedlings. SideLook software (version 1.1.01, 2005, M. Nobis, available at www.appleco.ch) was used to automatically threshold images (divide into open sky versus other pixels), which were then analyzed with the GLA software (version 2.0, 1999, Institute of Ecosystem Studies, Millbrook, N.Y.).

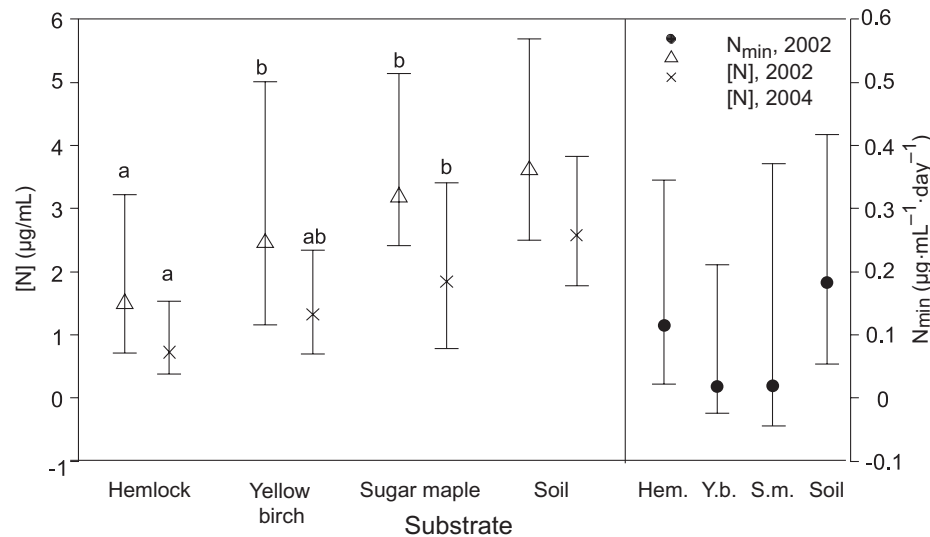
Greenhouse experiment

We carried out a 115 day (mid-July through early November) experiment at the Michigan State University Plant Science Greenhouses to compare mass and final N content of hemlock and yellow birch seedlings grown on hemlock, yellow birch, and sugar maple wood. In late May 2004, samples of stage III and stage IV wood of known species were collected from 20 logs of each species (60 in total) at the Sylvia Wilderness and the Porcupine Mountains sites. We had previously identified wood by microscopic examination (70–400 \times , using microscopes at the USDA Forest Products Laboratory in Madison, Wis.) of thin wood slices of each sample mounted on slides. From each wood sample, a 180 mL subsample was placed in each of two pots (the wood was embedded in moist perlite), one for hemlock seeds and one for yellow birch seeds. For 30 of the log samples (10 of each species), two additional subsamples were used for a fertilizer treatment. Pot locations were rerandomized and rotated every 2 weeks.

Eastern hemlock seeds (Ontario source, Ontario Tree Seed, Angus, Ont.) and yellow birch seeds (Michigan source, US Forest Service Toumey Nursery, Watersmeet, Mich.) were stratified in perlite and wet sand at 4 °C for 2 months before being placed on trays of wet perlite in the greenhouse in early July. One week later, after yellow birch seeds had germinated and most hemlock seeds had cracked seed coats but did not have visible radicles, nine seeds of either yellow birch or hemlock were pushed into the surface of the wood in each pot. The wood was saturated every day to ensure that seeds in the top layer of wood did not dry out. Yellow 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 cotyledons almost 3 weeks after yellow birch seedlings, and were not thinned. Throughout the experiment, seedlings were shaded with aluminum 70% shade cloth (Aluminet, Polysack USA, San Diego, Calif.). Seedlings were grown under natural light conditions in July and August and supplemented with standard greenhouse lighting (16 h per day) above the shade cloth for the remainder of the experiment. Temperatures in the greenhouse ranged from 21 to 35 °C.

