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 alleghaniensis_ (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...
with hardwood forests often show a pronounced patch structure, (Mladenoff & Stearns 1993). Remnant primary hemlock–the mature hemlock–hardwood forest in Michigan has been followed by harvesting began. Since that time, more than 99% of the hemlock–hardwood forest covered large areas of Upper seedlings to survive (Finzi (L.) Carr.) forests intermixed with sugar maple-dominated leaf litter in establishing. 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-shredding 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 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 cm² 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 died. 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.

**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 \( \chi^2, P > 0.41 \) 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>
<thead>
<tr>
<th>Site</th>
<th>Substrate</th>
<th>Seedling species, first-year seedlings</th>
<th>Seedling species, established seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tsuga</td>
<td>Betula</td>
</tr>
<tr>
<td>Huron</td>
<td>Tsuga</td>
<td>1.08 (0.41)</td>
<td>0.07 (0.04)</td>
</tr>
<tr>
<td></td>
<td>Betula</td>
<td>0.47 (0.17)</td>
<td>0.15 (0.10)</td>
</tr>
<tr>
<td></td>
<td>Acer</td>
<td>0.22 (0.05)</td>
<td>0.12 (0.09)</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>0.14 (0.04)</td>
<td>0.04 (0.02)</td>
</tr>
<tr>
<td>Porcupine</td>
<td>Tsuga</td>
<td>0.50 (0.18)</td>
<td>5.33 (2.47)</td>
</tr>
<tr>
<td></td>
<td>Betula</td>
<td>0.41 (0.17)</td>
<td>1.88 (0.66)</td>
</tr>
<tr>
<td></td>
<td>Acer</td>
<td>0.06 (0.06)</td>
<td>0.33 (0.24)</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>0.12 (0.04)</td>
<td>0.19 (0.06)</td>
</tr>
<tr>
<td>Sylvania</td>
<td>Tsuga</td>
<td>0.52 (0.45)</td>
<td>4.89 (3.24)</td>
</tr>
<tr>
<td></td>
<td>Betula</td>
<td>0.29 (0.13)</td>
<td>0.45 (0.16)</td>
</tr>
<tr>
<td></td>
<td>Acer</td>
<td>0.08 (0.05)</td>
<td>0.75 (0.31)</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>0.01 (0.01)</td>
<td>0.07 (0.02)</td>
</tr>
</tbody>
</table>

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 \( \chi^2, P < 0.0001 \) 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 (\( \chi^2, P < 0.045 \) 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 they 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).

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).
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

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

<table>
<thead>
<tr>
<th>Wood substrate</th>
<th>Seedling survival (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Betula</td>
</tr>
<tr>
<td>Tsuga</td>
<td>2003*</td>
</tr>
<tr>
<td>Betula</td>
<td>2003</td>
</tr>
<tr>
<td>Acer</td>
<td>2003</td>
</tr>
</tbody>
</table>

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).
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.

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.
Furthermore, the proportion of _Tsuga_ and _Betula_ trees that are still-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; Katot 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 & Kalmar 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**


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:
(This link will take you to the article abstract.)

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.


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