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silviculture

Potential Yields and Economic Returns of Natural Disturbance-Based Silviculture: A Case Study from the Acadian Forest Ecosystem Research Program

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Intrastand variability is promoted by many silvicultural systems designed to emulate natural disturbance regimes (natural disturbance-based silviculture [NDBS] systems) in the eastern United States and Canada but this variability is difficult to model in many growth-and-yield models, limiting application by the region's forest managers. We used a resampling approach to integrate intrastand variability into Forest Vegetation Simulator (FVS) growth-and-yield projections. We subsequently compared potential yield and financial returns over a 100-year period for two NDBS systems monitored in the Acadian Forest Ecosystem Research Program with two conventional systems: a two-stage uniform shelterwood and a single-tree selection system. NDBS systems produced the widest diameter distribution at the end of the harvest rotation and were more effective in recruiting large trees (>24 in.) and more diverse species relative to conventional silviculture systems. Projected merchantable yield and financial return were highest for the single-tree selection, followed by the two NDBS systems and finally the shelterwood; however, if standing merchantable value at the end of simulation was included, the NDBS systems ranked first and third overall financially. Our analysis suggests that NDBS systems are capable of sustaining a greater diversity in forest structure and composition while producing volume yields and financial returns that are competitive with conventional even- and uneven-aged silvicultural systems.

Keywords: expanding gap, irregular shelterwood, growth and yield, Forest Vegetation Simulator (FVS), natural disturbance-based silviculture, single-tree selection, uneven-aged management

During recent decades, biodiversity and sustainability concerns have altered forest management from a high-yield and low-cost emphasis on sustainable wood production, usually using only a few tree species, to an emphasis on a broader array of ecological objectives and services using a variety of tree species (Seymour et al. 2006, Bauhus et al. 2009, Gamfeldt et al. 2013). This shift toward ecosystem management and landscape ecology principles has driven development of alternative silvicultural strategies with labels such as "ecological forestry" (Seymour and Hunter 1999), "nature-based" silviculture (Larsen and Nielsen 2007, Zenner et al. 2013), and "natural disturbance-based management" (Bergeron et al. 2006, Long 2009). These strategies generally consist of managing forest biodiversity both through coarse-filter approaches that maintain a wide diversity of stand structures, ecosystems, and successional stages at multiple spatial and temporal scales (e.g., reserves of multiple ecosystem types) and through fine-filter approaches that maintain specific habitat elements for selected species (e.g., tree falls for denning sites; Hunter et al. 1988, Franklin 1993, Bauhus et al. 2009).

Unfortunately, conventionally applied even- and uneven-aged silviculture systems are poor models in this new ecological framework, because they generally homogenize stand structure and composition (Crow et al. 2002, Puettmann et al. 2009). Further, these systems commonly do not provide adequate legacy retention for biodiversity purposes (Franklin et al. 2007) because managers typically only use production cycles up to 150 years (Bauhus et al. 2009) and remove low-vigor individuals before they can contribute to snags and coarse woody debris pools (Goodburn and Lorimer 1998,

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Kenefic and Nyland 2007). Consequently, alternative silviculture systems have been designed using a premise that extant forest species are a result of their adaptation to dominant natural disturbance regimes (Keeton 2006, Seymour et al. 2006, Long 2009). Therefore, more closely emulating spatial and compositional patterns produced by these disturbances could help preserve essential habitat features and maintain a diverse and resilient ecosystem (Franklin 1993, Landres et al. 1999, Long 2009).

Outside of research studies, these natural disturbance-based silvicultural (NDBS) systems have yet to be widely implemented despite their theoretical underpinnings in disturbance ecology and forest dynamics. Most replicated NDBS system trials are relatively recent (often installed after 1990), and there are few long-term empirical studies to evaluate their intended effects on biodiversity (Simberloff 1999, Seymour et al. 2006, North and Keeton 2008). Comprehensive economic and production analyses of the existing examples of NDBS systems have also been lacking, largely because of the inability of standard growth-and-yield models to capture the spatial and temporal complexities of many NDBS systems (Arseneault and Saunders 2012).

In eastern North America, many NDBS systems use intrastand variability to approximate natural disturbances. Arseneault and Saunders (2012) showed that spatially implicit models could be used to estimate growth and yield in these systems. Here, we extend that work to analyze two NDBS systems to project forest growth, compositional change, yield, and economic returns for an entire 100-year rotation using the Northeast Variant of the Forest Vegetation Simulator (FVS-Northeast [NE]; Crookston and Dixon 2005, Dixon and Keyser 2008). We then compared and contrasted the relative structural differences, potential yields, and economic returns of these NDBS regimes to other conventional even-aged (i.e., two-stage shelterwood) and uneven-aged (i.e., single-tree selection) silviculture systems of the region.

Methods

Study Area

The Acadian Forest Ecosystem Research Program (AFERP) is located in the Penobscot Experimental Forest (PEF) near the towns of Bradley and Eddington in central Maine (44°51′ N, 68°37′ N). The PEF is approximately 4,000 acres and part of the Acadian Forest, a region dominated by a mixture of northern and boreal conifer species and northern hardwoods that encompasses the Maritime Provinces of Canada and northern New England (Sendak et al. 2003). The region experiences cold winters and warm summers (daily mean = 18° F and 68° F, respectively) with precipitation exceeding 40 in., which falls relatively evenly throughout the year. In the PEF, glacial till-derived soils predominate and range from well-drained loams, stony loams, and sandy loam ridges to poorly drained loams and silt loam flat areas and poorly drained silt and silty clay loams along watercourses and depressions (Brissette 1996, Saunders and Wagner 2008).