For the first month of the experiment, seedlings were watered to excess with well water that may have contained inorganic N. After this establishment period, 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 1 month, Scotts Proturf 38–0–0 Poly-S was applied to pots in the fertilizer treatment at 200 kg N/ha (0.319 g per pot). Surprisingly, this application of slow-release N quickly killed approximately half of the fertilized seedlings (with no detectable pathogen presence; Michigan State University Diagnostics Laboratory). Seed-

Fig. 1. Median N-mineralization rates (N_{\min}) and inorganic N concentrations ([N]) in wood in 2002 and 2004. N_{\min} is plotted on the secondary y axis. Points represent medians and whiskers show the interquartile range. ANOVAs with Tukey's HSD post-hoc comparisons performed on logarithm-transformed data indicate that [N] for hemlock logs was lower than that for both yellow birch and sugar maple logs in 2002 and lower than that for sugar maple logs in 2004 ($n = 128$ wood samples in 2002 and $n = 129$ in 2004).



lings 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 scanned under a dissecting scope (10–70 \times) within 36 h of harvest for evidence of mycorrhizal colonization. Seedlings were then dried at 65 $^{\circ}\text{C}$, weighed individually, pooled by pot, and ground with a mortar and pestle or a steel-ball pulverizer into a fine powder. The N content of ground seedlings was analyzed as previously described for field-grown seedlings. The remaining dried seedling powder from a subset of yellow birch seedlings (taken from seven randomly selected hemlock, six yellow birch, and seven sugar maple logs) was analyzed for boron, calcium, copper, iron, potassium, P, magnesium, manganese, and zinc concentrations (ppm; macronutrients have been converted to percent dry mass). Samples were microwave-digested at 205 $^{\circ}\text{C}$ for 30 min (MARS 5, CEM Corporation, Matthews N.C.) 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, Mass.). Hemlock seedlings did not vary in size in the greenhouse and were usually too small for micronutrient analysis and so were not analyzed for nutrients other than N.

Statistical analysis

With the exception of N_{\min} , data that required transformation, including seedling N content and mass, were successfully logarithm-transformed before analysis. Because N_{\min} data were resistant to transformation, they were analyzed using Wilcoxon/Kruskal–Wallis χ^2 tests. N_{\min} and [N] data, as well as seedling mass and N content data, are presented in the text and figures as medians, owing to non-normal distribution of the data. We used ANOVAs to test for differences in wood [N] across species, and to test the effect of wood species on seedling mass, seedling N content, and rates of

mycorrhizal colonization. Hemlock and yellow birch seedlings from a single log were pooled for statistical analyses of seedling mass and N content, while mycorrhizal colonization was analyzed for each individual seedling. We tested the correlation of seedling characteristics with wood nutrient supply using Pearson's correlations and single linear regressions, and used multiple linear regressions to test the effects of light (included as a covariate) and wood species on seedlings. Paired t tests and unequal-variance t tests were used to compare N_{\min} and [N] in wood versus soils and to test for the effect of mycorrhizal colonization and fertilization on seedling mass and N content. For all tests, P values less than 0.05 were considered significant and values from 0.05 to 0.10 borderline significant.

Results

N supply in wood and soil

N availability varied significantly across wood species (N_{\min} in 2002, Wilcoxon/Kruskal–Wallis χ^2 test, $P = 0.02$; [N] in 2002, ANOVA, $P = 0.004$; [N] in 2004, ANOVA, $P = 0.001$; Fig. 1, Table 1). [N] and N_{\min} were inversely ranked across species, with the highest N_{\min} and lowest [N] in hemlock logs and vice versa for sugar maple logs (Fig. 1). In all log species, NH_4^+ dominated [N]; NO_3^- was negligible in 2002, possibly because the samples were frozen before analysis, and approximately 30% of [N] in 2004, regardless of log species (data not shown). Within each individual log, N_{\min} was positively correlated with [N] measured at the start of the laboratory incubation (Pearson's correlation, $r = 0.35$, $P < 0.001$). It is important to note that because [N] was measured at different times of the growing season in 2002 and 2004 (late August and late May, respectively), 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. [N] values were higher in 2002 than in 2004, perhaps because of these methodological dif-

Table 1. Summary of median N-mineralization rates (N_{\min}) and N concentrations ([N]) for hemlock, yellow birch, and sugar maple wood and soil.

