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Decaying wood and tree regeneration in the Acadian Forest of Maine, USA☆

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ABSTRACT

We examined the effect of management history on the availability of decayed downed wood and the use of downed wood as a regeneration substrate in mixed-species stands in the Acadian Forest of Maine. Regeneration of red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), balsam fir (*Abies balsamea* L. Mill), and red maple (*Acer rubrum* L.) was quantified. Treatments included variants of selection cutting, commercial clearcutting (unregulated harvesting), and no harvesting for >50 years (reference). Area of wood substrate (wood $\geq$ Decay Class III and $\geq$10 cm on at least one end) was less in the commercial clearcut than in the reference; other treatments were not differentiated. Spruce and hemlock seedlings were found at higher densities on wood than paired forest floor plots of equal area, regardless of treatment. Conversely, fir and maple were less abundant on wood than forest floor plots in reference and selection treatments, but more or equally abundant on wood than forest floor plots in the commercial clearcut. These findings suggest that silvicultural treatment affects both the availability of decayed downed wood and seedling-substrate relationships, and that forest management in the Acadian Region should consider availability of downed woody material.

1. Introduction

Though tree mortality has traditionally been regarded as lost production in stands managed for commodities (Hagan and Grove, 1999), a number of studies have identified important relationships between decaying downed wood and tree seedling distribution. This topic has been the focus of many studies in the Pacific Northwest (Sollins, 1982, Harmon, 1987; Maser et al., 1988; Harmon and Franklin, 1989; Keeton and Franklin, 2005); much of that research identified strong relationships between tree seedling distribution and downed logs. For example, numerous studies from the Pacific Northwest have reported regeneration in *Picea-Tsuga-Thuja* forests nearly exclusive (94–98%) to woody material, though wood occupied a small portion (6–14%) of the forest floor (Christy and Mack, 1984; Graham and Cromack, 1982; Harmon et al., 1986; Harmon and Franklin, 1989). The importance of seedling-downed wood associations has also been noted in the Lake States (Eyre and Zilligitt, 1953; Corinth, 1995) and Rocky Mountain (USA) subalpine forests (Anderson and Winterton, 1996). Within the northern hardwood region of New York, McGee and Birmingham (1997) found a greater density of red spruce (*Picea rubens* Sarg.) and yellow birch (*Betula alleghaniensis* Britt.) seedlings on downed wood than nearby forest floor plots covering the same area. Internationally, significant relationships between tolerant conifers and decaying wood have been recorded in Japan (Takahashi et al., 2000; Narukawa and Yamamoto, 2003), Sweden (Hofgaard, 1993), and Poland (Szewczyk and Szwagrzyk, 1996).

The forests of Maine are located in an area where temperate and sub-boreal tree species' ranges overlap. The Acadian Forest was first described by Halliday (1937) in reference to the maritime provinces of Canada, but it was Braun (1950) who expanded this definition to include northern New England. The signature species of this region are red spruce and eastern hemlock (*Tsuga canadensis* L.). These shade-tolerant conifers are often present as advance regeneration, and in mixture with other softwood and hardwood species. Balsam fir (*Abies balsamea* L.) and red maple (*Acer rubrum* L.) are common associates of spruce and hemlock that can occur at higher densities and exhibit more rapid growth. The influence of management on competitive interactions between these species is of interest; our emphasis is treatment effect on the availability and use of downed wood as a regeneration substrate.

The Acadian Forest is a working forest and Maine's forestland represents a mosaic of management intensities. Recent data suggest that 95% of harvested acreage in the state is partially cut (Maine Forest Service, 2007). The effects of forest management history on the availability and use of wood for seedling establishment and

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☆ This research was conducted while J.K. Weaver was a graduate student in the School of Forest Resources at the University of Maine.

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growth are poorly understood in the Acadian Region. Objectives of the present study were to determine (1) the effect of a range of partial harvest treatments on available downed woody material substrates for germination and (2) the use of decaying logs as a regeneration substrate by eastern hemlock, red spruce, balsam fir, and red maple. Treatments investigated include variants of selection cutting, commercial clearcutting, and no harvest for >50 years (reference).

