Journal of Ecology 2008 doi: 10.1111/j.1365-2745.2008.01360.x

Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock–hardwood forests

Laura Marx* and Michael B. Walters

Department of Forestry and Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, 126 Natural Resources Building, East Lansing, MI 48824, USA

Summary

1. Seedlings of some tree species are strongly associated with decaying wood in the germination or establishment period. Despite recognition of this pattern in forests around the world, few studies have compared the ability of different species of decaying wood to support seedlings.

2. We measured the abundance, survival, and age distribution of seedlings of *Tsuga canadensis* (eastern hemlock), *Betula alleghaniensi*s (yellow birch), and *Acer saccharum* (sugar maple) among forest floor substrates at field sites in Upper Michigan, USA. Seedlings were censused on decaying wood of the same three species and on soil to determine whether species of decaying wood and soil differ in their ability to support seedlings. We hypothesized that *Tsuga* and *Betula* seedling abundance and survival are higher on *Tsuga* wood than on *Acer* wood or soil.

3. Independent of seed fall, light and size of wood piece, *Tsuga* wood generally supported the highest densities of first-year and established (> 1 year-old) seedlings of *Betula* and *Tsuga*. Averaged over three sites, established seedlings per metre square on *Tsuga* wood, *Betula* wood, *Acer* wood and soil were 0.42, 0.21, 0.08 and 0.01, respectively, for *Tsuga*, 0.60, 0.15, 0.10 and 0.01, respectively, for *Betula* and 0.09, 0.03, 0.04 and 0.98, respectively for *Acer*. Long-term seedling survival was also greatest on *Tsuga* wood which supported seedlings as old as 13 years, while on *Acer* wood seedlings > 3 years-old were rare. Despite a strong general pattern in seedling densities, there were large site differences perhaps related to water availability.

4. *Synthesis*. We conclude that the strong association of *Tsuga* and *Betula* seedlings with *Tsuga* decaying wood and not with *Acer* wood or soil, combined with the distribution of *Tsuga* wood, helps explain (i) the close *Tsuga–Betula* association, (ii) the maintenance of distinct, temporally stable *Tsuga*- and *Acer*-dominated patches; and (iii) the decline of *Tsuga* in selectively logged forests as mature trees are harvested and decaying *Tsuga* wood is scarce. Differences between *Tsuga* and *Acer* wood may reflect general differences in the suitability of conifer vs. angiosperm wood for seedling establishment.

Key-words: *Acer saccharum*, *Betula alleghaniensis*, coarse woody debris, decaying wood, patch structure, seedling establishment, *Tsuga canadensis*

Introduction

Established seedlings of some tree species are strongly associated with decaying wood (Cornett *et al.* 2001; Mori *et al.* 2004; Caspersen & Saprunoff 2005), which covers little of the forest floor under all circumstances and covers even less in areas managed by selective logging (Hura & Crow 2004; Newbery *et al.* 2007). Associations of seedlings with decaying wood, combined with the spatial distribution of wood, may be an important mechanism driving forest canopy composition by limiting seedling recruitment of certain species (Caspersen & Saprunoff 2005). Despite broad recognition of the importance of decaying wood in forest dynamics, wood is usually treated as a single category or categorized by decay class (e.g. Christy & Mack 1984; Harmon & Franklin 1989; Takahashi *et al.* 2000; Mori *et al.* 2004). Wood has rarely been identified to, and studied at, the species level (but see Stewart & Burrows

---

*Correspondence author. 19 Main Street, Chester, MA 01011. E-mail: lmarx@tnc.org

1994 and Cornett *et al.* 2001), and species-specific associations between decaying wood and established seedlings have been studied even less. 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. It is unknown if this pattern persists for older seedlings, but if it does and other forest systems show a similar pattern of preferential colonization of conifer vs. angiosperm wood, then species-specific associations between decaying wood and established seedlings could be an important mechanism underlying forest dynamics.

The hemlock–hardwood system is ideal for examining species differences in suitability of decaying wood for seedling establishment. Eastern hemlock-dominated (*Tsuga canadensis* (L.) Carr.) forests intermixed with sugar maple-dominated (*Acer saccharum* Marsh.) hardwood forest (hereafter called hemlock–hardwood forest) covered large areas of Upper Michigan and northern Wisconsin, USA until the late 1800s when harvesting began. Since that time, more than 99% of the mature hemlock–hardwood forest in Michigan has been converted to other cover types (Noss & Peters 1995), and by 1993 the *Tsuga* component occupied only 0.5% of the landscape (Mladenoff & Stearns 1993). Remnant primary hemlock–hardwood forests often show a pronounced patch structure, with *Tsuga*-dominated patches (3–30 ha, Davis *et al.* 1998) containing high admixtures of yellow birch (*B. alleghaniensis* Britton) (Frelich *et al.* 1993; Kotar *et al.* 1999) occurring adjacent to *Acer*-dominated patches (Frelich *et al.* 1993). Pollen core studies indicate that the boundaries between these remaining patches have changed little since their formation about 3200 years ago (Davis *et al.* 1993). Several mechanisms have been proposed to explain the long-term maintenance of patch boundaries. These mechanisms include diminished light, water and perhaps nitrogen levels beneath *Tsuga*-dominated stands which may allow *Tsuga* but not *Acer* seedlings to survive (Finzi *et al.* 1998; Campbell & Gower 2000; Catovsky & Bazzaz 2000) and the abundance of hardwood leaf litter in *Acer*-dominated stands, which smothers small first-year *Tsuga* seedlings growing on the forest floor but not the larger *Acer* seedlings (Koroleff 1954; Frelich *et al.* 1993). While proposed mechanisms offer a partial explanation for the maintenance of patch structure, they do not explain why the presence of leaf litter-shedding decaying wood pieces in *Acer*-dominated stands does not result in the establishment of *Tsuga* trees in *Acer*-dominated patches. In addition, these mechanisms do not explain why *Tsuga* patches almost always contain a large basal area component of *Betula*. The strong *Tsuga*–*Betula* association is puzzling, as *T. canadensis* is among the most shade tolerant tree species in North America and *B. alleghaniensis* is mid-tolerant. However, both species are small-seeded and drought-intolerant (Erdmann 1990; Godman & Lancaster 1990), and have been found to be associated with decaying wood in primary forests (Reif 1992; Corinth 1995).