Substrate	N_{\min} (2002), $\mu\text{g}\cdot\text{mL}^{-1}\cdot\text{day}^{-1}$	[N], $\mu\text{g}/\text{mL}$		
		2002	2004	pH
Hemlock wood	0.115	1.5	0.73	3.7
Yellow birch wood	0.018	2.45	1.33	3.9
Sugar maple wood	0.019	3.18	1.84	6.4
Wood species pooled	0.07	2.32	1.15	3.9
Soil	0.19	3.62	2.99	3.4 ($n = 34$)

Note: Mean pH values are listed for the three wood species. Values are summarized; for sample sizes, statistical significance, and interquartile ranges see Fig. 1 and the text.

ferences, but rankings across species were the same in 2002 and 2004.

Unlike Hart (1999), who measured N_{\min} on a mass basis, we found that on a volume basis, soils (0–10 cm depth) have greater [N] and N_{\min} than logs. Median N_{\min} were 0.07 and $0.19 \mu\text{g}\cdot\text{mL}^{-1}\cdot\text{day}^{-1}$ for wood and soil, respectively, in 2002 ($n = 121$ logs and 47 soils, Wilcoxon's test $P = 0.01$). Median [N] values in wood and soil were 2.32 and $3.62 \mu\text{g}/\text{mL}$ in 2002 ($n = 132$ logs and 79 soils, t test, $P < 0.001$) and 1.15 and $2.99 \mu\text{g}/\text{mL}$ in 2004 ($n = 128$ logs and 7 soils, t test $P < 0.001$).

The pH of wood species varied significantly: hemlock wood < yellow birch wood < sugar maple wood (ANOVA, $P = 0.014$, $n = 57$; Table 1). The pH values were not affected by the composition of the canopy surrounding each log (e.g., the effect of hemlock basal area on log pH (for methods see Marx 2005), ANOVA, $P = 0.664$, $n = 57$) and did not vary by field site (ANOVA, $P = 0.115$, $n = 57$).

Seedling mass and N content

Yellow birch seedling mass varied across wood species (Fig. 2, Table 2). The largest yellow birch seedlings grew on hemlock logs, and were larger than yellow birch seedlings on sugar maple logs in both the field (t test, $P = 0.003$) and the greenhouse (but $P = 0.09$). In contrast, hemlock seedlings did not vary significantly in size across wood species in either the field or the greenhouse (ANOVA, P values > 0.1) (Fig. 2). Paralleling trends in mass, yellow birch seedling N contents were greatest when seedlings were grown on hemlock logs in the field (ANOVA, $P = 0.003$; Fig. 2). However, there was no variation in yellow birch N content across wood species in the greenhouse (ANOVA, $P = 0.82$). Hemlock seedlings showed no consistent pattern of N content across wood species in the field or greenhouse.

Seedling N content and seedling mass were not significantly correlated with wood [N] or N_{\min} in either yellow birch or hemlock seedlings in the field or greenhouse (Pearson's correlation, $r < |0.52|$, P values > 0.12). In the field, this lack of correlation could have been due to unmeasured environmental factors, but in the greenhouse, light, water, and temperature were uniform across pots, leaving only resources inside each log or differences in the biotic communities within a log as sources of variation in seedling mass and N content. Canopy openness (a surrogate for light availability) did vary among seedlings (ranging from 1.9% to 15.2%) in the field, but not across wood species (ANOVA, $P = 0.24$ in 2002, $P = 0.76$ in 2004), so these two

factors were not confounded. We were unable to pool light measurements across years because seedlings were sampled from the site with the highest light availability in 2002 but not in 2004.

Mycorrhizae and fertilization

Seedling mycorrhizal colonization status varied with wood species. Mycorrhizae were rarely found on 2-year-old seedlings collected from the field: with all log species pooled, only 2 out of 45 (4%) seedlings in 2002 and 8 out of 186 (4%) seedlings in 2004 were colonized. However, mycorrhizal colonization was more common on older seedlings collected from the field in 2002, and colonization varied with wood species: 12% of yellow birch seedlings and 10% of hemlock seedlings on hemlock logs were mycorrhizal, compared with 0% of yellow birch seedlings and 3% of hemlock seedlings on yellow birch logs ($n = 50$ yellow birch and 88 hemlock seedlings older than 2 years). There were almost no older seedlings on maple logs (Marx 2005), so data on mycorrhizal colonization of seedlings on this wood species are not available. In the greenhouse, 20.3% of first-year yellow birch seedlings ($n = 237$ unfertilized seedlings) and 4.9% of hemlock seedlings ($n = 263$) were mycorrhizal. Hemlock and yellow birch logs supported greater percentages of mycorrhizal yellow birch seedlings (25% on each wood species) in the greenhouse than did sugar maple logs (11%, ANOVA for wood species, $P = 0.042$), while similar proportions of hemlock seedlings (3%–7%, ANOVA for wood species, $P = 0.56$) were colonized across wood species. The mass of mycorrhizal seedlings (hemlock: 13.6 ± 1.4 mg (mean \pm SE); birch: 44.8 ± 7.6 mg) was greater than that of non-mycorrhizal seedlings (hemlock: 10.8 ± 0.4 mg; birch: 29.9 ± 3.7 mg) (t test on logarithm-transformed data, $P < 0.0001$ for hemlock and $P = 0.02$ for yellow birch; Figs. 3a and 3c).

