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Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian Forest of Maine, USA


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ABSTRACT

Understanding the factors regulating the composition and abundance of natural regeneration in forest ecosystems is critical to sustainable management worldwide. Using a long-term silvicultural experiment in Maine, we partitioned the variation in natural regeneration and examined the contribution of overstory and understorey vegetation (biotic factors), substrate and soil attributes (abiotic factors), and silvicultural treatment. We hypothesized that silvicultural treatment (single-tree selection with 5, 10, and 20-year cutting cycles and diameter-limit cutting) would be less influential than abiotic and biotic factors in structuring regeneration pattern. Overall, treatment and site (biotic and abiotic) factors accounted for 26% of the variation in regeneration species composition, highlighting stochasticity of the regeneration process. In support of our hypothesis, regeneration pattern that could be explained was primarily associated with local site factors; overstorey and understorey vegetation uniquely accounted for 16% of the variation in species composition. Substrate and soil attributes along with silvicultural treatment accounted for 4% of variation, and uniquely accounted for 2% and 4%, respectively. In support of earlier reports, shifts toward hardwood dominance were apparent at early stages of cohort development and were associated with high harvest intensities. Our findings suggested that overstorey and understorey vegetation exhibit greater control over regeneration patterns than substrate and soil attributes, or silvicultural treatment, in partially harvested Acadian Forest mixedwood stands, and also indicated the potential for composition control through selective overstorey removal.

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1. Introduction

Natural regeneration is widely recognized as a complex and stochastic process (Paluch, 2005; Rodriguez-Garcia et al., 2010). Complexity describes the influence of a wide array of factors operating at a multitude of temporal and spatial scales. Stochasticity refers to the variation in outcome as opposed to a deterministic process. Throughout the regeneration stages, a wide range of biotic and abiotic factors interact to determine the amount, type, and distribution of natural regeneration. Spatial and temporal variation in these factors, coupled with interspecific differences in resource uptake and tolerance (Canham et al., 1994), result in multiple successional pathways that are difficult to predict. The most noted implication of regeneration complexity and stochasticity is the uncertainty in predicting future regeneration dynamics (Miina and Heinonen, 2008; Olson and Wagner, 2010). In practice, uncer-

tainty hinders our ability to evaluate long-term risk and plan strategically (Taylor et al., 2009). Moreover, the high degree of stochasticity in the process can be an impediment to achieving stand management objectives.

The many factors influencing forest regeneration can be divided into one of three broad categories: disturbance, abiotic, and biotic. Disturbance, whether anthropogenic (e.g. silvicultural treatment) or natural in origin, creates establishment sites and makes environmental resources (e.g., light, soil water, and nutrients) available for new individuals and survivors. Abiotic factors include the suite of physical attributes (e.g., temperature, soil texture, drainage, etc.), determining habitat suitability for germination, establishment, and survival (Harper et al., 1965). Biotic factors include neighborhood effects such as seed production and canopy distribution and composition, which can also influence temperature, humidity, and light levels (Canham et al., 1994; Frelich et al., 1998), as well as competition and predation.

These broad categories are encompassed within three explanatory models of plant community structure (Borcard et al., 1992; Wimberly and Spies, 2001): (1) disturbance control model; (2) abiotic control model; and (3) biotic control model. In all of these

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models, one set of variables at a time is presumed to have the most influential effect on the abundance and distribution of species assemblages. Although those models were previously viewed as mutually exclusive hypotheses, they are currently viewed in the context of multiple working hypotheses (Borcard and Legendre, 1994; Wimberly and Spies, 2001). Moreover, multivariate variance partitioning methods such as that developed by Borcard et al. (1992) have allowed for the evaluation and relative weighting of those competing models (e.g., Park, 2001; Wimberly and Spies, 2001). Although regeneration spatial pattern is not a determining factor, its inclusion serves as a synthetic indirect descriptor of the underlying generating processes (Borcard et al., 1992).

A comprehensive understanding of the natural regeneration process is crucial for sustainable forest management and conservation efforts (Smith et al., 1997; Nyland, 2002). Examination of the relative importance of disturbance, abiotic, and biotic factors in structuring natural regeneration is key to understanding the main drivers involved in regulating regeneration pattern (i.e., composition and abundance) (Maguire and Forman, 1983). Identification of those drivers constitutes a practical basis for modeling regeneration dynamics that allows for greater portability of those models (Blanco et al., 2009; Weiskittel et al., 2011). In addition, more effective silvicultural practices can be developed when the primary regulatory factors have been identified (Caspersen and Sapruff, 2005).

Recent shifts in North American forest management paradigms have placed greater emphasis on natural regeneration (Robinson, 2008; Blanco et al., 2009). Although economic reasons may have partly played a role in such shifts (Blanco et al., 2009), a greater impetus toward ecosystem management also underlies these changes (Kohm and Franklin, 1997). In the northeastern United States and eastern Canada, for example, the growing prominence of partial harvesting in response to changes in forest policy, coupled with an abundance of natural regeneration (Brisette, 1996), have strengthened the near-total reliance on natural regeneration for stand establishment. Limited understanding of how partial harvesting influences regeneration composition and abundance restricts our ability to design appropriate silvicultural prescriptions, accurately project future species composition and wood supplies, and assess impacts on wildlife habitat. Although there is a clear nomenclature for regeneration methods in silviculture (Smith et al., 1997), there is currently no consensus about how to classify partial harvesting as a broad category of incomplete removals that are now widely used across the northeastern United States and eastern Canada. This partial harvesting has been commonly described as any harvest that removes part of a stand (Brisette, 1996; Thorpe and Thomas, 2007).

In the Acadian Region, which is described as a transitional zone between the northern boreal forests and the northeastern broadleaf forests (Halliday, 1937), Brisette (1996) compared regeneration composition, abundance, and stocking among five partial harvesting intensities and found no differences among treatments. Greater frequency (repeated partial harvesting) also resulted in a few significant differences of small magnitude (Brisette, 1996). In Ontario's boreal mixedwood forests, high harvest intensities increased hardwood abundance and height growth at the expense of conifers (Man et al., 2008). Similarly, long-term compositional dynamics in the Acadian Region indicate that high harvest intensities of low frequency promote a shift toward hardwood dominance (Olson and Wagner, 2010), which is consistent with species shade tolerance and niche differentiation strategies. However, the roles of biotic and abiotic control models in creating or dampening these shifts remain unclear. Few studies have examined the combined effect of harvesting, understory vegetation, and physical environment on regeneration (Park, 2001; Man et al., 2008), and we lack

information about how these multiple factors interact to affect long-term patterns of regeneration.