Preliminary observations in Upper Michigan suggested that not only are *Tsuga* and *Betula* seedlings associated with decaying wood, but that they are more abundant on certain species of decaying wood. We hypothesized that *Tsuga* and *Betula* seedlings are strongly associated with *Tsuga*, and perhaps *Betula,* decaying wood and weakly associated with *Acer* wood and soil. This variation, combined with the greater quantity of *Tsuga* and *Betula* wood in *Tsuga*-dominated than in *Acer*-dominated stands, could help explain hemlock–hardwood patch structure and the *Tsuga*–*Betula* spatial association. We investigated this hypothesis by identifying decaying wood to species and measuring seedling abundance, survival rates and age distributions across decaying wood and soil at four sites. Our specific predictions were:

1. *Tsuga*-dominated stands contain more *Tsuga* and *Betula* wood than do *Acer*-dominated stands.

2. Independent of variation in light, seed fall, and wood piece size, *Tsuga* and *Betula* seedlings are more abundant on *Tsuga* and *Betula* wood than on *Acer* wood or soil, whereas *Acer* seedlings are more abundant on soil than on wood.

3. Survival and maximum age of *Tsuga* and *Betula* seedlings follow the same pattern among decaying wood substrates as for abundance; *Tsuga* wood > *Betula* wood > *Acer* wood.

Methods

FIELD SITES

Between 2002 and 2005, we studied four primary hemlock–hardwood forests in Upper Michigan (see Appendix S1 in Supplementary material). Three of these sites, the Porcupine Mountains Wilderness State Park (hereafter called Porcupine), Sylvania Wilderness Area in Ottawa National Forest (Sylvania), and the Huron Mountain Club Reserve (Huron), are characterized by a patchy distribution of forest types, with patches of *Tsuga*-dominated forest with high admixtures of *Betula* bordering hardwood forests dominated by *Acer* often with high admixtures of basswood (*Tilia americana* L.) (Pastor & Broschart 1990). These forests also contain minor components of several other species, including balsam fir (*Abies balsamea* (L.) Mill.), red maple (*Acer rubrum* L.), striped maple (*Acer pensylvanicum* L.), northern white cedar (*Thuja occidentalis* L.), and hop hornbeam (*Ostrya virginiana* (Mill.) K. Koch). Our study areas are in forests that have never been harvested except perhaps selectively for white pine (*Pinus strobus* L.) in the late 1800s (Woods 1981; Simpson *et al.* 1990). The fourth site, in the state-owned Sand River area near Skandia, MI (Sand River), is a small patch of *Tsuga*-dominated forest surrounded by areas that have been managed by selection silviculture methods for several decades. Unlike the other three sites, Sand River is poorly-drained, has been mainly cleared of *Betula* seed sources, and has lower deer browse pressure (D. Wilson, personal communication.). At each site, paired field plots (0.1 ha) were placed on either side of distinct hemlock–hardwood patch borders to allow comparison between *Tsuga*-dominated (> 55% basal area *Tsuga*) and *Acer*-dominated stands. In *Acer*-dominated patches we restricted selected plots to ones having 10–35% basal area in *Tsuga* trees to assure that we had a contrast in stand types and the factors that might cause differences between stand types (e.g. differences in seed availability, environmental factors and surface area and species composition of wood pieces) while at the same time ensuring that all the same components were present in plots of both stand types (e.g. *Tsuga* seed source and decaying wood). There were no obvious topographic differences between the members of each pair, and paired plots were separated by 40–110 m. Within these spatial, topographic and compositional constraints, plots were located randomly. Sixteen field plots were located: seven at Huron (one *Tsuga*-dominated plot had no suitable *Acer* plot nearby), four each at Sylvania and Porcupine, and one in the small *Tsuga*-dominated patch at Sand River where no adjacent uncut areas of hardwoods existed.

DECAYING WOOD AND SEED FALL

Within each field plot, every stump, downed bole, or large branch section > 10 cm in diameter was counted, dimensions and decay stage were recorded, and a small sample was collected for later species identification. These stumps, boles and branches will hereafter be referred to as wood pieces. Wood pieces in decay stage V (the most highly decayed stage, where wood is almost fully incorporated into surrounding soil; Graham & Cromack 1982) were not counted. Species of each of the 413 wood pieces present in field plots by 2004 was determined by microscopic examination of thin slices of wood (40× to 200×, microscopes at the USDA Forest Products Laboratory, Madison, WI, see Marx 2005 for details), and 47 pieces of species other than *Tsuga*, *Betula* and *Acer* were excluded from analysis.

Seed fall was measured beside the midpoint of 15 randomly selected wood pieces within each of 12 plots. Seed traps were constructed from 22-cm diameter plastic pots (366 cm^2 surface area) with half-an-inch wire mesh and plastic canvas used to exclude seed predators. 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, seeds were counted, and a subsample cut open to determine the percentage of seeds filled.

SEEDLING ABUNDANCE AND SURVIVAL

All tree seedlings (stems ≤ 30 cm in height in order to be comparable to Rooney & Waller 1998) growing on a wood piece were counted and identified to species, and their age class was recorded. Two age classes were used: first-year, and older than first-year (hereafter called established). For each wood piece, an identical seedling survey was conducted on an equal surface area of soil 1 m away from and in the same orientation as the wood piece. Soil plots were randomly placed on either side of the wood piece. Large seedlings/saplings (> 30 cm tall but not in canopy) were noted when they occurred on either wood pieces or soil, but individuals in this larger size class were rare or absent in most field plots due to factors including browsing by abundant white-tailed deer populations. In order to calculate the surface area available to seedlings, we assumed that stumps were flat and boles and branches were half-cylinders. Given that most boles were intermediate between flat surfaces and half-cylinders, seedling density for boles is a conservative estimate. In 2002 and 2004, age class was determined for all seedlings. In 2003, following a mast *Acer* and *Betula* seed year in 2002, *Acer* seedlings were often so abundant on soil, and *Betula* seedlings so abundant on wood pieces, that we determined age class for a subsample (every 10th or every 20th seedling). When calculating average seedling density across years, we excluded first-year *Betula* and *Acer* seedlings in 2003 and established *Betula* and *Acer* seedlings in 2004.

To measure rates of seedling survival, 190 seedlings growing on *Tsuga* (n = 18 wood pieces), *Betula* (n = 17), and *Acer* (n = 13) wood pieces were marked with plastic toothpicks in late August 2002, after the high-mortality period of June and July when many first-year seedlings die. Wood pieces were chosen via stratified (by wood species) random sampling from each site. On each wood piece, we started at one end and marked seedlings of each available species, up to 10 seedlings in total, without regard to seedling age. Marked seedlings were censused for survival in summer 2003–05.