2. Methods

Two replicates each of selection cutting on 5- and 20-year cutting cycles, commercial clearcutting, and reference (no harvesting for >50 years) were investigated on the Penobscot Experimental Forest (PEF) in the towns of Bradley and Eddington, Maine (N44°52.862′; W68°38.882′). A third reference stand was sampled on Lower Lead Mountain Island (N44°51.452′; W68°10.374′). Silvicultural treatments were applied by the U.S. Forest Service, Northern Research Station as part of their long-term research; treatments were initiated between 1952 and 1957. Prior to 1950, land use activities on the PEF were not well documented, but included a long history of periodic partial harvesting (Sendak et al., 2003; Kenefic et al., 2006). The selection stands were managed using the BD*q* (basal area (BA), maximum diameter, *q* factor) approach (Marquis, 1978; Guldin, 1991) with entries on 5- and 20-year cycles, resulting in ten and three harvests respectively. Overstory species composition goals (expressed as a percentage of residual stand BA) were: spruce species 35–55%; balsam fir and eastern hemlock 15–25% each; eastern white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marsh.), northern white-cedar (*Thuja occidentalis* L.) and other commercial species 5–10% each. The commercial clearcut treatment was not a silvicultural clearcut, but rather an unregulated, exploitative removal of all merchantable timber. This treatment was applied twice: in the 1950s and 1980s. The lower limit of merchantability was 16.5 cm dbh in the first harvest and 11.4 cm dbh in the second. Submerchantable and unmerchantable trees and those of non-commercial species were left standing. Mean BA (trees ≥2 cm dbh) and species composition determined from prism plots at the time of sampling are shown in Table 1.

For all treatments, harvesting was conducted first with horses then rubber-tired skidders and/or processors, and trees were delimbed with slash left in the woods. All harvests were done in winter, with snow cover, to minimize disturbance to the forest floor. Additional information about treatments can be found in Sendak et al. (2003).

Historical changes in BA for each treatment illustrate the timing and intensity of harvests (Fig. 1). No long-term inventory data are available for unmanaged areas used in this study.

Each stand was gridded on a 25-m interval. The intersection of north–south and east–west grid lines served as potential plot locations. A sub-sample of these grid points were randomly chosen for sampling. At chosen grid points, two 0.01-ha plots were sampled for downed wood in advanced stages of decay. The number of plots sampled per treatment was area-dependent, with a goal of capturing 5% of each stand. A five-class decay classification system following Sollins (1982) was used, in which ascending decay class corresponds to increased wood decay (Table 2). Pieces of wood ≥ Decay Class III (defined as bark sloughing or absent, advancing sapwood decay and beginning heartwood decay) and ≥10 cm on at least one end were included in this study, and will be referred to as decayed downed wood (DDW). The length and width of logs or stumps matching these criteria were recorded and surveyed for presence of tree seedlings; seedling species and height class were recorded. A paired forest floor plot of equal dimensions was established 1.0 m north of each piece of DDW. Attention to the location of the paired forest floor plot avoided situations where undersampling of the forest floor could occur (i.e. sampling at the base of large trees or under tree crowns). In these rare circumstances, plots were either offset or placed 1.0 m south of each piece of DDW. Seedling species and height class were also recorded within that paired plot. Trees were assigned to one of three height classes (≤0.1 m, between 0.1 and 1.3 m, and ≥1.3 m) and densities calculated by regeneration substrate. The third height class included all trees ≥1.3 m regardless of diameter.

Table 1
Mean basal area (m^2/ha, trees ≥2 cm dbh) and species composition of the study areas at the time of sampling; S.E.s are shown in parentheses.

	5-Year selection cutting	20-Year selection cutting	Commercial clearcutting	Reference (no harvest ≥ 50 years)
Total BA (m^2/ha)	25.7 (1.51)	25.8 (1.97)	25.5 (0.68)	48.3 (1.67)
Red spruce (%)	16.9	24.8	2.6	27.7
Eastern hemlock (%)	48.1	38.2	1.5	51.9
Balsam fir (%)	15.6	16.8	42.5	1.1
Red maple (%)	8.2	5.5	20.3	7.2
Other softwood (%)	8.2	5.5	6.0	8.8
Other hardwood (%)	3.0	9.2	27.1	3.4