An array of natural disturbances at a variety of spatial scales creates irregularly aged, mixed-compositional stands in the PEF. Natural disturbances range from individual treefall gaps from wind events and senescence, cumulatively affecting approximately 1.0% of the Acadian Forest annually (Fraver and White 2005), to insect outbreaks, ice storms, microbursts, and other partial canopy disturbances affecting larger spatial scales 0.5–2.0 times in a given area per century (North and Keeton 2008). Large-scale, stand-replacing events, such as hurricanes and fire, are exceedingly rare in the Acadian Forest Region (Seymour et al. 2002).

The AFERP has two NDBS treatments plus an unharvested experimental control. The NDBS treatments are hybrid systems (*sensu* Seymour 2005) and use expanding-gap harvesting to emulate 1% year^{-1} disturbance intensity. Each treatment was replicated three times across nine 22- to 28-acre research areas within irregularly aged, mixed-conifer hardwood sites (Table 1, Figure 1). Treatment installation occurred in the winters of 1995–1997. Pretreatment forest inventories were conducted in the summer before harvest and repeated every 5 years thereafter. Twenty sampling locations were randomly chosen from intersections of a 123.6 × 123.6-ft grid overlying each research area. At each sample location, overstory trees (≥3.7 in. dbh) and saplings (0.6–3.7 in. dbh) were quantified in 0.124- and 0.025-acre nested circular plots, respectively. Saunders et al. (2013) provide a more detailed description of the study area, experimental design, and inventory systems.

FVS Growth Model and Analysis

We used FVS-NE (release version Feb. 16, 2011; Dixon and Keyser 2008), an empirical distance-independent, tree-level growth-and-yield model, to simulate stand development of the AFERP treatments (i.e., the large-gap and small-gap treatments described below) and two conventional, uniformly applied silvicultural systems appropriate for these stand types. Five treatments were simulated:

1. *Control*. The stand was left to grow and no harvesting occurred.
2. *Shelterwood*. A uniform two-stage shelterwood system in which the initial harvest leaves a residual basal area target of 104.5 ft^2 acre^{-1}, following Sendak et al. (2003). The overstory removal was simulated 10 years after the initial cut, and all merchantable trees were removed.
3. *Selection*. A single-tree selection system using the BDq method (Leak 1964), with a residual basal area target (B) of 100 ft^2 acre^{-1}, maximum diameter (D) of 20 in., and a diameter class quotient (q) of

Management and Policy Implications

Silvicultural systems designed to emulate the temporal and spatial patterns of natural disturbances often create structurally complex forests that provide a coarse filter approach to conserving biodiversity. Skeptics of this management approach often cite lack of growth, yield, and economic data for these silvicultural systems as reasons not to implement them. Novel uses of existing growth-and-yield models can provide some guidance to the relative performance of natural disturbance-based silvicultural systems in comparison with conventional silvicultural systems, with which managers have more experience. As a case study in northeastern North America, gap-based silvicultural systems appear to provide more structural complexity than either single-tree selection or shelterwood systems and provide comparable to slightly higher merchantable yield and financial returns over a 100-year period. Therefore, natural disturbance-based silvicultural systems could be incorporated much more widely than presently within public and private landholdings without fear of significant economic loss.

Table 1. Initial basal area of the tree species found within the AFERP study sites.

Latin name	Species	BA (ft^2 $acre^{-1}$)	Group
Pinus resinosa	Red pine	3.72	Intolerant conifers
Pinus strobus	White pine	20.65	Intolerant conifers
Abies balsamea	Balsam fir	12.36	Tolerant conifers
Picea glauca	White spruce	1.94	Tolerant conifers
Picea rubens	Red spruce	8.32	Tolerant conifers
Picea spp.	Other spruce species	<0.01	Tolerant conifers
Thuja occidentalis	Northern white-cedar	12.97	Tolerant conifers
Tsuga canadensis	Eastern hemlock	38.41	Tolerant conifers
Betula alleghaniensis	Yellow birch	1.47	Intolerant hardwoods
Betula papyrifera	Paper birch	11.77	Intolerant hardwoods
Betula populifolia	Gray birch	0.32	Intolerant hardwoods
Fraxinus americana	White ash	1.10	Intolerant hardwoods
Fraxinus nigra	Black ash	0.51	Intolerant hardwoods
Fraxinus spp.	Other ash species	<0.01	Intolerant hardwoods
Populus grandidentata	Bigtooth aspen	4.20	Intolerant hardwoods
Populus tremuloides	Quaking aspen	5.34	Intolerant hardwoods
Prunus serotina	Black cherry	0.07	Intolerant hardwoods
Quercus rubra	Northern red oak	3.03	Intolerant hardwoods
Acer rubrum	Red maple	32.71	Tolerant hardwoods
Acer saccharum	Sugar maple	2.99	Tolerant hardwoods
Fagus grandifolia	American beech	2.79	Tolerant hardwoods
Fraxinus pennsylvanica	Green ash	0.20	Tolerant hardwoods
Ostrya virginiana	Eastern hophornbeam	0.41	Tolerant hardwoods
Tilia americana	American basswood	1.04	Tolerant hardwoods

Total basal area (BA) by site was 166.4 ± 5.6 ft^2 $acre^{-1}$ (mean ± SE). Shade tolerance groups used for summarizing results included both shade-tolerant and shade-intolerant to intermediately shade-tolerant conifers and hardwoods as reported in Burns and Honkala (1990).