Seedling age distributions were determined by collecting established *Tsuga* and *Betula* seedlings from 88 wood pieces in 2002 and 16 additional wood pieces in 2004 using an unbiased systematic sampling design in the area surrounding our non-destructive sampling field plots (see Marx 2005 for more detailed methods). In 2004 seedlings were collected to increase numbers of seedlings from *Acer* wood pieces. These pieces only rarely supported seedlings so we had to sample over a much larger survey area to achieve a similar sample size compared to the other wood species. For seedlings ≥ 2 mm in diameter immediately above the root collar, we counted growth rings using a 50× dissecting microscope. Second- and third-year seedlings < 2 mm in diameter were aged in the field by counting bud scars (field aging of *Tsuga* is highly imprecise above 3 years of age). Light availability 30 cm above each wood piece from which seedlings were sampled was estimated by analysis of canopy photographs (GLA Version 2.0, 1999, Institute of Ecosystem Studies) taken with a digital camera (Nikon Coolpix 995, set to grayscale) fitted with a fisheye lens.

STATISTICAL ANALYSES

Unless indicated otherwise, analyses were done with JMP statistical software (version 5.1, SAS Institute Inc, Cary, NC). The Sand River site was excluded from all statistical analyses as there was no plot replication for *Tsuga*-dominated plots and there was no *Acer*-dominated plot. Data from this site were instead compared qualitatively to other sites. Experimental units and analyses varied among measured characteristics.

ANOVA was used to examine the effects of stand type (*Acer*-dominated, *Tsuga*-dominated) and site (Porcupine, Sylvania, Huron) on decaying wood coverage and wood diameter, and plots were experimental units. For significant effects, means comparisons were made with Student's t-tests between stand types and with Tukey–Kramer HSD among sites. Variation in light availability among sites and wood species was also analyzed with ANOVA, but in this case wood pieces rather than plots were the experimental units. For the analysis of variation in light availability above different species of wood, the equal variances assumption of ANOVA was not met, so a Welch ANOVA, which allows unequal variance among groups, was used. Results were similar to a standard ANOVA.

The effects of wood species, site and stand type on seed fall density were analyzed with non-parametric tests because seed fall density distribution was strongly left skewed and could not be transformed to a normal distribution. The Kruskall–Wallis test was used to test differences between the three wood species and sites and Wilcoxon rank-sum was used for the two-sample tests for stand types and to compare seed fall on *Acer* vs. *Tsuga* wood when Kruskall–Wallis tests revealed significant differences among decaying wood species.

For analyses of seedling survival, seedlings were the experimental units and nominal logistic regression was used to test differences in probability of seedling survival among the three wood species. For years in which regressions were significant, a single contrast was performed (Fisher's exact test) between survival on *Tsuga* and *Acer* wood.

For seedling abundance data, wood pieces were the experimental units. The large number of zero values obtained for seedlings (as many as 97% of wood pieces within a study site lacked seedlings), while biologically meaningful, made the data impossible to normalize by transformation. Because of this we used negative binomial regression (SAS 9.1.3, proc GLM, distribution = negative binomial, SAS Institute Inc.) to examine the effects of site, stand type and substrate on seedling counts. Surface area (of wood and/or soils) was included in the models as a covariate in order to normalize seedling counts by substrate surface area. Seedling count differences independent of wood piece size are interpreted as differences in density and are presented and discussed as such.

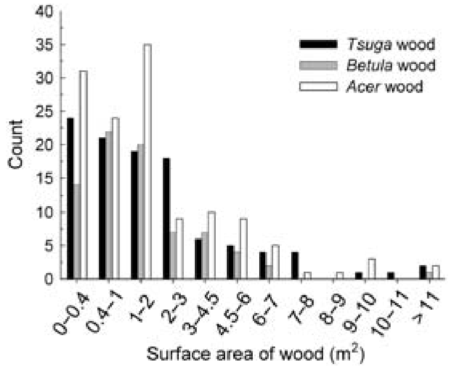

Fig. 1. Wood piece size distribution of *Tsuga* ($n = 105$), *Betula* ($n = 77$), and *Acer* ($n = 130$; field sites pooled) wood pieces.

Results

DECAYING WOOD AND SEEDLING DISTRIBUTIONS

Total decaying wood coverage did not vary significantly with stand type (ANOVA, $P = 0.22$) or site ($P = 0.23$) due to large variation among plots. On average, wood pieces covered 5.3% of forest floor area in *Tsuga*-dominated stands and 4.3% in *Acer*-dominated stands. Wood pieces covered 6.2% of the forest floor at Porcupine and 4.4% at both Sylvania and Huron. For all sites pooled, *Tsuga* wood pieces comprised 35% of the wood surface area in *Tsuga*-dominated stands, *Betula* 18%, and *Acer* 29%, with 18% of area made up of minor species, vs. 27%, 18%, 48% and 8%, respectively, in *Acer*-dominated stands. There was no difference in the average decay stage of wood pieces among sites or between the two stand types (mean = 2.9 and median = 3.0 for both, stages follow Graham & Cromack 1982). At Porcupine, but not at Sylvania or Huron, *Tsuga* wood pieces had a greater average diameter than *Acer* pieces (ANOVA, $P = 0.015$, *Tsuga* = 32.1 cm, *Acer* = 22.7 cm), but the size distribution of wood pieces did not vary significantly among species or sites (sites pooled, Fig. 1). For example, 31% of *Acer* wood pieces had > 2 m^2 surface area and these comprised 72% of the total surface area, which was similar to the values for *Tsuga* pieces (39% and 78%, respectively).

The same general pattern of seedling abundance occurred at each site; both first-year and established *Tsuga* and *Betula* seedlings were more abundant on *Tsuga* than on *Acer* wood pieces with the exception of established *Betula* seedlings at Huron (Table 1). Averaged over Sylvania, Porcupine and Huron, established seedlings per metre square on *Tsuga* wood, *Betula* wood, *Acer* wood and soil substrates were 0.42, 0.21, 0.08 and 0.01, respectively, for *Tsuga* seedlings, 0.60, 0.15, 0.10 and 0.01, respectively, for *Betula* seedlings and 0.09, 0.03, 0.04 and 0.98, respectively, for *Acer* seedlings. Thus *Tsuga* and *Betula* seedlings were at least five times more abundant on *Tsuga* wood pieces than on *Acer* pieces, and at least 42 times more abundant than on soil. On wood pieces that supported seedlings, *Tsuga* and *Betula* seedling densities were positively correlated (averaged across years, 2004 excluded for *Betula*, $r = 0.50$, $P < 0.0003$ at Porcupine). Density of established *Tsuga* seedlings was greater in *Tsuga*-dominated than in *Acer*-dominated plots at Porcupine but because this difference was due to a single *Tsuga*-dominated plot (negative binomial regression χ^2, $P > 0.41$ in all years at Porcupine with plot removed) we pooled stand types for analyses of seedling abundance.