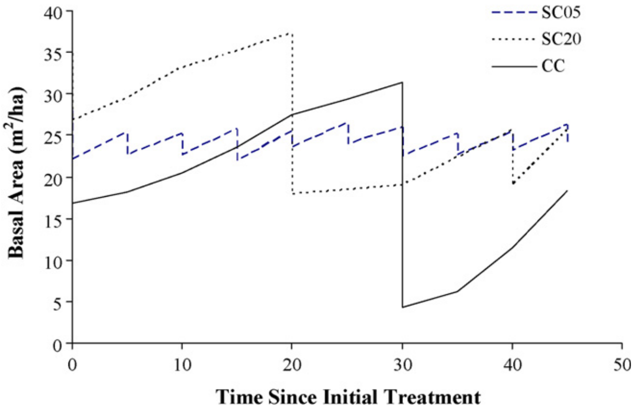

Fig. 1. Graphs of BA (m^2/ha) before and after harvests for 5-year selection (SC05), 20-year selection (SC20), and commercial clearcut (CC) on the Penobscot Experimental Forest (PEF). Treatments were not simultaneously administered, and inventories have been standardized to reflect time since initial treatment. Treatment abbreviations apply throughout. Data provided by the U.S. Forest Service.

The area of DDW was calculated in terms of two-dimensional ground area covered by the woody material. Logs were assumed to be elongated trapezoids (area = $(\Sigma B_1{:}B_2 \times L)/2$, where B_1 and B_2 are end widths of the log and L is length) and stumps were assumed to be ellipses (area = $(1/2)(A_1) \times (1/2)(A_2) \times \Pi$, where A_1 represented the length of the shortest axis and A_2 represented the length of the longest axis).

One-way analysis of variance (ANOVA) was applied using SYSTAT (11.0) software to determine if there were statistically significant differences in downed wood availability (m^2/ha) among sampled treatments. As necessary, post hoc tests using Bonferroni multiple comparisons were applied to determine significant differences between treatment means. Conclusions of statistical significance were evaluated using $\alpha = 0.1$ due to low replication ($n = 2$ for managed stands and $n = 3$ for reference stands); means are presented ± standard error (S.E.).

A Wilcoxon Signed Rank Test (Devore and Peck, 1997) was used to compare seedling densities between paired downed wood and forest floor plots. SYSTAT (11.0) was used for this analysis with $\alpha = 0.1$ set *a priori* to confer statistical significance. Given the relatively low seedling densities across all treatments for the third

Table 2
Downed wood classification scheme (from Sollins, 1982).

Character	Class description				
	I	II	III	IV	V
Bark	Intact	Mostly intact	Sloughing or absent	Detached or absent	Detached or absent
Structural integrity	Sound	Sapwood somewhat decayed; heartwood mostly sound	Heartwood mostly sound; supports own weight	Heartwood rotten, does not support own weight, branch stubs pull out	None
Branch system	Current-year twigs present	Larger twigs present, branch system entire	Large branches present, longer than log diameter	Branch stubs present, shorter than log diameter	Absent
Invading roots	Absent	Absent	Sapwood only	Throughout	Throughout

height class ($\geq$1.3 m), analyses were conducted on the first two height classes only.

3. Results

3.1. Treatment effect on downed wood substrate availability

Though DDW represented a small amount of available substrate (<2%), there were significant differences in wood substrate availability (m^2/ha) among treatments ($p = 0.06$). The reference had a greater area of DDW (114.8 ± 16.4 m^2/ha) than the commercial clearcut (62.2 ± 8.7 m^2/ha) ($p = 0.05$). There were no differences between either the 5-year selection (83.6 ± 4.3 m^2/ha) or 20-year selection (83.3 ± 14.8 m^2/ha) and any other treatment ($p = 0.73$–0.77).

3.2. Seedling densities

Hemlock seedlings $\leq$0.1 m in height were significantly more abundant on DDW than adjacent forest floor in all treatments ($p < 0.10$); hemlock between 0.1 and 1.3 m in height were more abundant on wood than forest floor plots in the 20-year selection and reference ($p = 0.09$ and <0.01, Fig. 2). In the commercial clearcut, hemlock seedlings were found only on DDW. Red spruce seedlings $\leq$0.1 m in height were significantly more abundant on wood than paired forest floor plots in the 5-year selection, 20-year selection, and reference ($p < 0.01$); spruce 0.1–1.3 m in height were more abundant on wood than forest floor plots in the 20-year selection and reference ($p = 0.09$ and <0.01, Fig. 3). Spruce seedling densities did not differ between wood and the forest floor plots in the commercial clearcut ($p = 0.32$).