The objective of this study was to evaluate the relative importance of silvicultural treatment and local abiotic and biotic site factors (overstory and understory vegetation, and substrate and soil attributes) in structuring the species composition and abundance of natural regeneration. Few significant differences among the five partial harvesting intensities examined by Brisette (1996) suggested a greater influence of abiotic and biotic control models relative to the disturbance control model. Thus, we hypothesized that silvicultural treatment would be less influential than overstory and understory vegetation, or substrate and soil attributes, in structuring regeneration pattern.

2. Materials and methods

2.1. Study area

This study was conducted within the Penobscot Experimental Forest (PEF), a 1618-ha mixedwood forest in Bradley and Eddington, Maine (44.87°N, 68.63°W). The climate is cool and humid with mean annual precipitation of 106 cm; 48% falls in May through October, and an annual frost-free period of 140–160 days. The area is of gentle terrain ranging in elevation from 24 to 76 m above sea level. Soil parent material is mainly glacial till derived from fine-grained, sedimentary rock. Soil drainage varies from well-drained on till ridges to very poorly-drained in the flats. Plaisted (isotic, frigid Oxyaquic Haplorthods) and Howland (isotic, frigid Aquic Haplorthods) soil series which are characterized as very deep coarse loams occur on till ridges, whereas loamy Monarda (mixed, active, acid, frigid, shallow Aerice Endoaquepts) and Burnham (mixed, superactive, nonacid, frigid, shallow Histic Humaquepts) series occupy flat areas (Safford et al., 1969; USDA-NRCS Soil Survey Division, 2013).

A mixture of northern conifers dominate the site with red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern white-cedar (*Thuja occidentalis* L.), and eastern white pine (*Pinus strobus* L.) as main components. Hardwood species include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), and aspen (*Populus* spp.) (Brisette, 1996; Sendak et al., 2003; USDA-NRCS Soil Survey Division, 2013). The area is recognized as part of the Acadian Region and the natural disturbance regime is predominantly small-scale gap openings with wind, insect, and senescence as the primary mortality agents (Arseneault et al., 2011).

2.2. Experimental design

Ten partially harvested stands within the USDA Forest Service long-term silviculture experiment on the PEF (Sendak et al., 2003) were selected for this study. The study stands consist of five silvicultural treatments: single-tree selection cutting on 5, 10, and 20-year cycles and fixed and modified (flexible) diameter-limit cutting (Table 1); each treatment was initially applied to two management units (stands) between 1952 and 1957. Selection treatments were applied using the *BDq* method (Guldin, 1991), where *B* is residual basal area (BA, for trees ≥ 1.3 cm DBH), *D* is maximum residual diameter at breast height (DBH), and *q* is a quotient determining the number of trees in each diameter class (Brisette, 1996; Sendak et al., 2003). A fixed *q* of 1.4 (for 2.5-cm DBH classes) was used and *D* was 48.3, 45.7, and 40.6 cm for the 5-yr (S05), 10-yr (S10), and 20-yr (S20) selection treatments, respectively. *B* values for S05, S10, and S20 were 26.4, 23.0, and 18.4 m² ha⁻¹, respectively. Species compositional goals were defined as a proportion

Table 1
Post-harvest overstory (trees ≥ 1.3 cm DBH) conditions for the entry immediately before the 2006 and 2007 sampling of five silvicultural treatments, with mean reduction in basal area (i.e., mean removal) over the course of the USDA Forest Service long-term silviculture experiment at the Penobscot Experimental Forest, Maine.

Harvest method	n^a	Density ^b trees ha ⁻¹	Basal area ^b m ² ha ⁻¹	QMD ^{bc} cm	Conifer ^d %	Hardwood ^d %	Removal ^b m ² ha ⁻¹
Selection 5-yr (S05)	33	2553 (384)	24.2 (0.9)	13.1 (0.7)	90	10	3.1 (0.1)
Selection 10-yr (S10)	35	4803 (527)	22.3 (0.9)	9.0 (0.6)	83	17	5.6 (0.3)
Selection 20-yr (S20)	37	5555 (731)	18.9 (0.7)	8.2 (0.6)	87	13	11.5 (0.4)
Fixed diameter limit (FDL)	33	3907 (499)	12.1 (0.6)	7.7 (0.6)	81	19	17.5 (0.6)
Modified diameter limit (MDL)	31	4226 (356)	22.7 (0.8)	9.4 (0.7)	83	17	10.3 (0.6)

^a Number of permanent sample plots.

^b Values represent means and standard errors (in parenthesis).

^c Quadratic mean diameter.

^d Proportion of basal area (m² ha⁻¹).

of residual BA as follows: spruce, 35–55%; balsam fir and eastern hemlock, 15–25% each; eastern white pine, paper birch, northern white-cedar, and other, 5–10% each. Selection treatments included cultural provisions such as timber stand improvement and pre-commercial thinning to remove cull trees, improve composition (e.g., increase spruce), and release desirable trees. In practice, control of species composition and tree quality and vigor were given priority over strict adherence to the structural guidelines.

Species-specific diameter thresholds were used in the diameter-limit harvests; these limits varied over the course of the experiment (Russell et al., 2012). After the initial entry, fixed diameter-limit cutting (FDL) was applied when volume regrew to pre-harvest levels; this occurred every 21–24 years. Modified (flexible) diameter-limit cutting (MDL) was applied on a 20-year interval. FDL and MDL treatments differed in: diameter thresholds (higher in the MDL); adherence to the thresholds (inflexible in FDL and flexible in MDL to allow markers to capture mortality in smaller size classes or leave some trees exceeding the diameter thresholds); and variability in harvest interval. Most recent FDL DBH thresholds were: 11 cm for balsam fir; 24 cm for spruce and eastern hemlock; 27 cm for pine; 19 cm for paper birch and northern white-cedar; and 11 cm for tamarack (*Larix laricina* (Du Roi) K. Koch) and other hardwoods. Recent MDL DBH thresholds were: 17 cm for balsam fir; 37 cm for spruce and pine; 32 cm for eastern hemlock; 19 cm for northern white-cedar; 24 cm for paper birch; and 14 cm for other hardwoods.