Despite the same general trend of established *Tsuga* and *Betula* seedling density across substrates at each site, there

Table 1. Mean *Tsuga*, *Betula* and *Acer* seedling density per metre square (SE in parentheses) on forest floor substrates

		Seedling species, first-year seedlings			Seedling species, established seedlings		
Site	Substrate	*Tsuga*	*Betula*	*Acer*	*Tsuga*	*Betula*	*Acer*
Huron	*Tsuga*	1.08 (0.41)	0.07 (0.04)	0.39 (0.28)	0.19 (0.08)	0.13 (0.08)	0.02 (0.02)
	Betula	0.47 (0.17)	0.15 (0.10)	0.20 (0.09)	0.07 (0.04)	0.01 (0.01)	0.02 (0.02)
	Acer	0.22 (0.05)	0.12 (0.09)	0.15 (0.06)	0.05 (0.04)	0.14 (0.14)	0 (0)
	Soil	0.14 (0.04)	0.04 (0.02)	1.89 (0.24)	0.01 (0.00)	0 (0)	2.44 (0.50)
Porcupine	*Tsuga*	0.50 (0.18)	5.33 (2.47)	0.15 (0.08)	0.70 (0.21)	1.22 (0.53)	0.09 (0.03)
	Betula	0.41 (0.17)	1.88 (0.66)	0 (0)	0.41 (0.18)	0.16 (0.09)	0.05 (0.05)
	Acer	0.06 (0.06)	0.33 (0.24)	0.01 (0.01)	0.02 (0.02)	0.02 (0.01)	0 (0)
	Soil	0.12 (0.04)	0.19 (0.06)	0.18 (0.04)	0.01 (0.00)	0.01 (0.00)	2.63 (0.52)
Sylvania	*Tsuga*	0.52 (0.45)	4.89 (3.24)	0.23 (0.18)	0.76 (0.68)	0.44 (0.35)	0.17 (0.17)
	Betula	0.29 (0.13)	0.45 (0.16)	0.12 (0.06)	0.27 (0.15)	0.28 (0.26)	0.03 (0.03)
	Acer	0.08 (0.05)	0.75 (0.31)	0.37 (0.23)	0.36 (0.10)	0.14 (0.08)	0.11 (0.06)
	Soil	0.01 (0.01)	0 (0.02)	0.88 (0.15)	0.02 (0.02)	0.01 (0.00)	4.74 (0.76)

Established seedlings are older than 1 year. *Tsuga* densities are averaged over 2002–04, while *Betula* and *Acer* densities exclude 2003 for first-year seedlings, and 2004 for established seedlings because 2002 was a mast seed year. $n = 302$ wood pieces and soils in 2002, $n = 308$ in 2003 and $n = 312$ in 2004.

were significant differences among sites (negative binomial regression χ^2, $P < 0.0001$ for both species in all years). For example, established *Tsuga* and *Betula* seedlings on wood pieces were most abundant at the wettest of the three main sites (Porcupine) and least abundant at the driest (Huron). At Sand River, our only site with a high water table (soil water in July 2003 = 79.1%, vs. an average of 55.5% for the other sites, see Marx 2005 for methods and Supplementary Appendix S1 for climate data), *Tsuga* seedlings were 20 times greater on wood pieces (7.82 m^{-2}), and 50 times greater on soil (1.03 m^{-2}) than average values across the three other sites (0.40 and 0.020 m^{-2}, respectively). In addition to site differences, sites and substrates interacted. Density of established seedlings varied among wood species at Porcupine in all years (χ^2, $P < 0.045$ in all cases, Supplementary Appendix S2) and at Sylvania for *Tsuga* seedlings in 2002 ($P = 0.029$). At Huron, our driest site and that with the fewest established seedlings, variation in seedling density across wood species was not significant (Supplementary Appendix S2).

Acer seedling densities showed a pattern opposite that of *Tsuga* and *Betula* seedlings, with 47–244 times as many established *Acer* seedlings on soil as on wood pieces, depending on site (Table 1). The year 2002 was a mast seed year for *Acer*, and first-year *Acer* seedlings in 2003 and established seedlings in 2004 were so abundant that we excluded these two cases from analyses where we averaged seedlings across years. Without this exclusion, *Acer* established seedling density on *Tsuga* wood at Porcupine rises from 0.09 seedlings m^{-2} to 0.64 seedlings m^{-2}.

LIGHT AVAILABILITY, WOOD PIECE SIZE AND SEED FALL

Light is a critical resource limiting seedling survival in forest understoreys, and if it were confounded with wood species then light availability, rather than intrinsic differences among wood species, could explain seedling–decaying wood associations. Light varied among sites (ANOVA, $P < 0.0001$), with wood pieces at Huron having higher mean GLI (7.6%) than wood from Sylvania (3.6%) and Porcupine (3.9%). However, among sites light availability did not vary consistently among wood species, and within sites differences were modest. For example, at Porcupine *Acer* wood pieces had negligibly lower light availability than *Tsuga* wood pieces (3.5% vs. 4.1%, respectively, ANOVA, $P = 0.001$) whereas the pattern was opposite at Sylvania (3.8% vs. 3.2%, respectively, Welch ANOVA, $P = 0.013$), and at Huron light availability did not differ significantly across wood species (8.4% vs. 7.1%, ANOVA, $P = 0.080$). In addition, light–seedling density relationships were weak for both *Tsuga* and *Betula* at all sites (Marx 2005).

If the average surface area of wood pieces varied by species, this also could affect seedling-wood associations if seedling density varied with wood piece size. However, surface area distributions of wood pieces did not vary among species (Fig. 1), and regardless of size, *Tsuga* wood pieces were generally more likely to support *Tsuga* and *Betula* seedlings than *Acer* wood pieces (Fig. 2).

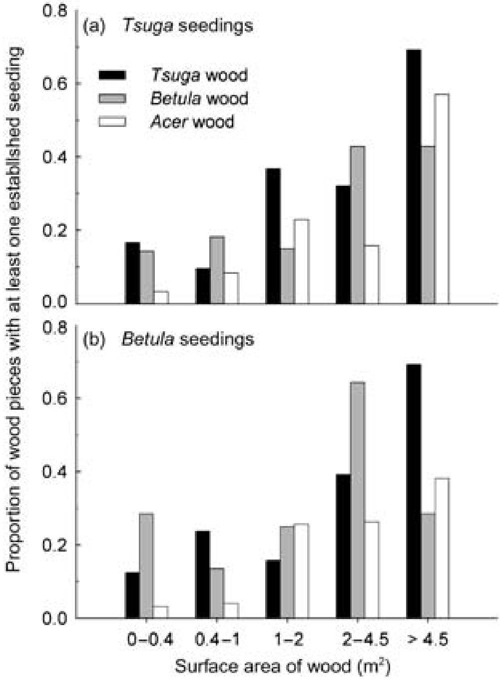

Fig. 2. Probability of *Tsuga* (a) and *Betula* (b) established seedling presence in at least one of the years 2002–04 on wood pieces, by wood surface area class and species for data pooled from Porcupine, Huron and Sylvania. $n = 105$ *Tsuga*, $n = 77$ *Betula* and $n = 130$ *Acer* wood pieces.