Balsam fir seedlings $\leq$0.1 m in height were more abundant on wood than paired forest floor plots in the commercial clearcut ($p = 0.03$), but were not differentiated in the reference or selection treatments ($p = 0.13$–0.56, Fig. 4). Density of fir seedlings between 0.1 and 1.3 m tall was lower on wood than paired forest floor plots in the reference and selection treatments ($p = 0.02$–0.03); there were no differences in fir seedling densities between substrates in the commercial clearcut ($p = 0.17$). Densities of red maple $\leq$0.1 m in height were lower on wood than paired forest floor plots in the reference treatments and 5-year selection ($p < 0.01$–0.01, Fig. 5). Red maple seedlings 0.1–1.3 m in height were also less abundant on wood than forest floor plots in the 5-year selection ($p = 0.03$), but undifferentiated in the other treatments ($p = 0.11$–0.72).

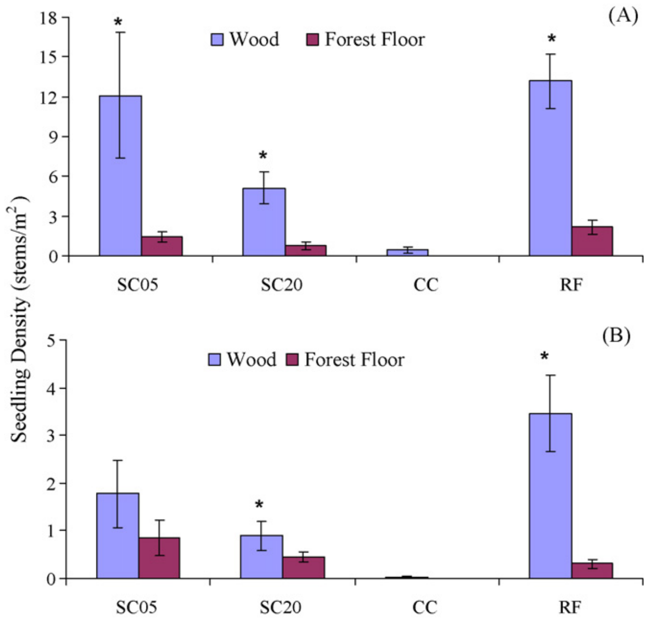

Fig. 2. Eastern hemlock seedling densities on wood and paired forest floor plots in the 5- and 20-year selection (SC05 and SC20), commercial clearcut (CC) and reference (RF) treatments, for (A) seedlings $\leq$0.1 m in height and (B) seedlings >0.1 m but <1.3 m in height. Significant differences ($p < 0.1$) in seedling densities between paired microsites are shown with an (*).

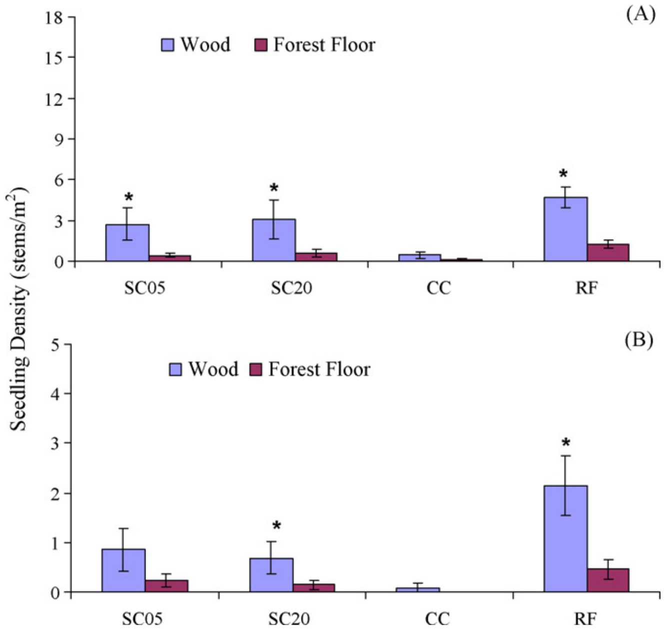

Fig. 3. Red spruce seedling densities on wood and paired forest floor plots in the 5- and 20-year selection (SC05 and SC20), commercial clearcut (CC) and reference (RF) treatments, for (A) seedlings $\leq$0.1 m in height and (B) seedlings >0.1 m but <1.3 m in height. Significant differences ($p < 0.1$) in seedling densities between paired microsites are shown with an (*).