N-fertilized yellow birch seedlings growing on hemlock and sugar maple logs in the greenhouse were significantly larger than their unfertilized counterparts growing on the same log (median seedling mass was 0.08 g when fertilized and 0.04 g when unfertilized; paired t test, $P = 0.0004$ ($n = 10$ pairs); Fig. 3b). Fertilized seedlings on these two wood types also had greater N contents (fertilized = 0.0022 g, unfertilized = 0.0007 g, $n = 9$ pairs, $P = 0.0001$). However, yellow birch seedlings growing on yellow birch logs did not respond to fertilization with increased mass or N content (mass: median fertilized = 0.02 g, unfertilized = 0.03, $P = 0.71$; N content: fertilized = 0.0006 g, unfertilized =

Fig. 2. Median seedling mass (a) and median N content (b) of yellow birch and hemlock seedlings growing on three different wood species. Differences are significant at $P < 0.05$ for mass and N content in field-grown yellow birch seedlings only (yellow birch: $n = 50$ logs with birch seedlings in the field and $n = 60$ in the greenhouse; hemlock: $n = 48$ and 59 , respectively).

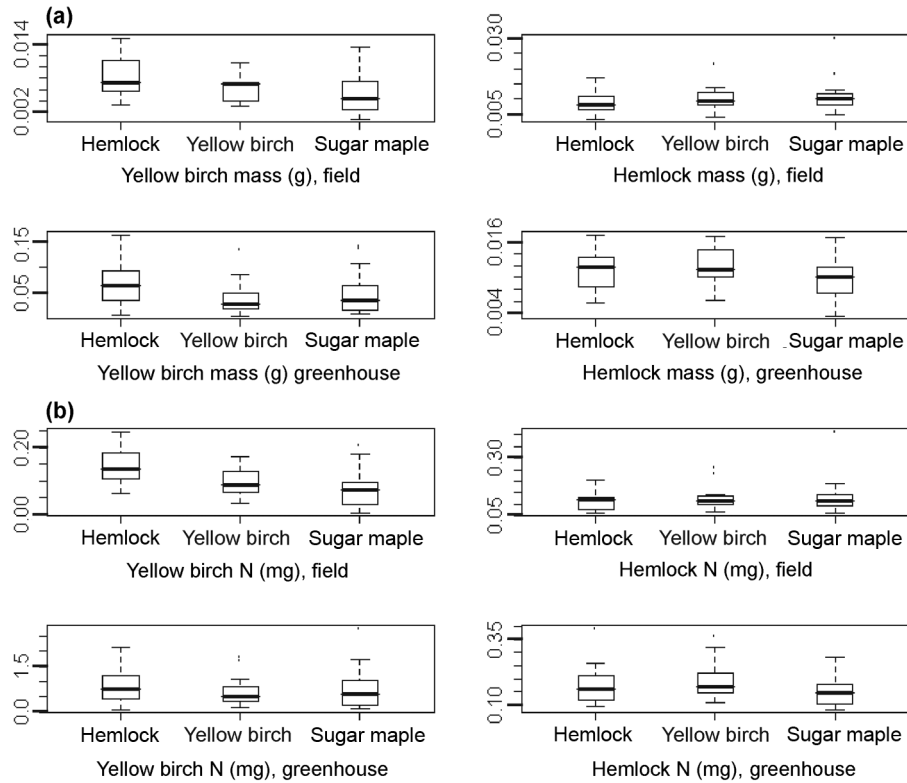


Table 2. Effects of log species and light on mass and N content of seedlings from the field and greenhouse.