2.3. Measurements

Permanent sample plots (PSPs) were established within each treatment stand in the early 1950s. PSPs were established in a systematic grid with 13–21 sampled points per grid. Each PSP consists of three concentric circular fixed-area subplots: 0.008 (added in 2000), 0.02, and 0.08 ha. Three circular regeneration subplots (0.0004 ha each) were established at the circumference of the 0.02-ha subplot in the early 1960s (Brissette, 1996) (Appendix A).

Trees ≥ 11.4 cm DBH are tallied in the 0.08-ha subplot. Before 2000, trees 1.3 to <11.4 cm DBH were tallied in the 0.02-ha subplot. Since 2000, trees 1.3 to <6.4 cm DBH have been tallied in the 0.008-ha subplot and trees 6.4 to <11.4 cm DBH have been tallied in the 0.02-ha subplot (Sendak et al., 2003). PSPs have been measured pre- and post-harvest and at 5-year intervals between harvests.

As part of an understory vegetation survey in 2006 and 2007, tree seedlings <0.6 m in height were identified and tallied within two of the regeneration subplots at each PSP (Bryce, 2009). Because tree seedling density was not a response of focus for the understory vegetation survey, there were eight subplots on which seedlings were counted up to 50 and greater density was noted but not quantified. Those records occurred in seven PSPs across the ten

stands and were mainly recorded for the prolific balsam fir. Understory vegetation (i.e., herb and shrub) cover was estimated using five cover classes (<5 ; 5–25; 26–50; 51–75; 76–100%). Ocular estimates of substrate cover were obtained for each of the following categories using the same classes: mineral soil, rock, downed wood, hardwood litter, and conifer litter. Soil attributes (i.e., thickness of the organic horizon, thickness of the eluvial horizon, and depth to redoximorphic features) were quantified after excavating a soil pit at the perimeter of each PSP. A hemispherical canopy image was obtained at 0.6 m above each regeneration subplot to provide an indirect estimate of the light regime (Jennings et al., 1999). Hemispherical images were obtained using a Sigma 8-mm 180° circular fisheye lens attached to a Canon EOS Rebel camera. Proportion of canopy openness was calculated using the Gap Light Analyzer imaging software (Frazer et al., 1999). Using data from this survey, Olson et al. (2011) reported on the occurrence of nonnative invasive plants.

2.4. Analytical approach

Although a total of 26 tree species were recorded, 14 occurred in less than 5% of the PSPs and were not included in this analysis. When seedlings were noted to occur at densities greater than 50 per plot, the maximum number recorded (i.e., 50) was used in analysis. Only a few records (eight) of densities greater than 50 occurred, representing 0.7% of the total number of records, and their influence on the analysis and underestimation of balsam fir was assumed negligible. Seedling counts by species from the two regeneration subplots were averaged to obtain an estimate for each PSP. For this analysis, a total of 292 regeneration subplots from ten treatment stands were available. Substrate and understory cover from the two regeneration subplots were also averaged using each class midpoint. Overstory (trees ≥ 1.3 cm DBH) BA for the eleven most abundant species was calculated for each PSP using pre-harvest inventory for the entry immediately before sampling. Seedling density among the five treatments was compared at the plot level using one-way ANOVA at a significance level of 0.05; the variance contribution of stands and PSPs was examined. For one-way ANOVA, treatment was considered a fixed effect, whereas stands were considered random effects (Pinheiro and Bates, 2009); the plot was the experimental unit in this local-scale analysis. ANOVA and variance contribution were conducted using SAS PROC MIXED and PROC VARCOMP, respectively (SAS Institute Inc, 2000).

Seedling density estimates were square root transformed to reduce the range of species variation and arranged in a Q matrix, where PSPs served as rows and species served as columns. Treatment (intensity, time since last harvest, and canopy openness) and site factors (eleven overstory species, cover of understory vegetation, five substrate categories, and three soil attributes)

were also arranged in Q matrices with PSPs as rows. Site factors were arranged in two matrices to reflect biotic (overstory and understory vegetation) and abiotic (substrate and soil attributes) influences. Harvest and site matrices were standardized to unit length to remove the arbitrary effect of factor units. To account for any variation based on the spatial location of a PSP (a surrogate for unmeasured and spatially structured environmental variation), a third degree polynomial of PSP coordinates was used (Borcard et al., 1992). All terms of the third degree polynomial were used as an initial spatial matrix that was subsequently reduced using forward selection based on Akaike's information criterion and significance from permutation tests (Park, 2001).

Cluster analysis and non-metric multi-dimensional scaling (NMS) were used to group PSPs based on similarities in regeneration composition and abundance. In cluster analysis, flexible beta ($\beta = -0.25$) linkage and Bray-Curtis coefficient were used. Flexible beta groupings were superimposed on the NMS graph to avoid misrepresenting groups that were distinct in higher dimensions (Legendre and Legendre, 1998). Indicator species analysis (ISA) was used as an objective criterion for pruning the resulting dendrogram (Dufréne and Legendre, 1997; McCune and Grace, 2002). Indicator values were obtained for each species at each step of cluster formation and statistical significance of indicator values was assessed using a Monte-Carlo randomization test with 10,000 permutations. Indicator values combine relative abundance and relative frequency to provide a measure of species faithfulness and exclusiveness to a specific group. The number of groups was chosen based on maximum number of significant indicators and minimum average *P* value (McCune and Grace, 2002). NMS used a Bray-Curtis coefficient as the distance measure. Flexible beta clustering, ISA, and NMS were performed using PC-ORD software (McCune and Mefford, 1999). In NMS, the slow and thorough option (i.e., 400 maximum number of iterations, 0.00001 instability criterion, 6 starting number of axes, 40 real runs, and 50 randomized runs) of the autopilot procedure was used.