Seed fall could also affect seedling abundance patterns among wood species. Seed fall density varied across sites and ranked Huron > Porcupine > Sylvania for all seed species (Kruskall–Wallis, $P \leq 0.0002$ in all cases, data shown in Marx 2005). *Tsuga* and *Betula* seed fall density was greater in *Tsuga*-dominated plots and *Acer* seed fall density was greater in *Acer*-dominated plots as is expected given differences in canopy composition (Wilcoxon rank-sum, $P < 0.0001$ in all cases). Given that *Tsuga*-dominated plots contained both more *Tsuga* and *Betula* wood pieces and more *Tsuga* and *Betula* seeds, it is possible that the seedling–wood species pattern we observed is partly due to differences in seed fall onto different wood species. Two lines of evidence suggest that the contribution of seed fall to seedling abundance patterns is minor. First, when analyzed with stand types pooled in order to be comparable to analyses of seedling density, seed fall does not vary among wood species with one exception. The exception is that more *Tsuga* seeds fell onto *Betula* wood than on *Acer* and *Tsuga* wood at Porcupine (Kruskall–Wallis $P = 0.001$). The seedling density patterns at this site (Table 1) indicate a different pattern, with greater *Tsuga* seedling abundance on *Tsuga* than on *Acer* wood, despite no difference in *Tsuga* seed fall on these wood species (Wilcoxon rank-sum, $P > 0.05$). Second, differences in mean *Betula* seed fall on *Tsuga* vs. *Acer* wood pieces were 8-fold at Porcupine and 1.5-fold at Sylvania whereas respective differences in mean established seedling densities were 61-fold at Porcupine and 3-fold at Sylvania (Table 1).

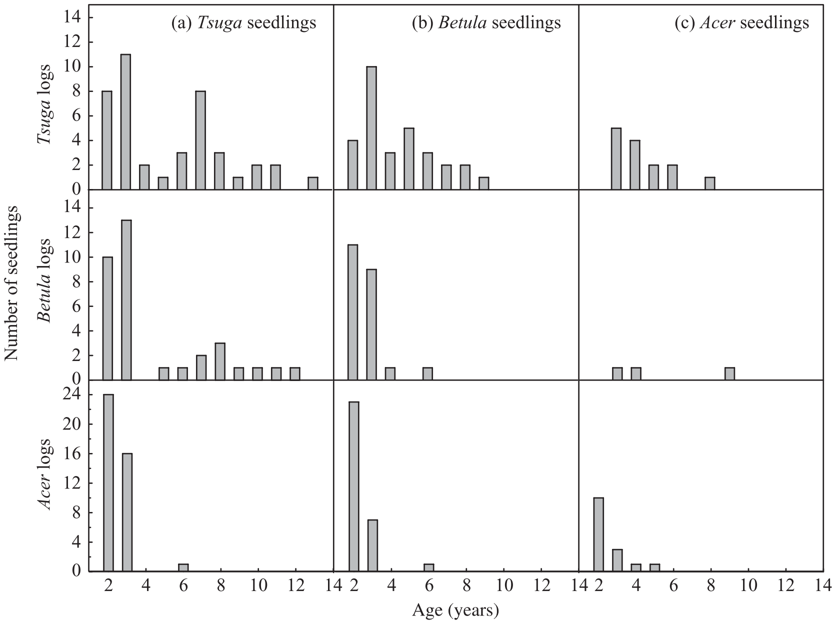

Fig. 3. Age distribution of *Tsuga*, *Betula* and *Acer* seedlings on different wood species. Note the different y-axis scale for *Acer* logs. $n = 42$ *Tsuga*, $n = 30$ *Betula* and $n = 34$ *Acer* wood pieces; field sites pooled.

Table 2. Percent survival of *Betula* and *Tsuga* seedlings growing on decaying wood substrates

Wood substrate	Seedling survival (%)					
	Betula			*Tsuga*		
	2003*	2004	2005	2003*	2004	2005*
Tsuga	62.7	20.9	11.6	90.3	67.7	55.2
Betula	56.5	26.1	13.0	66.7	46.2	35.9
Acer	26.3	15.8	10.5	65.4	46.2	28.0

Seedlings were marked in late summer 2002 and censused in summer of the years indicated. $n = 96$ *Tsuga* and $n = 85$ *Betula* seedlings. *Percent seedling survival on *Tsuga* wood was significantly greater than that on *Acer* wood (Fisher's exact test, $P < 0.05$).

SEEDLING SURVIVAL

Mortality across 3 years was high, with only 50 of the original 190 marked seedlings surviving to 2005. *Tsuga* seedlings had highest survival on *Tsuga* wood pieces and lowest survival on *Acer* wood (Table 2). Survival of marked *Betula* seedlings was significantly greater on *Tsuga* wood than on *Acer* wood from 2002 to 2003, even when first-year seedlings (which had higher mortality rates than established seedlings) were excluded (data not shown). When seedling survival was remeasured in 2004 and 2005, *Betula* survival was low and did not vary across wood species. *Acer* was not included in our marked seedling experiment, however, only 33% ($n = 95$, sites pooled) of the established *Acer* seedlings on wood in the 2004 census survived to the 2005 census in our field sites, where the *Acer* seedling population was predominantly from a 2002 mast seed year.

The age distribution of *Tsuga* and *Betula* seedlings on wood (Fig. 3) is consistent with our marked seedling survival data (Table 2). Only 3% of established *Tsuga* plus *Betula* seedlings were older than 3 years on *Acer* wood pieces, whereas 54% and 23% were older than 3 years on *Tsuga* and *Betula* wood, respectively. Nine percent of *Tsuga* seedlings and no *Betula* seedlings were ≥ 10 years-old on *Tsuga* and *Betula* wood pieces. Across all wood species, 41% of *Acer* seedlings were > 3 years-old, but none were > 9 years-old (Fig. 3) and as described above, *Acer* seedlings were rare on wood of all species.