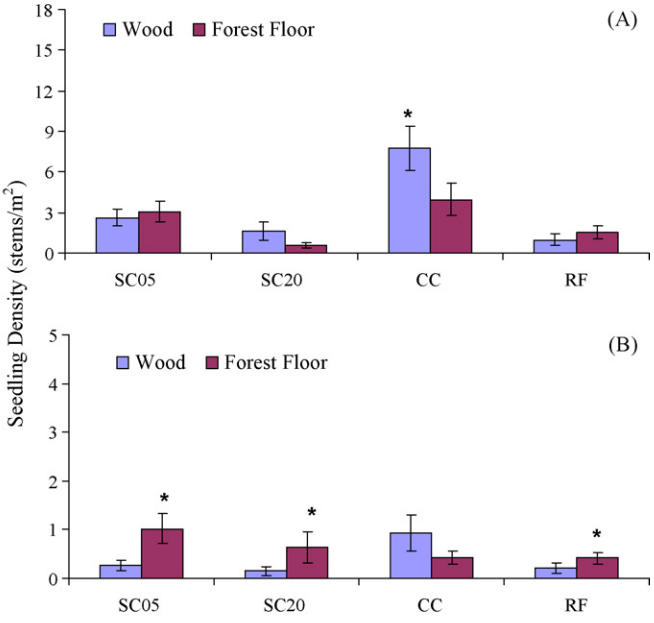

Fig. 4. Balsam fir seedling densities on wood and paired forest floor plots in the 5- and 20-year selection (SC05 and SC20), commercial clearcut (CC) and reference (RF) treatments, for (A) seedlings ≤ 0.1 m in height and (B) seedlings >0.1 m but <1.3 m in height. Significant differences ($p < 0.1$) in seedling densities between paired microsites are shown with an (*).

4. Discussion

4.1. Wood substrate availability

Downed wood $\geq$ Decay Class III occupied a relatively small percentage (approximately 1–2%) of the forest floor in this study. This is consistent with other studies in eastern North America (McGee and Birmingham, 1997; McGee, 2001) and northern Europe (Hofgaard, 1993; Szewczyk and Szwagrzyk, 1996), but far less than levels reported in the Pacific Northwest (Harmon, 1987). Such differences may be due to forest type, management history, and sampling protocol (i.e. variation in definition and inclusion of individual decay classes).

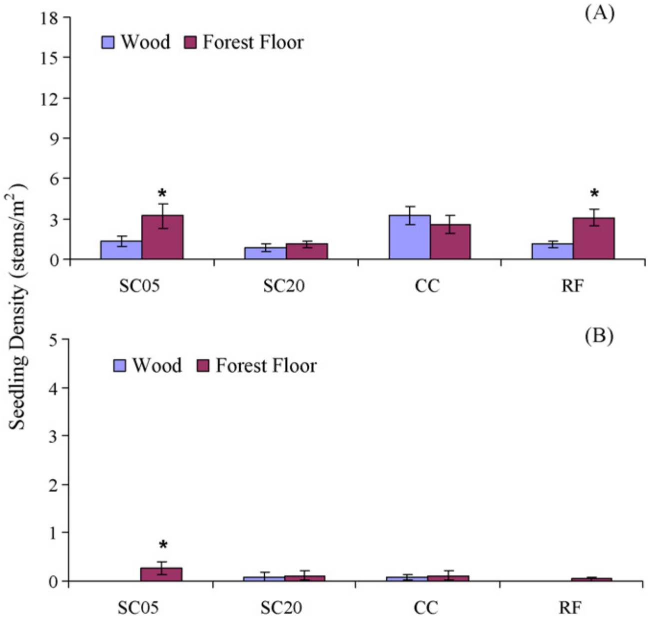

Fig. 5. Red maple seedling densities on wood and paired forest floor plots in the 5- and 20-year selection (SC05 and SC20), commercial clearcut (CC) and reference (RF) treatments, for (A) seedlings ≤ 0.1 m in height and (B) seedlings >0.1 m but < 1.3 m in height. Significant differences ($p < 0.1$) in seedling densities between paired microsites are shown with an (*).