To relate regeneration patterns to the treatment at the PSP level, it was necessary to quantify treatment in more detail than merely assigning one of the five types. Using an approach similar to Olson and Wagner (2010), harvest intensity for each PSP was quantified using long-term inventory data. Intensity was calculated as reduction in BA (trees ≥ 1.3 cm DBH) between pre- and post-harvest conditions for the entry immediately before sampling. Plot-level reduction in BA was expressed in both absolute and relative (proportional) terms. Time since last harvest reflected the lag period between treatment and sampling and was used to account for differences in regeneration patterns due to variable harvest times. Redundancy analysis (RDA) was used to relate regeneration patterns to single and pairwise-combined predictor matrices (i.e., treatment, site, and spatial location) and determine the proportion of variance accounted for by each of these constraints (Borcard et al., 1992; Park, 2001; Peres-Neto et al., 2006). Variance partitioning was carried out using adjusted *R*-squares to provide more accurate estimates of the influence of explanatory factors using samples (Peres-Neto et al., 2006). Adjusted *R*-square values may be negative for shared variation due to correlations among predictor variables. Treatment and site matrices were reduced using forward selection based on Akaike's information criterion and significance from permutation tests to restrict the analysis to important explanatory factors. Partial redundancy analysis (pRDA) was used to determine the unique contribution and relative importance of treatment, site, and location matrices. Multivariate variance partitioning and redundancy analyses were performed using the *vegan* package (Oksanen et al., 2011) in R (R Development Core Team, 2008). Significance

tests for RDA axes were performed using Monte-Carlo randomization tests.

3. Results

Mean seedling density for the 12 most abundant species did not differ ($P = 0.88$) among the five silvicultural treatments and ranged from 34,669 trees ha^{-1} for S20 to 47,479 trees ha^{-1} for S05. Within-stand variability (PSP to PSP) in seedling density was the dominant source of variation (84%), whereas stand-to-stand variability accounted for a smaller proportion (16%) of variance. Across all treatments, conifer seedlings were the most abundant (Table 2). Treatment mean BA reduction was between 2.0 and 17.9 $\text{m}^2 \text{ha}^{-1}$ with a wider range of values at the PSP level (Table 2). Pre-harvest overstory was predominantly coniferous; red maple and paper birch were the most prominent hardwoods (Table 2).

3.1. Unconstrained variation

Pruning the dendrogram using ISA as a criterion resulted in the identification of six groups (Fig. 1A). Three of those groups were compositionally distinct (groups 2, 3, and 5), whereas the other three were composed of species mixtures with a limited number of PSPs within each group. The first distinct group (group 2) was composed mainly of balsam fir as identified by ISA (Table 3). This group included 25% of the total number of PSPs. The second distinct group (group 3) was composed of red spruce and eastern hemlock and included a greater proportion (40%) of the total number of PSPs. The third distinct group (group 5) included a small proportion (6%) of PSPs, but was mainly composed of northern white-cedar, as well as hardwood species such as red maple, paper birch, and gray birch. Across the six groups, mean density ranged from 5560 to 73,993 seedlings ha^{-1} for the six most abundant species and reflected a similar pattern to that identified using ISA (Fig. 2).

NMS resulted in a three-dimensional solution with 31%, 33%, and 22% of total unconstrained variation represented by the first three axes, respectively. Stress value for NMS was 15.6, indicating an acceptable solution (McCune and Grace, 2002). Balsam fir and spruce-hemlock groups were separated along the third axis indicating the influence of a gradient in structuring regeneration pattern in these stands (Fig. 1A). This gradient, however, did not seem to be related to treatment (Fig. 1B). In addition, these groups did not seem to separate along the first or second axes in a systematic manner.

3.2. Variance partitioning

Parsimonious models that included three of the four silvicultural treatment factors, six of the twelve overstory and understory vegetation (biotic) factors, five of the eight substrate and soil attribute (abiotic) factors, and two of the nine location terms were selected. The four reduced predictor matrices (treatment, biotic, abiotic, and spatial location) and their joint effects accounted for 26% of the total variation in regeneration composition and abundance (Fig. 3). Although the unique variance contribution of each predictor matrix was low, they were all significant ($P < 0.05$), as suggested by permutation tests. The unique contribution of treatment, after deducting the covariance of site (biotic and abiotic factors) and location matrices, was 4%, whereas the variance fraction shared with abiotic factors (4%) was similar to that explained by treatment alone. Overstory and understory vegetation alone accounted for four times the amount of variation (16%) explained uniquely by silvicultural treatment, whereas substrate and soil attributes uniquely accounted for 2% of variance. Spatial location

Table 2
Summary statistics for the analysis variables across five silvicultural treatments of the USDA Forest Service long-term silviculture experiment at the Penobscot Experimental Forest, Maine.

	Variable	Mean ^e	SD ^e	Range ^c Min ^d	Max ^e
Response (Y) ^a	Balsam fir (trees ha ⁻¹)	18,067	20,947	0	126,021
	Red spruce (trees ha ⁻¹)	3106	4698	0	25,946
	Eastern hemlock (trees ha ⁻¹)	7066	8750	0	75,366
	Northern white-cedar (trees ha ⁻¹)	1379	3000	0	17,297
	Red maple (trees ha ⁻¹)	8606	8189	0	44,478
	Paper birch (trees ha ⁻¹)	1676	6796	0	55,598
Treatment (H)	Basal area (m ² ha ⁻¹) ^b	7.8	6.8	0.0	27.7
	Canopy openness (%)	10.7	7.1	3.1	39.5
	Time since last harvest (year)	9.0	2.4	5.0	12.0
Biotic (B)	Understory vegetation (%)	146	72	24	349
	Balsam fir (m ² ha ⁻¹) ^b	4.6	3.4	0.0	18.4
	Red spruce (m ² ha ⁻¹) ^b	6.4	4.5	0.0	21.2
	Eastern hemlock (m ² ha ⁻¹) ^b	8.9	6.4	0.0	32.4
	Northern white-cedar (m ² ha ⁻¹) ^b	1.7	2.2	0.0	13.1
	Red maple (m ² ha ⁻¹) ^b	3.1	2.4	0.0	14.1
	Paper birch (m ² ha ⁻¹) ^b	1.0	1.3	0.0	8.8
Abiotic (A)	Mottling (cm)	22.1	14.7	1.3	57.2
	Eluvial horizon (cm)	3.2	3.7	0.0	15.2
	Downed wood (%)	16	12	0	52
	Conifer litter (%)	53	27	3	88
	Hardwood litter (%)	48	26	1	88

^a The six most abundant regeneration species (tree seedlings ≤ 0.6 m in height).

^b Trees ≥ 1.3 cm DBH.

^c n = 146 for all variables.

^d Minimum.

^e Maximum.