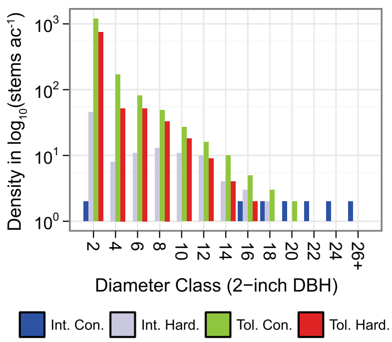

Figure 1. Initial diameter distribution by 2-in. classes, pooled across all AFERP experimental sites.

1.5 with 2-in. diameter class widths, following Leak (2003). Trees eligible for harvest were removed in descending order within each diameter class until the residual basal area target was achieved.

4. *Large-gap*. A modification of an irregular group shelterwood system, this area-based harvest removes 20% of the stand area on a 10-year cutting cycle (Figure 2A). Initial gap sizes averaged 0.49 acre and expanded outward on two to four sides every cutting cycle. Harvests only occurred during the first half of a 100-year rotation; the stand was then allowed to "rest" for the second half.
5. *Small-gap*. A modification of a group selection system, this area-based harvest system removes 10% of the stand area on a 10-year cutting cycle (Figure 2B). Initial gap sizes averaged 0.25 acre and expanded outward on two to four sides every other cutting cycle, resulting in two gap cohorts, each having a 20-year regeneration period. Harvests occurred throughout a 100-year rotation.

In both gap systems, reserve trees of long-lived (e.g., white pine, spruces, and eastern hemlock) or uncommon species (<5% of basal area; e.g., red oak and yellow birch) were retained within gaps at a basal area density of 16.1 ft^2 $acre^{-1}$ or approximately 10% of the pretreatment stocking. Low-quality, short-lived species (e.g., aspen, birch, fir, and red maple) were targeted for removals (Seymour 2005, Saunders et al. 2013).

Simulations for each system were run on all pretreatment, plot-level data (i.e., plots were treated as individual stands) to allow integration of intrastand variability in growth responses and comparison of development using the same starting conditions. All simulations were projected for 100 years using 10-year cycles. We used a data partitioning and a raster-based simulation model created in R version 2.11.1 (R Development Core Team 2011) by Arseneault and Saunders (2012) to incorporate intrastand variability of tree growth responses, which are commonly observed within group- or gap-based silvicultural systems (e.g., Puettmann et al. 2009), within projections of the two AFERP treatments. Using empirical data for the AFERP sites (Arseneault et al. 2011), we defined edges as within approximately one mature tree height (i.e., 66 ft) of harvested gaps and applied a 20% increase in base FVS-NE growth rates; increases attenuated to default values after 20 years (i.e., two cutting cycles).

FVS-NE currently does not have a full-establishment model for regeneration, and the long-term effects of expanding-gap harvests on regeneration establishment, survival, and recruitment are unknown. Consequently, we simulated pretreatment conditions by using regeneration inputs for the large- and small-gap treatments derived from the proportion of initial seedling and sapling importance values. Sapling importance values were calculated as sums of relative dominance (%), relative frequency (%), and relative density (%), whereas seedling importance values were sums of relative frequency and relative density. Regeneration inputs for the shelterwood and single-tree selection systems were estimated using regeneration abundance data reported for those systems at the PEF (Brissette 1996). Initial regeneration records were added to the input tree list with a 0.4-in. dbh and limited to a maximum of 2,000 trees $acre^{-1}$ to minimize bias in projected basal area growth and mortality (Ray et al. 2009). Regeneration survival (i.e., all stems <4 in. dbh) during harvesting was assumed to be 80%, which is within the ranges reported in Stokes et al. (2009) and consistent with postharvest observations after the gap expansion treatments in 2005–2007.

The basal area maximum within all FVS-NE simulations was set at 203.7 ft^2 $acre^{-1}$, which corresponded to the 85th percentile of the pretreatment basal area distribution across all plots and is representative of mature stand conditions in these stand types (Saunders and Wagner 2008). The large-tree diameter growth model was calibrated with the observed 10-year diameter growth rates from plots >66 ft from harvested gaps but truncated to protect against bias due to measurement errors. Negative increments (approximately 3.4% of records) were entered as 0, and increments greater than the 95th percentile by species were capped at the 95th percentile. The small-tree height model was not calibrated because