An important aspect of efficient commodity-production silviculture is harvesting trees before they die; it is logical that this would lead to less dead wood recruitment from natural tree death. In fact, a number of studies (for example, Hansen et al., 1991; Duvall and Grigal, 1999; Fraver et al., 2002) found a decrease in downed wood availability in managed forests. Only the most heavily harvested stands (commercial clearcuts) in the present study had less area of DDW than the references; there were no other treatment differences. This is consistent with Duvall and Grigal (1999), who reported fewer differences in downed logs between managed mature red pine (*Pinus resinosa* Ait.) stands and references than between managed immature stands and references in the Great Lakes region, USA. The PEF selection stands contain numerous trees with >100 years at breast height, and some >200 years (Kenefic and Seymour, 1997; Seymour and Kenefic, 1998), as well as stems as large as 55–70 cm dbh (U.S. Forest Service unpublished data). Though trees in the commercial clearcuts have not been aged, a preponderance of sapling-sized trees, intolerant hardwoods, and harvest-induced sprout clumps (U.S. Forest Service unpublished data) indicates that they can reasonably be classified as less mature than the selection stands.

Other possible explanations for our findings include undocumented partial cuttings in the references >50 years ago (potentially affecting current levels of DDW in those stands), and the intensity and timing of the more recent harvests in the treated stands. Though silvicultural treatments reduce recruitment of dead wood due to natural mortality, tree-length harvesting with in-woods delimbing, as conducted on the PEF, adds downed woody material in the form of logging residues (Duvall and Grigal, 1999; Fraver et al., 2002). Such residues are often smaller than the 10-cm diameter threshold used for sampling in this study, but some may contribute initially to the amount of wood in Decay Classes I and II (not included in this study) and later to the amount $\geq$ Decay Class III. Inputs of larger DDW in managed stands can include stumps, decayed lower bole pieces, and windthrow of residuals. Conversely, felling and skidding activities may fragment DDW and accelerate structural loss (Freedman et al., 1996). The type of silvicultural treatment also affects stand structure and thus the likelihood of recruitment of dead wood of various sizes. Garber et al. (2005) found significant differences in rate of snag creation and size of snags by treatment and species on the PEF; they found larger snags in the references than commercial clearcuts. Such factors affect subsequent downed wood recruitment and longevity.

4.2. Wood-seedling associations

Early researchers in the eastern United States reported prolific tolerant conifer regeneration on downed logs in unmanaged stands across the northeastern region (Knechtel, 1903; Westveld, 1931). Unlike those early studies, the observations in the present study were recorded across a gradient of partial cutting treatments. Despite a relative scarcity of wood as a regeneration substrate, decaying pieces of wood generally supported a higher density of red spruce and eastern hemlock seedlings than adjacent forest floor. However, unlike forested ecosystems of the Pacific Northwest (Harmon and Franklin, 1989) or northern Sweden (Hofgaard, 1993), tolerant conifer regeneration in the Acadian Forest does not appear to be exclusively dependent on decaying wood. Rather, our findings are consistent with those of McGee and Birmingham (1997) for the Adirondack region, where density of small seedlings (<0.5 m) was greater on wood than adjacent forest floor plots. Additionally, we found few tolerant conifers in the $\geq$1.3 m height class growing on downed wood. This is consistent with a study by Szewczyk and Szwagrzyk (1996) in *Fagus-Abies-Picea* forests of the Carpathian Mountains; they found wood to be a suitable regeneration medium for spruce and fir, but did not find seedlings >0.25 m in height on wood though seedlings of that size were abundant on the forest floor.

McGee (2001) suggested that influences operating at the stand level such as light conditions may factor substantially into recruitment patterns. While this link was not established in the study stands (Weaver, 2007), slow growth of tolerant conifers in the understory (Seymour and Kenefic, 1998; Wu et al., 1999) and temporal changes in substrate availability due to litter accumulation and decay (Hofgaard, 1993) may account for the small number of trees ≥1.3 m in height growing on decayed downed wood ≥Decay Class III. It is also plausible that seeds landing on highly decayed wood germinated successfully and recruited to larger sizes, but evidence of this legacy is difficult to identify without extraction and soil analysis (McFee and Stone, 1966). Alternatively, low nutrient levels in wood relative to soil (Harmon et al., 1986) may be suppressing growth of seedlings on decayed downed wood and limiting recruitment to the third height class (≥1.3 m).