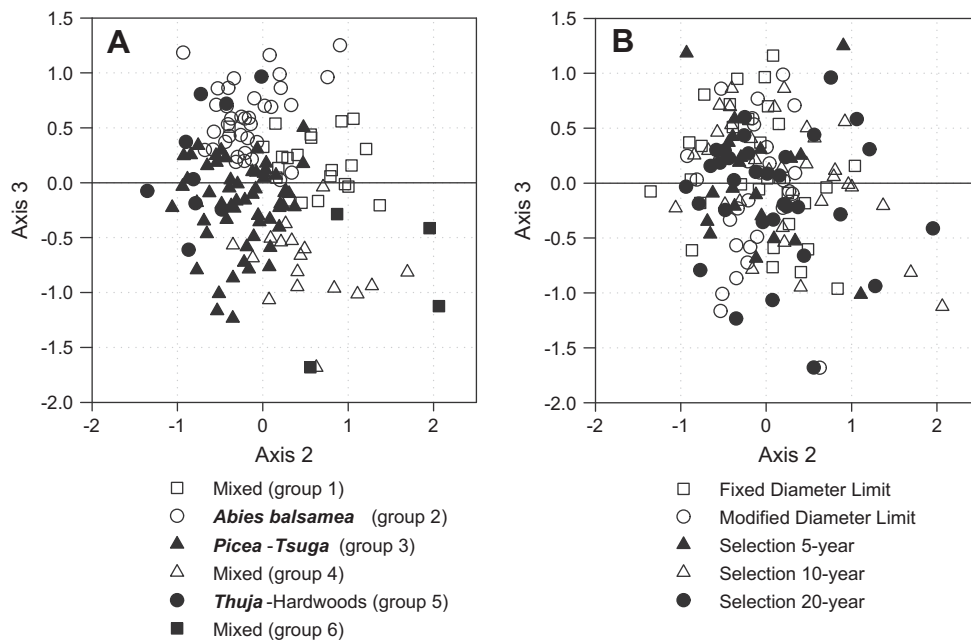


Fig. 1. Ordination of permanent sample plots along the second and third axes of non-metric multi-dimensional scaling, with groupings from flexible beta clustering (A) and silvicultural treatment (B).

accounted for 2% of the variation with minimal joint influences with treatment and site (Fig. 3).

3.3. Local site effects

The six factors used to characterize biotic effects were the most influential in structuring regeneration pattern (Fig. 3). Both axes of

pRDA, first and second, were significant ($P = 0.005$). After removal of treatment, abiotic, and location effects, regeneration groups were separated along a gradient corresponding to overstory composition (i.e., potential seed sources) (Fig. 4A). Regeneration groups were also structured along a gradient of decreasing understory cover (Fig. 4A). Mixed and hardwood-white-cedar groups occupied sites with low amounts of herb and shrub cover, whereas the

Table 3
Observed indicator value for each species by flexible beta groupings with *P* value for maximum value (in bold) using a Monte Carlo randomization test of 10,000 permutations.

Species	Group						<i>P</i> value ^a
	1	2	3	4	5	6	
Balsam fir	19	36	16	3	11	10	0.0001
Red spruce	1	24	29	5	4	0	0.0285
Eastern hemlock	4	25	25	8	15	4	0.0329
Northern white-cedar	0	3	17	0	32	0	0.0144
Red maple	17	20	16	14	29	0	0.0004
Paper birch	1	2	1	0	63	0	0.0003
White pine	0	15	10	0	0	0	0.2186
Birch	0	2	2	1	10	0	0.2734
White ash	1	1	2	0	19	0	0.0746
Gray birch	1	0	0	1	42	0	0.0021
Red oak	4	1	0	0	12	0	0.2202
American beech	1	4	1	0	0	1	0.6392

^a Proportion of permutations with a maximum indicator value that is equal to or greater than the maximum observed indicator value.

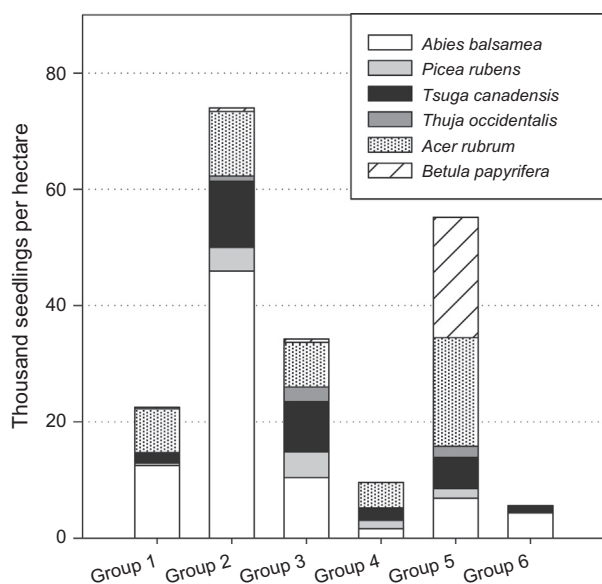


Fig. 2. Seedling density (trees ha⁻¹) by the six most abundant species for each of the groups obtained in flexible beta clustering.

balsam fir group occupied sites toward the opposite end of this gradient. The spruce-hemlock group occupied an intermediate position along the herb and shrub cover gradient.

In relation to unique abiotic effects, regeneration groups were ordered along a gradient of decreasing conifer litter cover (Fig. 4B). The balsam fir group occupied microenvironments of high conifer litter cover along this gradient, while spruce-hemlock occupied sites of relatively lower litter cover. The hardwood-white-cedar group occupied a high position along the second pRDA axis and represented an association with microenvironments of higher downed wood and thicker eluvial horizons (Fig. 4B). The first pRDA axis was significant (*P* = 0.005), whereas the second pRDA axis was not significant (*P* = 0.130).