Discussion

SEEDLING DISTRIBUTION AND SURVIVAL

The consistent differences we found in *Tsuga* and *Betula* seedling survival and density among decayed wood substrates provide strong support for our hypothesis that there are species-specific differences in the suitability of wood pieces as seedling establishment substrates. *Tsuga* and to a lesser extent *Betula* wood is more favourable for seedling establishment than *Acer* wood. Seedling age class structures (Fig. 3) provided the most compelling support for our hypothesis as nearly all *Tsuga* and *Betula* seedlings > 3 years-old were restricted to *Tsuga* and *Betula* wood. In addition to *Tsuga*, *Betula* and *Acer* wood, we recorded seedling density data on one to eleven *T. occidentalis*, *Abies balsamea*, *Ostrya virginiana*, *T. americana*, *A. rubrum*, *P. strobus* and *Quercus sp.* wood pieces. Sample sizes of these wood species preclude all but speculation, but among the conifers, *Tsuga* and possibly *Thuja* wood, but not *Abies* wood, appear to serve as establishment sites for large numbers of *Tsuga* and *Betula* seedlings while *Pinus* was too rare for speculation. Of the six angiosperm species, only *Betula* supported *Tsuga* and *Betula* seedlings.

Acer seedlings are unlike *Tsuga* and *Betula* seedlings in that *Acer* seedlings are rare on all wood species substrates and abundant on soil. There is no clear pattern in density or

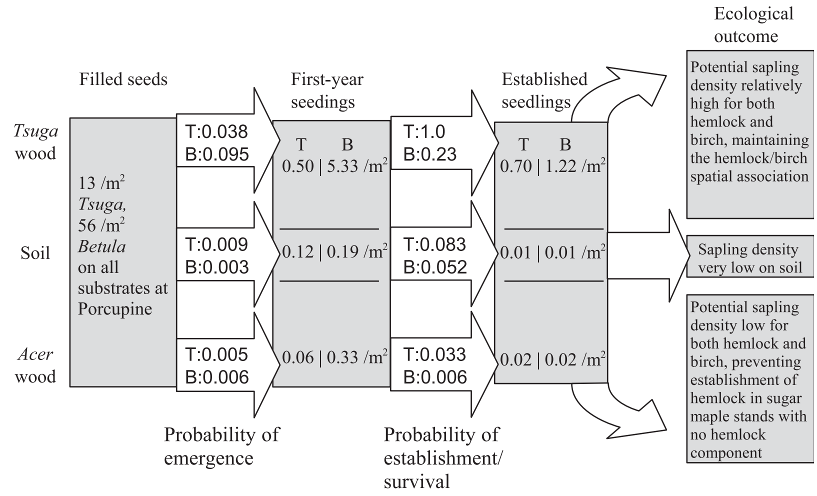

Fig. 4. Seed and seedling densities (in boxes) and estimated probabilities of survival between life stages (in arrows) for *Tsuga* and *Betula* on *Tsuga* wood pieces (top left to right), soil (middle) and *Acer* wood pieces (bottom). Data are from Porcupine only. Survival probabilities were estimated by dividing seedling density in a life stage by seedling/seed density in the previous life stage. Probability of establishment/survival is therefore the ratio of established seedlings of all ages, not only second-year seedlings, to first-year seedlings.

survival of *Acer* seedlings among wood species, and unlike the many *Tsuga* seedlings > 10 years-old on *Tsuga* wood, there are no *Acer* seedlings > 9 years-old on any wood species. It appears that *Acer* seedlings can germinate and survive for a few years at relatively low density on decaying wood, but they have low longer-term survival (as suggested in Tubbs 1995). These differences may be due to the combination of *Acer*'s relatively large seed, with greater ability to colonize litter-covered soil (Mori *et al.* 2004) and survive resource shortfalls (e.g. Walters & Reich 2000), and *Acer*'s possible inability to acquire nutrients on decayed wood (Marx & Walters 2006).

Despite having the most abundant first-year *Tsuga* seedlings on wood pieces of any site, established seedlings were the least abundant at Huron which is consistent with the low established seedling densities found in prior regeneration surveys (Graham 1941; Nelson 1997; Rooney & Waller 1998). This implies that high early mortality is the primary cause for low established seedling populations at Huron. Possible mortality agents include frost, pathogens (although O'Hanlon-Manners & Kotanen 2004 suggests that at least for seeds, wood pieces provide a refuge from fungal pathogens), browsing by deer, and/or drought. The large differences in established seedling densities among sites, with the driest, Huron, having the lowest seedling density, and the wettest, Sand River, having the highest, indicates that the ability of wood pieces to support established seedlings depends strongly on local climate and/or hydrology. Sand River also had the smallest difference between seedling abundance on wood pieces and on soil of any field site. Seedlings appear to be both more abundant overall and less restricted to wood pieces at Sand River.

Possible mechanisms explaining species-level differences in seedling abundance and survival on wood pieces are beyond the scope of this paper. Briefly, intrinsic factors that we have found to be important in explaining differences in seedling establishment and survival on different species of wood in our model system include variation in wood decay patterns and rates (see Marx 2005) and differences in nutrient availability and mycorrhizas (see Marx & Walters 2006). In contrast to intrinsic, wood species-based characteristics, we found in this study that the extrinsic or sampling-based factors of light availability, wood piece size, and *Tsuga* and *Betula* seed fall did not contribute strongly to differences in seedling density and survival among wood species. Negligible and inconsistent differences in light availability among wood species (this study) combined with weak light–seedling density relationships (Marx 2005) indicate that light does not explain differences in seedling density and survival among wood species. Similarly weak relationships between seedling density and seed fall are consistent with the assertions of McEuen & Curran (2004) and Caspersen & Saprunoff (2005) that regeneration of small-seeded, wind-dispersed species *Tsuga* and *Betula* are limited by recruitment rather than by seed dispersal.

ECOLOGICAL AND MANAGEMENT IMPLICATIONS

Despite variation among sites, collectively our results indicate that species-level differences in seedling density and survival on wood may help maintain the boundaries of adjacent *Tsuga*-dominated and *Acer*-dominated patches. Similar numbers of seeds fall on *Tsuga*, *Betula* and *Acer* wood pieces and soil, but immediate differences in seedling abundance are apparent across substrates and those differences become more pronounced as first-year seedlings become established and surviving established seedlings become the potential sapling pool (Fig. 4). At Porcupine, established *Tsuga* seedling density on *Tsuga* wood was 70 times greater than on soil and 35 times greater than on *Acer* wood. This pattern serves as a positive feedback loop for *Tsuga* establishment in *Tsuga*-dominated stands where decaying *Tsuga* wood is common. Conversely, this pattern may limit *Tsuga* establishment in *Acer*-dominated patches where *Tsuga* wood is rare to absent and *Acer* seedlings can dominate the established seedling pool on a forest floor characterized by smothering leaf litter.