Knechtel (1903) noted straight lines of tolerant conifer saplings; he suggested that these had germinated on downed wood that was no longer identifiable. Similar patterns in sapling positions were seen in the present study (personal observation), but without soil analyses these observations are anecdotal. Future research should focus on recruitment patterns of red spruce and eastern hemlock regenerating on downed wood.

Seed size may also play a role in regeneration patterns observed in this study. The small seeds of red spruce and eastern hemlock might become lodged in grooves of wood more easily than the larger seeds of balsam fir and red maple (Anderson and Winterton, 1996; Szewczyk and Szwagrzyk, 1996; McGee and Birmingham, 1997). Logs provide an elevated microsite that may help to prevent smothering and crushing of small seeds from excessive leaf litter accumulations (Korstian, 1937; Wang and Kemball, 2005). Small seeds also have fewer stored resources and may benefit from the moisture (Fraver et al., 2002) and nutrient capital (Sollins, 1982; Takahashi et al., 2000; Laiho and Prescott, 2004) associated with decaying logs, though the latter has been debated within the literature (Holub et al., 2001). In addition, litter accumulation on logs and associations with ectomycorrhizae fungi (Harmon et al., 1986; Harvey et al., 1987) may alleviate nutrient stress (Harmon, 1987; Takahashi et al., 2000), though log geometry or unique features on the log surface (i.e. bryophyte mats) may affect litter accumulations and subsequent nutrient capital. In the present study, leaf litter accumulations on downed wood were not quantified, but leaf and bryophyte cover was noted (personal observation).

The fact that balsam fir was significantly more abundant on downed wood than adjacent forest floor plots only in the commercial clearcut suggests that changes in forest floor or stand conditions have affected balsam fir regeneration dynamics in that treatment. Earlier studies on the PEF showed that repeated commercial clearcutting shifted stands from overstory softwood domination to overstory hardwood domination (Sendak et al., 2003). These changes contributed to a high proportion of hardwood leaf litter (Weaver, 2007), likely making seedling radical penetration to organic and/or mineral soil more difficult (there was little exposed mineral soil). This is supported by evidence of other studies (e.g. Moore, 1926; Place, 1955) that suggest seedling radical morphology determines survival across various regeneration mediums. Small radicals and few stored nutrients within the seed capsule favor substrates that maintain high moisture environments (Korstian, 1937). By comparison, seeds with large radicals and stored reserves within the seed capsule allow for penetration of otherwise formidable barriers such as that posed by hardwood leaf litter (Walters and Yawney, 1990).

4.3. Silvicultural implications

Managers interested in retaining a component of red spruce and eastern hemlock in partially harvested stands in the Northeast generally, and the Acadian Region specifically, should consider deadwood dynamics. Permanently retaining some large reserve trees, which will eventually die and fall over, will help to replenish this important pool. Existing large DDW can also be conserved by pre-harvest designation of logging trails so as to avoid this rare substrate during timber extraction. Timing of harvest also may play an important role in substrate availability. In the present study, winter harvests minimized disturbances to the forest floor, and likely helped to protect the integrity of decayed downed wood.

Though the present study did not identify wood as an exclusive regeneration substrate for spruce and hemlock, our findings illustrate that wood is an important seedbed for these tolerant conifers; this was generally not the case for their common competitors balsam fir and red maple which occur at equal or greater densities on the typical forest floor microsites. Because the forest floor will always be the most dominant condition by far, the more DDW can be enhanced via silviculture, the greater the likelihood that spruce and hemlock will comprise viable components of the regeneration stratum and future overstory.

5. Conclusion

Total wood availability (expressed as a percent of the forest floor) was comparable to results reported in earlier studies from a broad spectrum of global geographic locations. Our findings suggest that wood is a more important (or at least more utilized) regeneration substrate for red spruce and eastern hemlock than for balsam fir (with the exception of the commercial clearcut where there were fewer hospitable regeneration substrates) and red maple. Studies directed at recruitment patterns of seedlings on wood and forest floor to larger sizes are needed. In the interim, landowners and foresters interested in maintaining a red spruce and/or eastern hemlock component in partially harvested stands within the Acadian Forest should consider dead wood retention and recruitment when crafting management plans.

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