3.4. Treatment effects

Only the first pRDA axis was significant (*P* = 0.005). This axis reflected a gradient from past harvests of low intensity to more recent harvests with higher basal area removal and canopy openness values (Fig. 4C). Mixed and hardwood-white-cedar

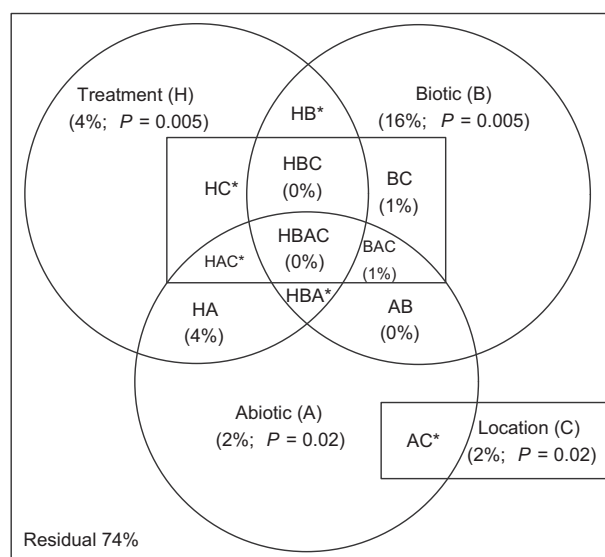


Fig. 3. Venn diagram of regeneration composition and abundance variance partitioning among treatment (H), biotic (B), abiotic (A), and location (C) predictor matrices. Treatment, biotic, abiotic, and location matrices contained three, six, five, and two factors, respectively. Starred values are <math><0.05</math>.

groups were associated with more recent, higher intensity removals. Shade-tolerant balsam fir and spruce-hemlock groups, on the other hand, were associated with older and lower intensity harvests.

4. Discussion

Silvicultural treatment and biotic, abiotic and location factors were directly related to regeneration pattern to allow for maximum explanation of variation in composition and abundance. Despite the use of these various factors, overall explanation of total variation was relatively low (26%). Thus, highlighting the degree of complexity and stochasticity involved in the regeneration process (Paluch, 2005; Weiskittel et al., 2011), especially at early development stages such as that captured in this study. This result also underscores the difficulty of developing predictive regeneration models (Weiskittel et al., 2011) and the practicality of using established seedlings as a starting point in model development (Ferguson et al., 1986; Schweiger and Sterba, 1997).

4.1. Biotic control model

The variation in regeneration patterns that could be accounted for was associated primarily with local site factors. Our results indicated a greater influence of the biotic control model in relation to abiotic and disturbance control models (Figs. 3 and 4A), thus supporting the hypothesis of a lesser role of harvest intensity in structuring regeneration pattern within these stands. In an earlier study, Brissette (1996) attributed the finding of few statistically significant differences among the silvicultural treatments analyzed in this study to considerable within-stand heterogeneity. Results from our study support this interpretation.

An examination of the natural regeneration pattern at the PSP level is consistent with the theory of neighborhood dynamics (Pacala et al., 1996; Canham and Uriarte, 2006). Within the context of this theory, regeneration is viewed as a neighborhood process governed by interactions at fine spatial scales. Our analysis of regeneration patterns at the PSP level allowed us to examine the simultaneous influence of a wide variety of factors operating at a neighborhood scale. Our results suggested that biotic effects, such

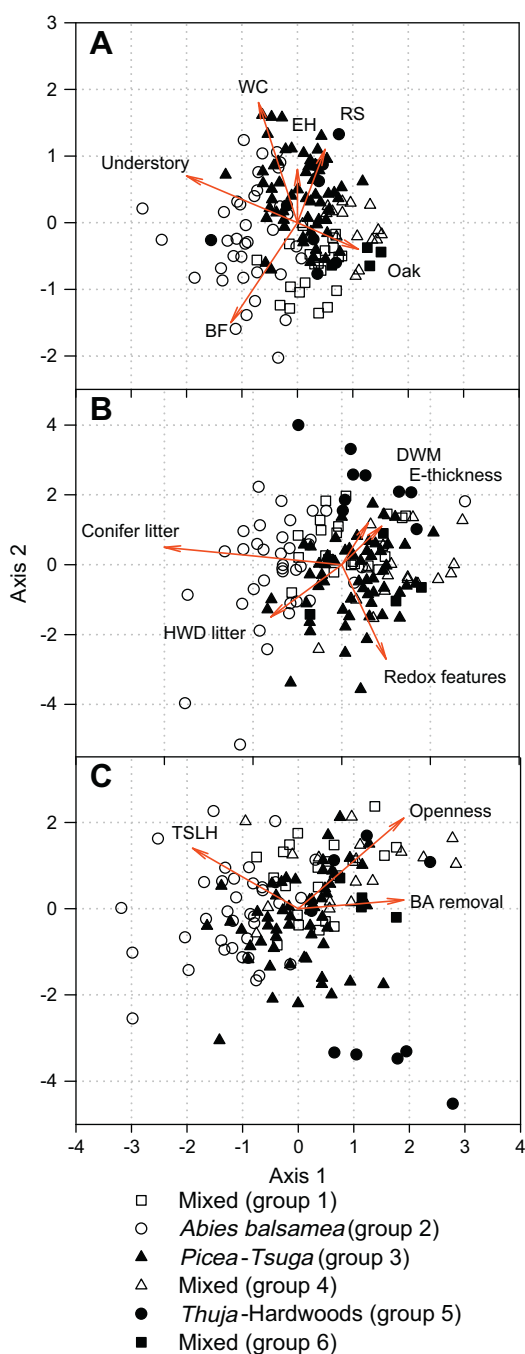


Fig. 4. Biplots showing the relationship between regeneration groups (symbols) and: six biotic factors (BF-balsam fir; RS-red spruce; EH-eastern hemlock; WC-northern white-cedar; Oak; understory herb and shrub cover) (A); five abiotic factors (Conifer litter; DWM-downed wood; E-eluvial horizon thickness; depth to redoximorphic features; HWD-hardwood litter) (B); three treatment factors (TSLH-time since last harvest; Openness-canopy openness; BA-basal area removal intensity) (C)-after deducting the covariance of remaining factors.

as canopy composition and understory competition, can be more important than the type of partial harvesting used (or natural disturbance that creates small canopy gaps) in structuring regeneration at the neighborhood scale.

Despite the presence and noted lingering of advance natural regeneration in northern conifer stands (Seymour, 1995; Weaver, 2007), pre-harvest overstory composition was a reasonable predictor of regeneration composition. This is in support of the principle of initial floristic composition, in which vegetation development is closely related to initial on-site flora (Egler, 1954). In our study,

this on-site flora was the product of pre-harvest overstory composition. Our results are consistent with those of White (1991), who attributed post-harvest regeneration pattern in a clearcut northern hardwood stand to pre-harvest stand composition. Similarly, Wilson and Maguire (1996) reported a significant relationship between overstory structure and germinant density of balsam fir and eastern hemlock within the Penobscot Experimental Forest. In central Ontario, seed supply limitation was reported as the primary cause of germinant recruitment failure for balsam fir, whereas establishment limitation was the primary cause of recruitment failure for eastern hemlock (Caspersen and Sapruff, 2005). The positive association of regeneration patterns with pre-harvest overstory composition in our study suggested a greater importance of seed supply relative to establishment limitation in partially harvested mixed conifer stands of the Acadian Region. However, the influence of overstory on regeneration patterns is not necessarily restricted to that of seed supply. For example, canopy influence on understory light levels has been reported to be more conducive to the survival of conspecific seedlings (Canham et al., 1994). Such interspecific differences in light transmission by canopy trees have probably played a role in the positive association of overstory composition to the regeneration pattern observed in this study.