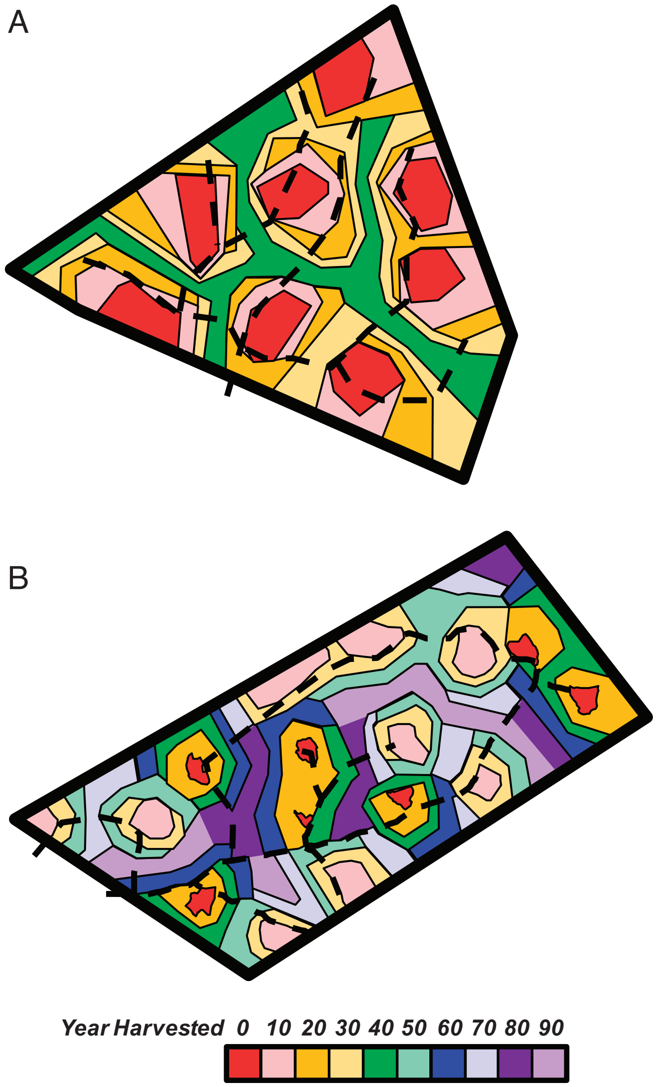

Figure 2. Schematic diagram of planned harvests for the large-gap (A) and small-gap (B) treatments within the AFERP. For the large-gap treatment, harvesting only occurs in the first 50 years of the 100-year projection. An example of a skid trail network is shown with the black dashed line.

height is not measured for saplings in AFERP inventories. Last, site quality was estimated for every plot using local estimates of depth to water table and the site-classification system from Briggs (1994); all estimates were then scaled to represent a moderately productive site with a mean balsam fir site index$_{50}$ of 65 ft.

FVS-NE outputs included the default stand-level estimates such as density and basal area by projection cycle. Diameter distributions by 2-in. classes were also produced for four species groups based on relatedness and shade tolerance (Table 1). Other structural metrics, many of which require spatially explicit data, cannot be estimated from FVS output or are directly calculated from diameter within the FVS modeling framework (e.g., height and canopy cover) and provide no additional discriminatory power among stand structures. Default FVS-NE merchantability standards were used (Dixon and Keyser 2008). Assuming a 4-in. minimum top, softwood and hardwood pulp had minimum dbhs of 5 and 6 in., respectively. Softwood sawtimber had a 9-in. dbh threshold with a 7.6-in. minimum top; hardwood sawtimber had an 11-in. dbh threshold with a 9.6-in. minimum top. Harvest revenue was then estimated using mean stumpage prices for pulpwood and sawtimber from 1996 to 2009 across all counties in Maine, as reported in stumpage price reports published by the Maine Forest Service (1996–2009). Stumpage values were adjusted for inflation using the producer price index for all commodities, and all revenues are reported in constant year 2000 dollars. Based on historical trends, we assumed real annual increases of 0.6 and 0.7% for pulpwood stumpage prices and 4.6 and 2.2% for sawtimber stumpage prices for hardwoods and softwoods, respectively (Wagner and Sendak 2005). Conversion rates among cords, tons, and board feet for sawlogs followed Maine Forestry Service (1996–2009) reports; we also used the heuristic assumption that a cord contained approximately 85 merchantable cubic feet of solid wood for pulpwood.

The database extension to FVS-NE (Crookston et al. 2005) was used to manage data input and output with Microsoft Access 2010 (Microsoft Corporation, Redmond, WA). Analysis of model outputs used a nonparametric resampling approach to estimate mean and confidence intervals for various stand-level outputs reported over time by FVS-NE. The plyr (version 1.4; Wickham 2011) and reshape (version 0.8.4; Wickham 2007) packages were used to manipulate data in R, and confidence intervals were estimated using the stats package (version 2.12.1; R Development Core Team 2011). Figures were produced using the ggplot2 package (version 0.8.9; Wickham 2009).