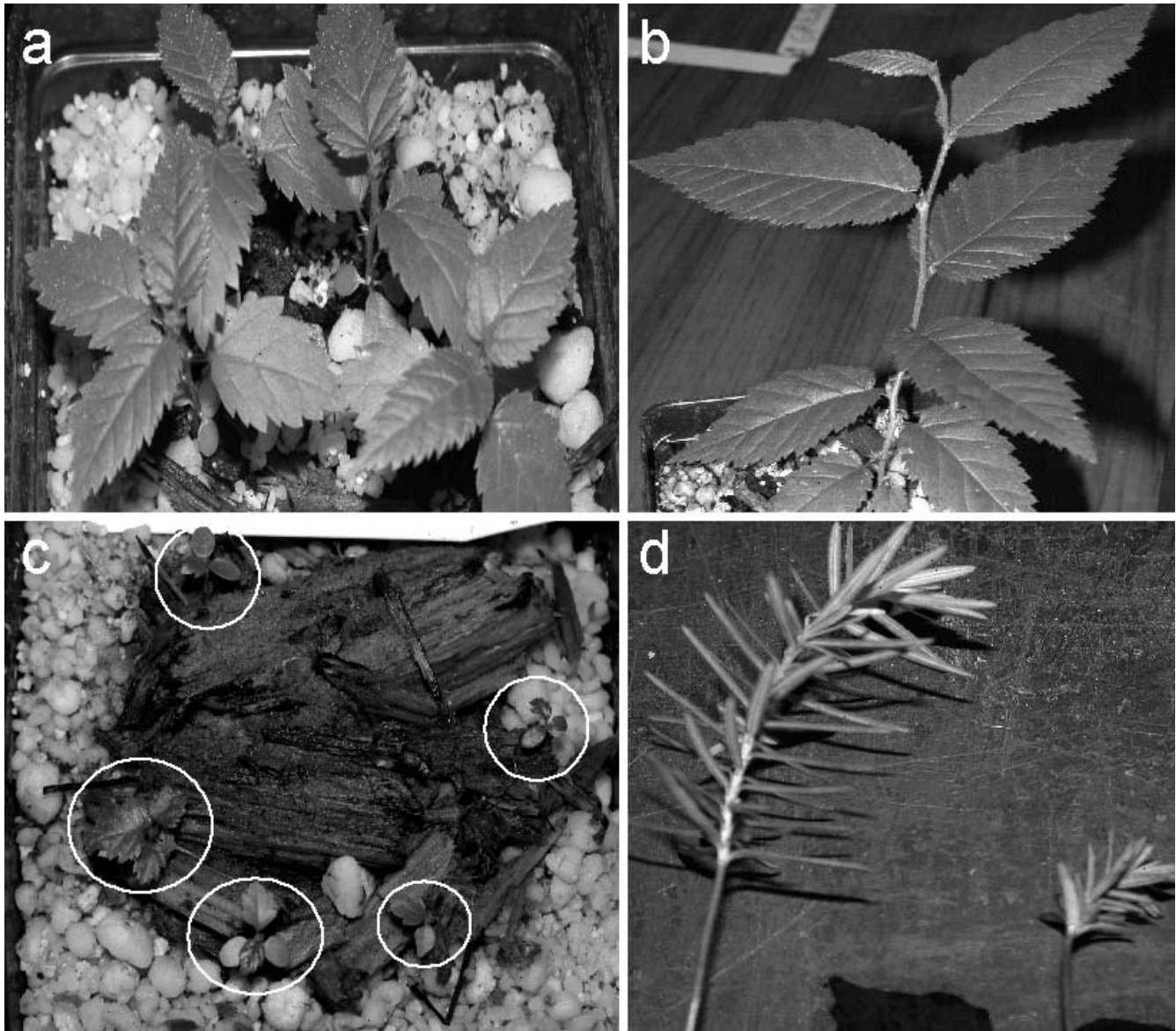
Seedlings	Response	Effect of log species	Effect of canopy openness
<i>Betula alleghaniensis</i>			
Field, 2002 ($n = 17$ logs)	Mass	0.204	0.162
	N content	0.035	0.749
Field, 2004 ($n = 33$ logs)	Mass	0.013	0.364
	N content	0.011	0.734
Greenhouse ($n = 60$ logs)	Mass	0.064	—
	N content	0.817	—
<i>Tsuga canadensis</i>			
Field, 2002 ($n = 22$ logs)	Mass	0.921	0.049
	N content	0.735	0.21
Field, 2004 ($n = 26$ logs)	Mass	0.734	0.081
	N content	0.673	0.027
Greenhouse ($n = 59$ logs)	Mass	0.104	—
	N content	0.220	—