Herb and shrub cover have been previously shown to influence regeneration patterns (Maguire and Forman, 1983; Dibble et al., 1999; Valkonen and Maguire, 2005). Herb and shrub cover have clearly played an important role in the structuring of regeneration patterns in our study (Fig. 4). Our results showed a positive association between understory cover and balsam fir abundance, implying a facilitative effect for or tolerance by balsam fir regeneration under heavy understory cover. In contrast, Wilson and Maguire (1996) showed that balsam fir germinant density was negatively correlated with herb cover. However, balsam fir and eastern hemlock survival were positively correlated with herb cover (Wilson and Maguire, 1996). Greenwood et al. (2008) described how early life cycle strategies such as delayed germination and greater root to shoot ratio provide balsam fir with a competitive advantage over red spruce. Such early life strategies may have resulted in greater survival of balsam fir under heavy understory cover.

Recently, the relative importance of plant community assembly controls has been the focus of discussion (Levine and Murrell, 2003; Chave, 2004; Caspersen and Sapruff, 2005). According to Chave (2004), the neutral theory of Hubbell assumes equivalence in the likelihood of birth and death of all individuals in a community, thus implying that community structure is largely dependent on dispersal. In a review of available literature, Levin and Murrell (2003) contended that empirical evidence in support of neutral theory and the role of seed dispersal in species coexistence was limited. Caspersen and Sapruff (2005) concluded that niche differences are more important than dispersal limitations in structuring forest communities at local scales. Chave (2004) viewed neutral and niche differentiation theories as complementary and suggested bridging both theories. At a first glance and as mentioned previously, our results suggested greater importance of dispersal in species relative abundance control, which provides support for the neutral theory. However, in relating pre-harvest overstory to regeneration pattern, measures of community structure such as composition and abundance were used. These measures do not rule out other biotic influences of tree canopy and most certainly confound the interpretation of the relative influence of seed dispersal in relation to niche differentiation. Therefore, our results do not favor one of the two theories over the other. Such comparisons are better examined using studies that focus on seed dispersal manipulation and empirically-based dispersal kernel modeling (Levine and Murrell, 2003).

4.2. Disturbance control model

Relative to harvesting, a greater influence of environmental factors on regeneration pattern, including biotic and abiotic effects such as overstory and understory vegetation, and substrate and soil attributes, as examined in this study were previously reported (Park, 2001; Rodriguez-Garcia et al., 2010). Wimberly and Spies (2001) suggested that the relative importance of disturbance and environmental controls was dependent on the community attribute examined, in which community composition was largely structured by environmental controls whereas community structure was largely a function of disturbance. Our results are consistent with these earlier reports. In our study, removal intensity was the primary factor used in characterizing silvicultural treatment. Other factors such as frequency of removal were not included in the analysis. Because sampling of regeneration across multiple years was not included in the response, characterization of silvicultural treatment using intensity alone was sufficient.

Similarly, our analysis did not incorporate all potential explanatory factors within the biotic and abiotic control models. For example, the influence of seed predation and seedling browsing on natural regeneration is well established in the Acadian Region (Abbott and Hart, 1961; Abbott, 1962; Kanoti, 2005; Berven, 2011). Differential seed predation by deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Clethrionomys gapperi*), in which balsam fir is avoided, may have contributed to differences in species relative abundance observed in the present study (Abbott and Hart, 1961). Preferential browsing of red spruce may have also played a role (Berven, 2011). The relative importance of seed predation and browsing, within the biotic control model, on regeneration dynamics remains unclear (Hart et al., 1968). Furthermore, we do not know how the proportion of variance attributed to each control model in our study would vary temporally. Given seed crop periodicity and interannual variation in substrate (i.e., litter) cover, it is likely that the proportion of variance would fluctuate from year to year. It is unlikely, however, that the relative importance of these control models would drastically change temporally. In an earlier study, Brissette (1996) reported little effect of repeated partial harvesting on regeneration within our stands. In general, harvest intensity and frequency are negatively and strongly correlated, where high intensity harvests are usually of low frequency (Olson and Wagner, 2010).

The effect of canopy gaps on the physical environment (Dey and Macdonald, 2001; Beckage and Clark, 2003), and the consequent influence on natural regeneration is reflected by the shared variance (4%) between silvicultural treatment and abiotic factors. The effect of this source of variance was equivalent to that uniquely accounted for by treatment. Coarser scale (i.e., greater than that captured at the PSP level) variability in canopy structure as influenced by treatment and a limited range of examined partial harvest intensities (i.e., five treatments with mean reduction in BA ranging from 2.0 to 17.9 m² ha⁻¹) may have contributed to the low fraction of variance accounted for by treatment alone. Nevertheless, the indication of a greater role of the biotic control model at the PSP level implies a limited degree of control over natural regeneration using partial harvest intensities such as those used in this study. This, however, does not negate the influence of silvicultural treatment on composition control of pre-harvest overstory and consequently regeneration pattern. Olson and Wagner (2010), examined the long-term neighborhood dynamics in relation to treatment history and initial overstory within the Penobscot Experimental Forest. Changes from initial overstory composition were proportional to intensity and frequency of removal, with lighter more frequent removals resulting in maintenance of northern conifers and heavier less frequent removals resulting in hardwood dominance (Olson and Wagner, 2010). Similarly,

examination of stand-level response over the first 40 years of the experiment showed that single-tree selection on a 5-yr cutting cycle was effective in reducing overstory hardwoods, and that selection and modified diameter-limit treatments were effective at increasing the proportion of spruce basal area (Sendak et al., 2003).