Results

Forest Structure

There were strong differences among the treatments in projected stand development. In the control treatment, positive basal area accretion occurred during the first 40 years (Figure 3), at which point the stand reached maximum site capacity of 203.7 ft^2 acre^{-1}. Subsequent density-dependent mortality resulted in a final density of 65 trees acre^{-1} and quadratic mean diameter (QMD) of 24.0 in., respectively. The shelterwood treatment, on the other hand, lost basal area during the first 20 years (Figure 3) because of the establishment and overstory removal cuts, although growth in subsequent cycles of the new stand resulted in a final structure at maximum site capacity consisting of 133 trees acre^{-1} with a QMD of 16.7 in. Conversely, the single-tree selection treatment had minimal basal area accretion after the 1st decade as all growth in excess of the BDq structural targets was removed in every cutting cycle (Figure 3). This led to a relatively stable structure with mean basal area and QMD varying between 150 and 157 ft^2 acre^{-1} and 3.0 and 3.2 in., respectively, until the end of the simulation,

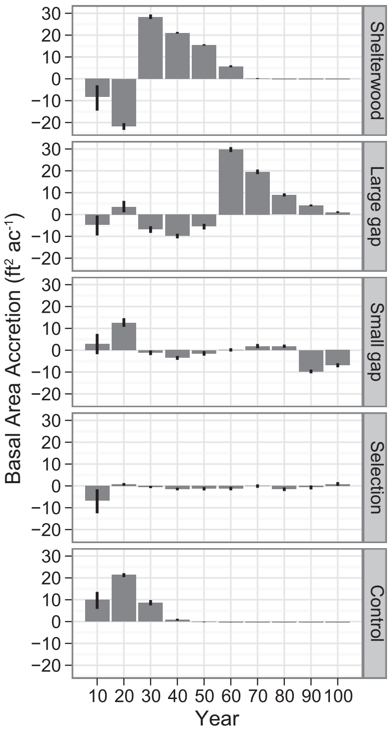

Figure 3. Basal area accretion (ft^2 acre^{-1}) by year for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments. Basal area accretion for a given year is calculated based on the previous 10 years of growth (i.e., one cutting cycle). Error bars are the 95% confidence interval.

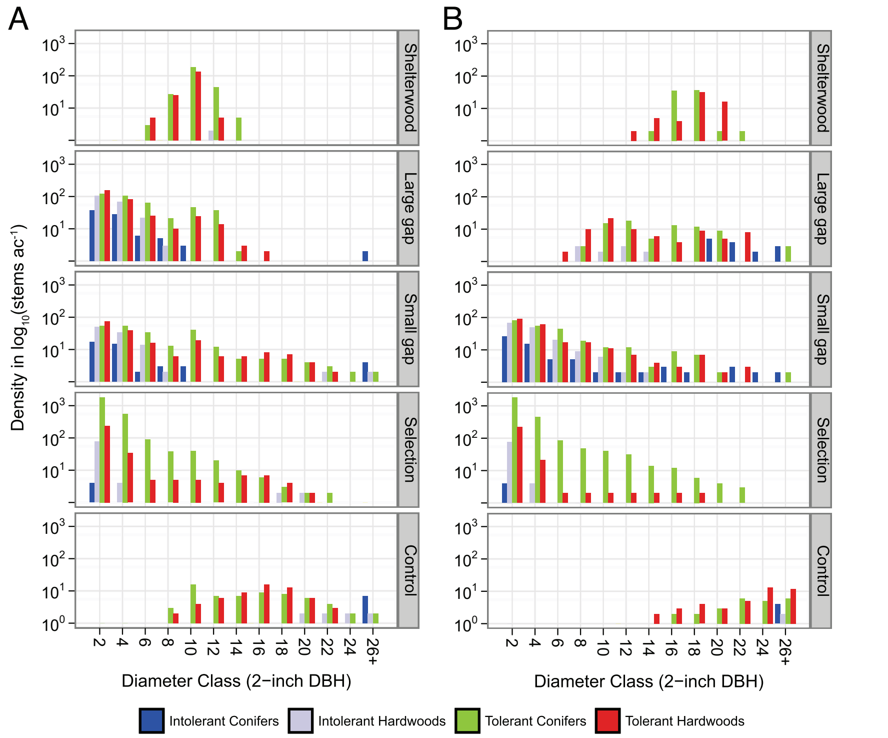

Figure 4. Simulated diameter distribution by 2-in. classes for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments at the midpoint (A) and end (B) of the 100-year projection.

whereas mean density decreased slightly from 3,200 to 2,830 stems acre^{-1}.

Basal area accretion in the two NDBS systems was intermediate to that for the shelterwood and the selection treatment (Figure 3). Once both gap cohorts had been established in the small-gap treatment, projected estimates of density, basal area, and QMD were also relatively stable and varied between 521 and 746 trees acre^{-1}, 161 and 178 ft^2 acre^{-1}, and 6.5 and 7.9 in., respectively, for the remainder of the simulation. In the large-gap treatment, structure was stable during the initial cutting cycles, with projected estimates of density, basal area, and QMD varying between 933 and 1,370 trees acre^{-1}, 139 and 161 ft^2 acre^{-1}, and 4.6 and 5.5 in., respectively. Density declined to 169 trees acre^{-1}, and QMD increased to 14.9 in. by the end of the projection.

From a relatively diverse assemblage of species groups and size classes, simulations of the control treatment suggest that, by the midpoint of the projection (Figure 4A), the diversity of species groups across the diameter distribution will begin to wane. Consistently high stocking would probably suppress most regeneration and, consequently, few trees in the seedling and sapling size classes exist at the end of the projection (Figure 4B). The final diameter distribution is predicted to be predominantly composed of shade-tolerant conifer and hardwood species, although some intolerant conifers and hardwoods still persist in the largest size class.