Note: Values are P values from two-way ANOVA effect tests. Data were logarithm-transformed before analysis. In all cases the interaction between log species and canopy openness was not significant ($P > 0.250$) in preliminary analyses and the term was removed from the ANOVAs shown here (Bancroft 1964).

0.0005 g, $P = 0.15$, $n = 8$ pairs; Fig. 4). Despite statistically significant differences in mass when wood species were pooled, hemlock seedlings did not respond to fertilization with a biologically meaningful increase in mass (median fertilized = 0.011 g, unfertilized = 0.010 g, paired t test with all species pooled, $n = 14$, $P = 0.03$), and differences within individual wood species were not significant. Hemlock seed-

lings did have higher N contents when fertilized (fertilized = 0.0003 g, unfertilized = 0.0002 g, $n = 14$ pairs, $P = 0.004$), but again these differences are not biologically meaningful. One possible confounding factor in the fertilized seedling pots was that as a result of fertilizer burn, many fertilized pots had only two or three seedlings per pot at harvest, rather than four. Hemlock seedlings never grew tall enough

Fig. 3. Greenhouse-grown seedlings, showing great variation in size. (a) Mycorrhizal yellow birch seedlings growing on a hemlock log. (b) Fertilized yellow birch seedlings. (c) Non-mycorrhizal yellow birch seedlings growing on a yellow birch log. (d) Non-mycorrhizal hemlock seedlings on a single sugar maple log.



to directly compete for light by shading each other, but some fertilized yellow birch did shade others in the same pot by the end of the experiment. Fertilized yellow birch may have been larger because of a combination of more N and fewer competitors.

Micro- and macro-nutrients

To determine why N fertilization affected seedlings on some wood types but not others, we compared micro- and macro-nutrient concentrations in a subset of our greenhouse-grown yellow birch seedlings (Table 3). For two 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 the seedling zinc concentration varied significantly with wood species (Table 3), but showed no significant correlation between seedling mass and nutrient concentration. Although the P concentration in yellow birch seedlings did not vary significantly among log species, it explained a high percentage of the variation in seedling mass, especially when yellow birch logs were excluded from the analysis (with yellow birch logs excluded: linear regression, $R^2 = 0.46$, $n = 11$, $P = 0.01$; Table 3). In addition, mean N:P ratios were smaller on hemlock (11.4) and sugar maple (13.9) logs than on yellow birch logs (17.5, mean across species = 14.1, ANOVA, $P = 0.03$), the log species on which seedlings also had the lowest mean P concentration. Seedling mass decreased as the N:P ratio increased, and when all log species were pooled, the N:P ratio explained more variation in yellow birch seedling mass than the P con-

Table 3. Concentrations of macronutrients (calcium, N, P, potassium; percentage of plant dry mass) and micronutrients (boron, copper, iron, magnesium, manganese, zinc; ppm, or mg/kg dry plant material) in whole yellow birch seedlings grown on three species of wood in the greenhouse.

	Hemlock wood	Yellow birch wood	Sugar maple wood	<i>B. verrucosa</i> ratio, expected % dry mass ^a	Correlation with yellow birch mass (species pooled) ^b
Macronutrient concn. (% dry mass)					
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*
Macronutrient concn. (ppm)					
Boron	48.36 (4.09)a	52.24 (7.08)a	50.59 (3.10)a		0.19
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		0.28
Zinc	187.92 (31.57)a	360.42 (54.41)b	136.98 (21.44)a		-0.058

Note: Each concentration represents the mean of a composite sample (four entire yellow birch seedlings from a single pot make up each sample; $n = 5-7$ for each wood species), followed by 1 SE in parentheses.