The association of mixed and hardwood-white-cedar groups with sites of low herb and shrub cover reflected the pioneer status and species' shade tolerance, in which pioneer and shade intolerant hardwoods such as paper birch and intermediate red maple occupy these sites. This outcome was also apparent in the association of those groups with more recent, higher intensity removals. The association of northern white-cedar with these sites is consistent with seed substrate requirements and shade tolerance of the species (Hofmeyer et al., 2009; Larouche et al., 2011). Our results support reports of shifts toward hardwood dominance with higher harvest intensities (Man et al., 2008; Olson and Wagner, 2010). In addition, our results indicated that those shifts can be apparent at early stages of cohort development (i.e., the regeneration phase).

4.3. Abiotic control model

Regeneration pattern was weakly structured by abiotic controls. Similar conclusions were reported by Maguire and Forman (1983) and Kneeshaw and Bergeron (1996). Northern white-cedar was associated with microenvironments of higher downed wood (Hofmeyer et al., 2009; Boulfroy et al., 2012), however the strength of this relationship was weak. Despite the low variance contribution, natural regeneration pattern in our study was structured along a gradient of conifer litter cover. Litter accumulation is known to hinder establishment and growth of both balsam fir and red spruce (Frank, 1990; Caspersen and Sapruff, 2005; Weaver, 2007; Weaver et al., 2009). Balsam fir rapid root development and ability to penetrate deeper humus layers relative to red spruce provide balsam fir with a competitive advantage under heavy litter accumulation conditions (Place, 1955; Bakuzis, 1965; Greenwood et al., 2008). According to Messaoud and Houle (2006), small-seeded species (e.g., red spruce and eastern hemlock) are more negatively influenced by litter accumulation than large-seeded species (e.g., balsam fir), which have greater reserves. Brissette (1996) attributed greater abundance of balsam fir to seed characteristics in which heavier seeds of balsam fir provide an advantage over lighter seeds of red spruce and eastern hemlock. Greenwood et al. (2008) suggested that differences in early life stage behavior between balsam fir and red spruce contribute to differences in their abundance. The observed role of litter in structuring regeneration in our stands suggests control potential through seedbed preparation (e.g., scarification) strategies to promote red spruce and eastern hemlock over balsam fir. In a seedbed treatment trial on the Penobscot Experimental Forest, red spruce and hemlock germinant density increased with removal or mixing of litter with the mineral soil (Davis and Hart, 1961). It is not clear how such strategies alone would be able to, if at all, compensate for the prolific reproduction of balsam fir (Seymour, 1992).

4.4. Modeling implications

Stochasticity of the regeneration process was reflected in our results, and supported using established seedlings as a starting point in the development of regeneration models. Although there is merit to developing regeneration models at each stage of the life cycle, approaches that use established seedlings as a starting point not only allow for the use of commonly available inventory data but may also reduce the impact of stochastic processes operating at earlier life cycle stages. Our results illustrated a strong relationship between overstory composition and understory competition on one hand, and natural regeneration composition and abundance

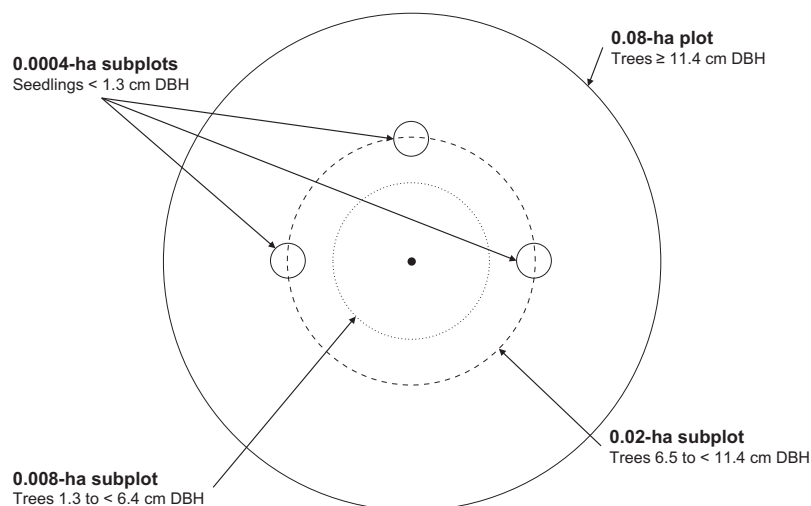


Fig. A1. Permanent sample plot (PSP) layout for the USDA Forest Service long-term silviculture experiment at the Penobscot Experimental Forest, Maine.

on the other. Regeneration modeling efforts in partially harvested stands should exploit this relationship. Further, the interaction of silvicultural treatment with substrate and soil attributes in structuring natural regeneration is as important as treatment alone, and should be considered in modeling efforts. Modeling approaches that emphasize the role of pre-harvest overstory composition and regeneration origin have potential in partially harvested northern conifer stands. Such emphasis is reflected in two available approaches; the REGEN expert system of Loftis (1989) and the empirically-based dispersal kernels relating natural regeneration spatial variation to parent tree spatial distribution (Ribbens et al., 1994). Future studies should explore these two approaches to modeling regeneration in partially harvested stands.

4.5. Management implications

In the Acadian Region, repeated partial harvests have selectively removed red spruce, resulting in long-term shifts in composition toward balsam fir and shade-intolerant or low-value, sprout-origin hardwoods (Seymour, 1995; Irland, 1999; McCaskill et al., 2011). From a management perspective, red spruce is a preferred species in this forest type owing to its longevity, low susceptibility to decay and spruce budworm (*Choristoneura fumiferana* Clemens), and high commercial value. The fact that overstory and understory composition accounted for a relatively high proportion of observed variation in regeneration composition in our study suggests that retention of spruce and removal of competing species may be effective silvicultural practices, both in terms of overstory manipulations (regeneration treatments) and cultural work (treatments in the submerchantable classes, e.g. site preparation prior to regeneration or release work). Seymour (1995), for example, suggested that removal of balsam fir in shelterwood establishment cuts can be very effective, if these cuts coincided with good spruce seed years. Such practices require high and uniform stocking of red spruce or other components.

Our results also suggest potential for favoring red spruce, hemlock, and northern white-cedar through seedbed preparation strategies including downed wood retention or soil scarification (Fig. 4B). The critical role of established vegetation in determining post-harvest regeneration outcomes, and the potential for refinement of those outcomes through treatments focused on vegetation composition and manipulation of substrate or soil attributes, are the important outcomes of this work for Acadian Forest managers.

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Appendix A

See Fig. A1.

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