Even with the initial influx of shade-intolerant regeneration, the shelterwood system became increasingly dominated by a mix of the shade-tolerant species (Figure 4A and B). Overall, the diameter distribution was normal with a narrow range, typical of single-cohort stands with little midstory or understory development. On the other hand, the single-tree selection system had a negative exponential distribution dominated by shade-tolerant conifers and hardwoods (Figure 4B). Intolerant species were present, however, in the sapling size classes, presumably from the frequent harvest entries.

Structural development in the two gap systems was, in some respects, intermediate to that in the two conventional systems. In the large-gap system, frequent harvesting during the first half of the projection provided a steady flow of regeneration that enabled shade-intolerant species groups to persist in the sapling and smaller poletimber size classes, although by the end of the projection, these size classes became dominated by tolerant species groups (Figure 4B) presumably due to high overall stand stocking and higher density-dependent mortality within lower canopy, shade-intolerant trees. The diameter distribution at the end of the projection became approximately bimodal, with a peak in density in the poletimber and smaller sawtimber size classes (8–12 in.) composed of surviving regeneration, largely shade-tolerant species from the most recent harvest entries, and a second peak in the larger sawtimber size classes (16–22 in.) composed of both trees retained during harvests and a component of surviving regeneration from areas harvested early during the rotation (Figure 4B). This resulted in a relatively broad and diverse diameter distribution for the large-gap system in comparison with the control or conventional systems.

The small-gap treatment resulted in an even more diverse and broad structure throughout the rotation (Figure 4). By the midpoint of the projection, when half of the stand had been harvested, developmental patterns in harvested areas resembled patterns observed in the large-gap treatment with a diversity of species groups throughout the sapling and poletimber size classes (Fig-

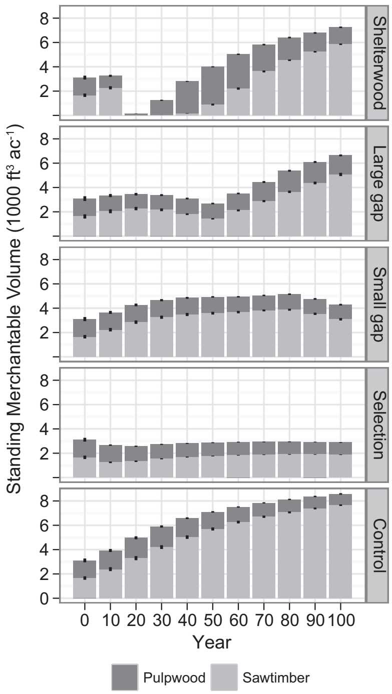

Figure 5. Standing merchantable volume (ft^3 acre^{-1}) by year for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments. The initial standing volume is shown in year 0; each cutting cycle is 10 years long. Error bars are the 95% confidence interval.

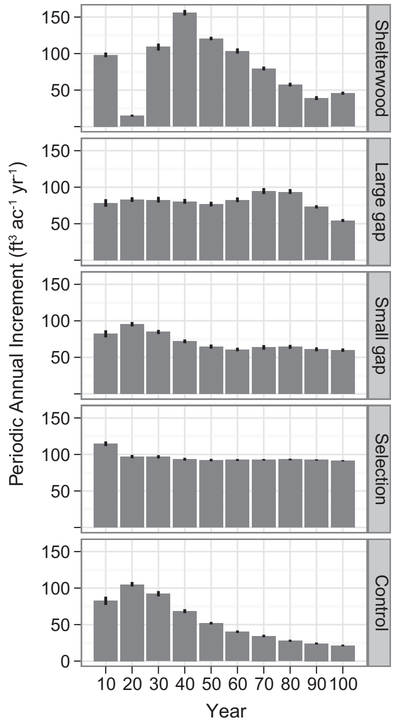

Figure 6. PAI (ft^3 acre^{-1} year^{-1}) by year for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments. PAI for a given year is calculated based on the previous 10 years of growth (i.e., one cutting cycle). Error bars are the 95% confidence interval.

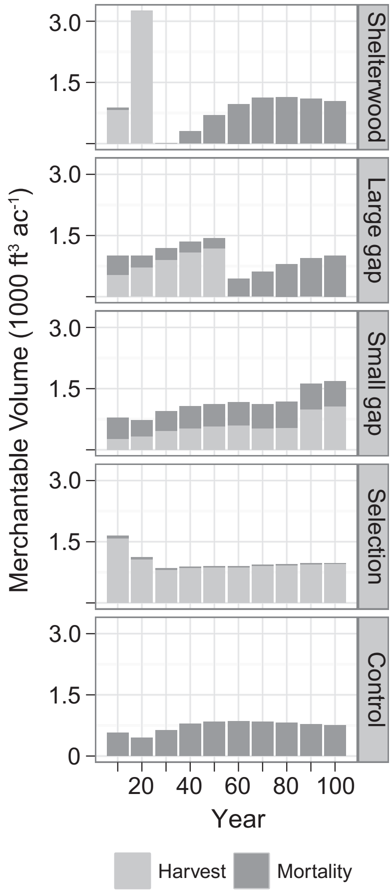

Figure 7. Merchantable volume harvested and lost to mortality (ft^3 acre^{-1}) by year for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments. Volume for a given year includes all harvests and mortality in the previous 10 years (i.e., one cutting cycle); it does not include harvest *in that* year (i.e., the start of the next cutting cycle). Error bars signifying the 95% confidence interval are not visible at this scale.

ure 4A). In the remainder of the stand yet to be harvested, structures resembled the control treatment because high stocking in these areas probably suppressed most regeneration, and shading removed most of the intolerant poles and small sawlog-sized trees. In the second half of the projection, these mature, highly stocked areas were harvested and replaced with young, diverse cohorts of all species groups. Relative to all other treatments systems, the distribution observed under the small-gap system had the greatest range and enabled intolerant species groups to persist across all size classes through the end of the 100-year projection (Figure 4B).