^aThe ratio of macronutrients to one another (N is set to 100) in *B. verrucosa* seedlings at optimum nutrition (Ingstad 1971) and the percent dry mass that would be expected in our data given these ratios and %N (setpoint for the ratios) of 1.60 are provided for comparison.

^bPearson's correlations between nutrient concentration and yellow birch mass; *, statistical significance ($\alpha = 0.05$).

Fig. 4. Response of yellow birch seedlings to fertilization with N when grown on different wood species. Data points represent mean values of yellow birch seedling mass, pooled by pot. Error bars represent 1 SE. Differences between fertilized and unfertilized seedlings are significant for hemlock ($P = 0.01$) and for sugar maple ($P = 0.02$) logs but not for yellow birch logs ($P = 0.71$) ($n = 18$ fertilized pots (6 hemlock, 8 yellow birch, and 4 sugar maple) and 60 unfertilized pots (20 of each species)).



centration alone (linear regression, $R^2 = 0.35$, $n = 16$, $P = 0.01$).

Discussion

Seedling mass

Our first prediction, that seedlings would be largest on hemlock wood, was correct for yellow birch but not hemlock seedlings in the field (Fig. 2). In the greenhouse, mass of both hemlock and yellow birch seedlings on hemlock logs was greater than on sugar maple logs, though this trend was

statistically weak. It is surprising that the differences in yellow birch mass across wood species in the greenhouse are only borderline significant, given the differences in seedling mass in the field and the many factors held constant for all seedlings in the greenhouse: light, temperature, seed source of seedlings, water availability, and exact seedling age (field-collected 2-year-old seedlings could have germinated in May, June, July, or August of the previous year). Yellow birch seedlings showed not only a strong trend towards larger seedlings on hemlock logs than on the other two log types in the greenhouse, but also large variation in seedling size, which reduced the statistical significance of this trend. Four months may not have been long enough for measurable differences in mass to be generated, and growth differences in hemlock may have been modest because some resources vary on a smaller spatial scale than the one we measured, thus contributing to high variability in hemlock seedling mass within a single log (Fig. 3d). Ectomycorrhizae, for example, were often found on some but not all hemlock seedlings within a single pot.

Growth differences were driven by wood species differences and not light in both the greenhouse, where light availability was uniform, and in the field. In the field, variation in light availability in the mostly closed-canopy forests we studied did not appear to be an important limiting factor for seedling growth. When light availability was included as a covariate with wood species in a regression model of mass of field-grown seedlings, light did not explain significant variation in yellow birch mass in the field in either 2002 or 2004. The significant effect of light on hemlock seedling mass in 2002 is the result of a spurious negative correlation between mass and light availability, based on a single high light, low seedling mass outlier.

N in wood, soil, and seedlings

Our second prediction was that hemlock wood has a

greater [N] and N_{\min} than sugar maple wood, and our third that seedling mass and N content are correlated with wood N availability. [N] was lowest and N_{\min} highest in hemlock log samples, and our values were comparable to the range of wood [N] measured in other species by Takahashi et al. (2000). Other authors have found, as we did, inverse relationships between N_{\min} and [N] (nitrification versus NO_3^- only; Robertson and Vitousek 1981), and although both measures have their limitations (Grenon et al. 2005), both are potential indicators of N available to plants. [N] is affected by vegetation density and uptake, and thus likely a more accurate measure of N availability for individual seedlings (Walters et al. 2006). Decaying hemlock logs contain more roots than sugar maple logs (L. Marx, personal observation), and greater root uptake could account for lower [N] despite higher N_{\min} in hemlock logs (Fig. 1). However, regardless of which measure of wood N availability was used, and whether wood species were pooled or tested separately, our third prediction was incorrect and there was no significant correlation between seedling N content or mass and wood N supply. Differences in N availability across species were only significant when we used the full set of wood samples collected in 2002 or 2004 (as in Fig. 1), and not significant when we examined only wood samples from logs that supported 2-year-old seedlings (as in Fig. 2). This was due to high variability in wood N availability in the smaller subset, which may have contributed to the lack of correlation between wood N and seedling characteristics. It is more likely, though, especially given the presence of seedlings even on logs with N_{\min} at or just below zero and the variation in P content of yellow birch seedling grown on different log species, that seedling growth is not limited by N but rather colimited by the supply of N and P. Four lines of evidence suggest that hemlock logs supply an optimal balance of these nutrients to seedlings.