Tsuga and *Betula* saplings were scarce in Huron, Porcupine and Sylvania due, in part, to high deer density. However, the preponderance of stilt-rooted *Tsuga* and *Betula* trees at all sites is strong circumstantial evidence for the importance of wood species-seedling associations in forest canopy dynamics.

Fig. 5. Paired *Tsuga* and *Betula* canopy trees. The *Betula* tree is labelled with a B, the *Tsuga* tree with a T. Photo was taken at Sylvania Wilderness Area, near Devil's Head Lake. This photo is in colour in the online version of this article.

Furthermore, the proportion of *Tsuga* and *Betula* trees that are stilt-rooted underestimates the proportion of seedlings that established on decayed wood since only wood pieces in the early decay stages have surfaces noticeably higher than the forest floor (L. Frelich, personal communication). Based on excavations of visible as well as buried decayed wood at the base of trees in the Porcupine Mountains, Lee Frelich and Craig Lorimer estimated that 70–80% of *Tsuga* and *Betula* trees in multi-age stands originally became established on wood pieces (L. Frelich, personal communication, From University of Minnesota via email to M. Walters).

Our seedling and wood piece distribution results also suggest an explanation for the close spatial association of *Tsuga* and *Betula* trees (Rogers 1980; Kotar *et al.* 1999; Figs 4 and 5). The apparent restriction of both *Tsuga* and *Betula* seedlings > 4 years-old to *Tsuga* or *Betula* wood, and the positive correlation between *Tsuga* and *Betula* seedling densities on each wood piece explain this pattern. At the individual tree scale, seedlings of *Tsuga* and *Betula* often become established on the same wood piece and can ultimately become pairs of canopy trees as evidenced by pairs of stilt-rooted *Tsuga* and *Betula* trees with tangled roots (Fig. 5). At the stand scale, the abundance of decaying *Tsuga* and perhaps *Betula* wood substrates in *Tsuga–Betula* stands and their absence in *Acer*-dominated stands can explain the close *Tsuga–Betula* association with or without their colonizing the same pieces of wood.

The restriction of *Tsuga* and *Betula* seedlings to wood may also help explain why established seedlings are often rare in forests managed by selection silvicultural systems, where mature trees are removed and thus decaying wood coverage is lower (Hura & Crow 2004). 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 & Lorimer 1996; Neumann & Peterson 2001), but these guidelines do not yet specify which species should be left. Our data show that the value of wood as a substrate for seedling establishment varies with species and wood species should be considered in management plans aimed at increasing the abundance of trees such as *Betula* and *Tsuga*, or influencing future species composition in stands impacted by the invasive pest, hemlock woolly adelgid.

Species-specific associations between wood and seedlings are, to our knowledge, little studied in other forest ecosystems, yet these associations could be an important determinant of forest composition in a wide range of forest systems. Decaying wood is an important seedling substrate for both conifer and hardwood seedlings in Scandinavian *Picea–Betula* and *Pinus–Betula* forests (Kuuluvainen & Kalmari 2003), for spruce saplings throughout the world (Eichrodt 1969; Simard *et al.* 1998; Bauer 2003; Brang *et al.* 2003 in Baier *et al.* 2007), for conifer seedling survival in Japan (Mori *et al.* 2004), for several species in South American (Lusk 1995) and New Zealand rainforests (Bellingham & Richardson 2006), and in other systems referenced in Harmon *et al.* (1986) review. Studies which have compared decaying wood by species have found that wood species vary in density of seedlings (*Picea–Tsuga* forests in the Pacific Northwest, Christy & Mack 1984; *Betula–Thuja* forests in northern Minnesota, Cornett *et al.* 2001; this study), wood decay fungal species (*Nothofagus* forests in New Zealand, Stewart & Burrows 1994), and in the long-term survival of seedlings (this study). The association of tree seedlings with particular species of wood, and perhaps especially with conifer vs. angiosperm wood, may play an important role in shaping forest composition and dynamics in systems beyond northern Michigan. Understanding this association will aid in both our mechanistic understanding of forest dynamics and our ability to manage and regenerate these forest systems.

Acknowledgements

Scott Kissman, Marcie Tidd and Laurie Gilligan assisted with field and laboratory work. This research was supported financially by a NSF Graduate Research Fellowship and a Doctoral Dissertation Improvement Grant (DEB-0410748) to L.M., by the Huron Mountain Wildlife Foundation, and by the Michigan Botanical Club Hanes Fund. We thank Kerry Woods and two anonymous referees for helpful comments on an earlier draft.

References

Baier, R., Meyer, J. & Gottlein, A. (2007) Regeneration niches of Norway spruce saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps. *European Journal of Forest Research*, **126**, 11–22.

Bellingham, P.J. & Richardson, S.J. (2006) Tree seedling growth and survival over 6 years across different microsites in a temperate rain forest. *Canadian Journal of Forest Research*, **36**, 910–918.

Campbell, J.L. & Gower, S.T. (2000) Detritus production and soil N transformations in old-growth eastern hemlock and sugar maple stands. *Ecosystems*, **3**, 185–192.

Caspersen, J.P. & Saprunoff, M. (2005) Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. *Canadian Journal of Forest Research*, **35**, 978–989.

Catovsky, S. & Bazzaz, F.A. (2000) The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. *Journal of Ecology*, **88**, 100–112.

Christy, E.J. & Mack, R.N. (1984) Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *Journal of Ecology*, **72**, 75–91.

Corinth, R.L. (1995) Coarse woody debris and regeneration of eastern hemlock. *Hemlock Ecology and Management: Conference Proceedings, September 27–28, 1995, Iron Mountain, MI.* (eds G.D. Mroz & J. Martin), pp. 193–194. University of Wisconsin-Madison, Madison.

Cornett, M.W., Puettmann, K.J., Frelich, L.E. & Reich, P.B. (2001) Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology*, **9**, 386–396.

Davis, M.B., Calcote, R.R., Sugita, S. & Takahara, H. (1998) Patchy invasion and the origin of a hemlock-hardwoods forest mosaic. *Ecology*, **79**, 2641–2659.

Davis, M.B., Sugita, S., Calcote, R.R., Ferrari, J.B. & Frelich, L.E. (1993) Historical development of alternate communities in a hemlock-hardwood forest in northern Michigan, USA. *Large-scale Ecology and Conservation Biology* (eds P.J. Edwards, R.M. May & N.R. Webb), pp. 19–39. Blackwell Scientific Publications, Oxford.