Volume Growth and Increment

Standing merchantable volume (Figure 5), periodic annual increment (PAI; Figure 6), and volume lost to mortality (Figure 7) over time differed markedly among treatments. In the control treatment, standing volume increased over time and product ratios shifted such that greater proportions of total merchantable volume met the 12-in. size threshold for sawtimber. For example, at the end of the rotation, 89% of the mean standing merchantable volume met the criteria for sawtimber. PAI peaked during the 2nd decade at more than 100 ft^3 acre^{-1} year^{-1} and continually declined once maximum site capacity was reached during the 3rd decade (Figure 6) as merchantable volume was lost to mortality at a rate between 71 and 85 ft^3 acre^{-1} year^{-1} (Figure 7).

In the shelterwood treatment, merchantable volume increased throughout the projection after the overstory removal cut (Figure 5). Relative to the control, PAI was higher, and it peaked during the 4th decade at 156 ft^3 acre^{-1} year^{-1} (Figure 6). By the end of the simulation, approximately 80% of the mean standing merchantable volume was sawtimber size (Figure 5), although a significant amount of merchantable volume had been lost to mortality in previous cutting cycles (Figure 7).

Unlike all other treatments, the selection treatment had relatively stable standing merchantable volume (Figure 5) and PAI (Figure 6) and minimal merchantable volume lost to mortality (mean = 3% of total volume; Figure 7). Merchantable standing volume at the end of the projection was lower than all that for other treatments, although 65% of that volume was sawlog-sized. PAI declined slightly throughout the projection, probably from the shift in composition toward slower growing, more shade-tolerant species in this treatment.

Volume development and increment patterns were more complex in both gap-based treatments. For example, in the large-gap treatment, total standing merchantable volume varied between 2,680 and 3,450 ft^3 acre^{-1} during the first half of the projection as the remainder of the prior stand was harvested. Subsequently, standing volume then increased to 6,650 ft^3 acre^{-1} at the end of the projection, 76% of which was sawlog-sized (Figure 5). PAI was also relatively stable in our simulations and varied from 77 to 83 ft^3 acre^{-1} year^{-1} during the first half of the projection and then increased until maximum site capacity was reached in the 7th

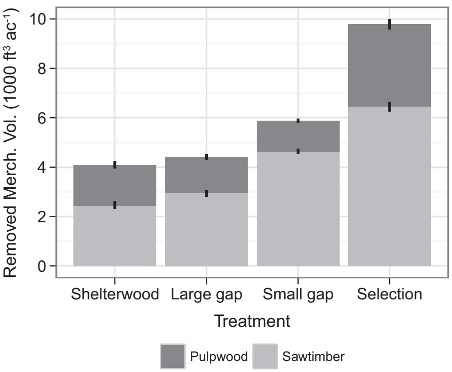

Figure 8. Total merchantable volume harvested (ft^3 acre^{-1}) at the end of the 100-year projection for the control, shelterwood, single-tree selection, large-gap, and small-gap treatments. Error bars are the 95% confidence interval.

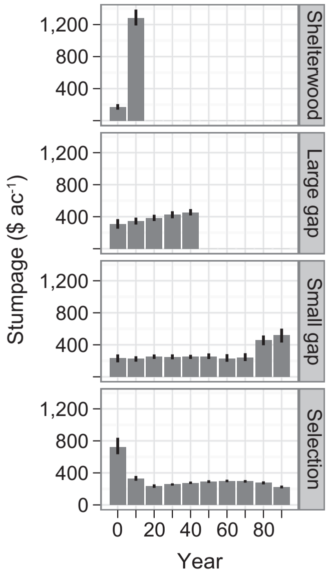

Figure 9. Total discounted stumpage returns from harvesting in a given year (constant 2000 dollars discounted at 4%) for the shelterwood, single-tree selection, large-gap, and small-gap treatments. Error bars are the 95% confidence interval.

and 8th decades (Figure 6). PAI then declined until the end of the projection as volume lost to density-dependent mortality increased after the last harvest (Figure 7). The small-gap treatment differed in that it slowly increased in standing volume until the 8th decade to 5,150 ft^3 acre^{-1} and then declined slightly until the end of the projection. Approximately 72% of the standing volume in the small-gap treatment was sawlog-sized at this time (Figure 5). After three harvests, PAI of the small-gap treatment was less variable than the large-gap treatment but lower than the selection treatment, varying from 60 to 64 ft^3 acre^{-1} year^{-1} during the last half of the projection (Figure 6). For both gap systems, mortality of merchantable material occurred every decade (Figure 7), probably due to previously harvested areas in these stands that were at high stocking and experiencing density-dependent mortality.