First, yellow birch seedlings grown on hemlock logs for just 4 months were significantly larger than those grown on sugar maple logs. The measurable differences in growth in such a short time with environmental factors held constant suggest that nutrients may be very important for short-term growth and survival of seedlings.

Second, mycorrhizal yellow birch and hemlock in the greenhouse were significantly larger than their non-mycorrhizal counterparts (Figs. 3a, 3c, and 4). 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 less chance of becoming colonized by ectomycorrhizae. This may be due to differences in ectomycorrhizal-fungus communities across wood species that parallel those in wood decay fungus communities (Kropp 1982), 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 colonized by mycorrhizae because they are larger and have a greater rooting volume, rather than larger because they are colonized with mycorrhizae.

A third reason why yellow birch seedlings, if not both yellow birch and hemlock, grow largest and survive best on hemlock logs may be that hemlock logs supply low but adequate 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 yellow birch logs, yellow birch seedlings had P concentrations lower than those required for optimal relative growth rate in silver birch, *Betula pendula* L. (Ericsson and Ingestad 1988), and high N:P ratios. Seedlings on this wood type also did not respond to N fertilization, unlike seedlings grown on hemlock and on sugar maple logs, suggesting that they were most limited by P. Thus, the N:P ratio explained only 13% of the variation in seedling mass on yellow birch logs. The N:P ratio explained 54% and 42% of variation in seedling mass on hemlock and sugar maple logs, respectively, and seedlings responded to N fertilization with increased growth, suggesting limitation by both nutrients. Adequate N and P availability in hemlock wood could be mediated by pH. Unlike soil, the pH of which is influenced by canopy composition and other external factors (Finzi et al. 1998), hemlock logs maintain a pH of about 4 regardless of environmental conditions around them. The near-neutral pH values found on sugar maple logs are less favorable for seedlings, as several nutrients are less available at these higher pH values including P (which drops off sharply at pH 7.5 in organic soils), N, potassium, manganese, and zinc (Smith 1989). Whether mediated by pH, mycorrhizal colonization, or a factor not measured here, the optimal N and P availability on hemlock logs as suggested by N:P ratios increased the growth (and, in the field, potentially the survival) of hemlock and yellow birch seedlings under greenhouse conditions.

Conclusions

Hemlock seedlings were unresponsive to N fertilization in the greenhouse, were similar in size and N content across wood species in the field and greenhouse, and showed no correlation between N availability in wood and seedling characteristics. Overall, hemlock was unresponsive to the factors measured here, a finding that is not surprising when its persistent seedling bank regeneration strategy is considered (Sutherland et al. 2000). We found no evidence that hemlock is limited by N, a result supported by fertilization experiments in other regions (Catovsky and Bazzaz 2002; Tripler et al. 2002). The presence of mycorrhizae, however, did benefit hemlock seedlings, presumably by increasing the seedlings' rate of uptake of nutrients, including N and P (Perez-Moreno and Read 2000). Future researchers might measure the amounts of P and micronutrients in individual large hemlock seedlings collected from or planted into logs in the field. Such seedlings would be large enough to yield sufficient dried plant material for micronutrient analysis of individual seedlings, and the results could either support or refute patterns of nutrient uptake demonstrated here in greenhouse-grown seedlings. Survival and abundance data from hemlock and yellow birch seedlings in the field do suggest that hemlock logs continue to confer an advantage to seedlings beyond the first year (Marx 2005).

Consistent with its gap-phase life-history strategy (Erdmann 1990), yellow birch responded strongly to large increases in light (greenhouse versus field) and nutrients. Fertilized seedlings were several times larger than unfertilized seedlings when growing on hemlock or sugar maple logs, but were mainly limited by P, and therefore unresponsive to N fertilization, when growing on yellow birch logs. Variation in yellow birch seedling mass could be directly related to the availability of N and P on different log species in the greenhouse, while in the field yellow birch seedlings were largest when growing on hemlock logs but showed no significant relationship between wood N availability and seedling mass. Alternative reasons for the increased mass and survival of yellow birch seedlings on hemlock wood in the field are explored in Marx (2005), but further experiments involving fertilization of yellow birch seedlings with both N and P and nutritional analysis of seedlings older than 2 years collected from wood of different species would be informative.

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