Erdmann, G.G. (1990) *Betula alleghaniensis* Britton yellow birch. *Silvics of North America: 2. Hardwoods* (eds R.M. Burns & B.H. Honkala), pp. 133–147. United States Department of Agriculture (USDA), Forest Service, Agriculture Handbook. 654.

Finzi, A.C., Canham, C.D. & Breemen, N.V. (1998) Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications*, **8**, 440–446.

Frelich, L.E., Calcote, R.R., Davis, M.B. & Pastor, J. (1993) Patch formation and maintenance in an old-growth hemlock-hardwood forest. *Ecology*, **74**, 513–527.

Godman, R.M. & Lancaster, K. (1990) *Tsuga canadensis* (L.) Carr. Eastern hemlock. *Silvics of North America: 1. Conifers* (eds R.M. Burns & B.H. Honkala), pp. 604–612. United States Department of Agriculture (USDA), Forest Service, Agriculture Handbook. 654.

Graham, R.L. & Cromack, K. Jr. (1982) Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Canadian Journal of Forest Research*, **12**, 511–521.

Graham, S.A. (1941) The question of hemlock establishment. *Journal of Forestry*, **39**, 567–569.

Harmon, M.E. & Franklin, J.F. (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology*, **70**, 48–59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., *et al.* (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.

Hura, C.E. & Crow, T.R. (2004) Woody debris as a component of ecological diversity in thinned and unthinned northern hardwood forests. *Natural Areas Journal*, **24**, 57–64.

Koroleff, A. (1954) Leaf litter as a killer. *Journal of Forestry*, **52**, 178–182.

Kotar, J. Kovach, J.A. & Brand, G. (1999) *Analysis of the 1996 Wisconsin Forest statistics by Habitat Type. Gen. Tech. Rep. NC-207*. USDA Forest Service, North Central Research Station, Saint Paul, MN.

Kuuluvainen, T. & Kalmari, R. (2003) Regeneration microsites of *Picea abies* seedlings in a windthrow area of a boreal old-growth forest in southern Finland. *Annales Botanici Fennici*, **40**, 401–413.

Lusk, C.H. (1995) Seed size, establishment sites and species coexistence in a Chilean rain-forest. *Journal of Vegetation Science*, **6**, 249–256.

Martin, J. & Lorimer, C.G. (1996) How to manage Northern hardwoods. *University of Wisconsin Forestry Extension Publication #81*. University of Wisconsin-Madison, Madison.

Marx, L.M. (2005) *Substrate Limitations to Tsuga canadensis and Betula alleghaniensis Seedling Establishment*. PhD thesis. Michigan State University, East Lansing.

Marx, L.M. & Walters, M.B. (2006) Effects of nitrogen supply and wood species on *Tsuga canadensis* and *Betula alleghaniensis* seedling growth on decaying wood. *Canadian Journal of Forest Research*, **36**, 2873–2884.

McEuen, A.B. & Curran, L.M. (2004) Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. *Ecology*, **85**, 507–518.

Mladenoff, D.J. & Stearns, F. (1993) Eastern hemlock regeneration and deer browsing in the northern Great Lakes Region: a re-examination and model simulation. *Conservation Biology*, **7**, 889–900.

Mori, A., Mizumachi, E., Osono, T. & Doi, Y. (2004) Substrate-associated seedling recruitment and establishment of major conifer species in an old-growth subalpine forest in central Japan. *Forest Ecology and Management*, **196**, 287–297.

Nelson, C.R. (1997) *Hemlock regeneration on the Nicolet National Forest, Wisconsin*. MS thesis. University of Wisconsin-Madison, Madison.

Neumann, D. & Peterson, G. (2001) Northern Hardwood Forest Management. *Michigan State University Extension Bulletin E2769*. Michigan State University, East Lansing.

Newbery, J.E., Walters, M.B. & Lewis, K.J. (2007) *Inonotus tomentosus* and the dynamics of unmanaged and partial cut wet-sub boreal spruce-fir forests. *Canadian Journal of Forest Research*, **37**, 2663–2676.

Noss, R.F. & Peters, R.L. (1995) *Endangered Ecosystems: A Status Report on America's Vanishing Habitat and Wildlife*. Defenders of Wildlife, Washington, D.C, p. 82.

O'Hanlon-Manners, D.L. & Kotanen, P.M. (2004) Logs as refuges from fungal pathogens for seeds of eastern hemlock (*Tsuga canadensis*). *Ecology*, **85**, 284–289.

Pastor, J. & Broschart, M. (1990) The spatial pattern of a northern conifer-hardwood landscape. *Landscape Ecology*, **4**, 55–68.

Reif, C.B. (1992) Specimens of *Betula alleghaniensis* and *Betula lenta* growing from century-old stumps. *Journal of the Pennsylvania Academy of Science*, **66**, 116–122.

Rogers, R.S. (1980) Hemlock stands from Wisconsin to Nova Scotia: transitions in understory composition along a floristic gradient. *Ecology*, **61**, 178–193.

Rooney, T.P. & Waller, D.M. (1998) Local and regional variation in hemlock seedling establishment in forests of the upper Great Lakes region, USA. *Forest Ecology and Management*, **111**, 211–224.

Simpson, T.B., Stuart, P.E. & Barnes, B.V. (1990) Landscape ecosystems and cover types of the reserve area and adjacent lands of the Huron Mountain Club. *Occasional Papers of the Huron Mountain Wildlife Foundation, No. 4*. Huron Mountain Wildlife Foundation, Big Bay, MI.

Stewart, G.H. & Burrows, L.E. (1994) Coarse woody debris in old-growth temperate beech (*Nothofagus)* forests of New Zealand. *Canadian Journal of Forest Research*, **24**, 1989–1996.

Takahashi, M., Sakai, Y., Ootomo, R. & Shiozaki, M. (2000) Establishment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growth *Picea–Abies* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research*, **30**, 1148–1155.

Tubbs, C.H. (1995) Aspects of eastern hemlock silvics important in silviculture: an overview. *Hemlock Ecology and Management: Conference Proceedings, September 27–28, 1995, Iron Mountain, MI* (eds G.D. Mroz & J. Martin), pp. 5–10. University of Wisconsin-Madison, Madison.

Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, **81**, 1887–1901.

Woods, K.D. (1981) *Interstand and Intrastand Pattern in Hemlock-Northern Hardwood Forests*. PhD thesis, Cornell University, Ithaca.

Received 12 August 2007; accepted 18 January 2008
Handling Editor: Frank Gilliam

Supplementary material

The following supplementary material is available for this article:

Appendix S1 Locations and characteristics of field sites.

Appendix S2 Model results of effects of wood species on seedling abundance.

This material is available as a part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2008.01360.x
(This link will take you to the article abstract.)