Yield and Value

There were significant differences in cumulative pulpwood and sawtimber merchantable volume harvested by the end of the harvest rotation across treatments (Figure 8). Across the four silvicultural systems, the shelterwood system harvested the least combined pulpwood and sawtimber volume (1,640 and 2,440 ft^3 acre^{-1}, respectively), whereas the single-tree selection yielded the highest volume (3,340 and 6,650 ft^3 acre^{-1}, respectively). The gap treatments were intermediate, with the small-gap (1,230 and 4,620 ft^3 acre^{-1}, respectively) yielding significantly more than the large-gap (1,490 and 2,930 ft^3 acre^{-1}, respectively).

At the end of the rotation, standing merchantable volume was inversely related to volume harvested; consequently, the control treatment had the greatest mean standing volume (8,570 ft^3 acre^{-1}), followed by the shelterwood (7,250 ft^3 acre^{-1}), large-gap (6,650 ft^3 acre^{-1}), small-gap (4,290 ft^3 acre^{-1}), and single-tree selection (2,890 ft^3 acre^{-1}) systems (Figure 5). Cumulative merchantable volume lost to mortality was similarly related, but lost volume was largely a function of the area of and duration that the stand experienced strong density-dependent mortality within the projection. The greatest merchantable volume lost to mortality occurred in the control treatment (7,330 ft^3 acre^{-1}), followed by the shelterwood (6,430 ft^3 acre^{-1}), small-gap (5,560 ft^3 acre^{-1}), large-gap (5,370 ft^3 acre^{-1}), and single-tree selection (360 ft^3 acre^{-1}) systems (Figure 7).

At a discount rate of 4%, the selection system had more than double the net present value (NPV) of the shelterwood ($3,200 and $1,450 acre^{-1}, respectively), largely due to the periodic harvest incomes and the relatively high value of the initial selection harvest, when all trees greater than 50 cm were removed according to the specified BDq residual structure (Figure 9). The two gap systems were intermediate, with NPVs of $1,940 and $2,960 acre^{-1} for the large- and small-gap treatments, respectively. Conversely, NPV of the standing timber at the end of the harvest rotation was inversely related to volume harvested. The control treatment had the greatest mean standing stumpage value ($4,340 acre^{-1}), followed by the shelterwood ($2,700 acre^{-1}), large-gap ($2,190 acre^{-1}), small-gap ($1,270 acre^{-1}), and selection ($430 acre^{-1}) systems. Therefore, FVS-NE projections suggested that the large-gap had highest total NPV of the harvested treatments ($4,230 acre^{-1}), followed by the shelterwood ($4,150 acre^{-1}), small-gap ($4,130 acre^{-1}), and, lastly, selection ($3,630 acre^{-1}).

Discussion

Assumptions and Validity

Modeling growth and yield of NDBS systems can be quite difficult for land managers. Here we made many simplifying assumptions that allowed us to isolate the impacts of intrastand structural and compositional variability among these complex systems and conventional, uniformly applied, even- and uneven-aged systems. For example, we assumed that there was a homogeneous increase in growth within all plots within one tree height (i.e., 66 ft) of a harvest gap; in reality, these increases would vary with factors such as gap size, tree species, and shade tolerance (Menard et al. 2002, Coates et al. 2003, Banal et al. 2007). We also assumed, because of some underlying weaknesses of the FVS-NE model (Ray et al. 2009, Arseneault and Saunders 2012), that regeneration occurred subsequent to harvest, when in fact advanced regeneration is ubiquitous in these forests (Brissette 1996). Furthermore, we did not simulate natural disturbance events, other than senescence, within the FVS projections and, therefore, made the assumption that natural disturbance agents affected all stands equally. Given that some disturbance agents are species-specific or size-dependent, this is unlikely. For example, one would expect the selection system, with a higher proportion of spruce and balsam fir, to be much more affected by spruce budworm (*Choristoneura fumiferana* Clem) outbreaks than the two AFERP treatments. Likewise, because ice storms are frequent in the Northeast (Irland 2000) and disproportionately increase mortality for both sapling- and sawtimber-sized trees in comparison with poles (Turcotte et al. 2012), the shelterwood would probably experience greater risk from ice damage over a longer period than the other silvicultural treatments.

Despite our simplifications and a lack

of empirical studies of expanding-gap harvest systems to which our results can directly be compared, we believe the projected patterns of forest development are reasonable estimates of stand dynamics in these forests. For example, during the first 40 years after treatment, gross volume growth was projected to be greater under single-tree selection relative to that for the shelterwood system. Volume growth in all harvest systems was also greater than that for the control, largely because of the higher mortality levels experienced in that treatment. Both results are generally consistent with forest development patterns observed under these systems elsewhere in the PEF (Sendak et al. 2003). Likewise, species composition under the single-tree selection treatments was projected to shift toward shade-tolerant species, which is consistent with many empirical reports of this silvicultural system (Smith and Miller 1987, Crow et al. 2002, Leak and Sendak 2002, Sendak et al. 2003). Although intolerant and moderately shade-tolerant species can persist in frequently disturbed areas within selection stands (Olson and Wagner 2010) or in unmanaged stands (Angers et al. 2005, Saunders and Wagner 2008), ingrowth of these species groups into sapling and pole timber size classes is often lacking (Smith and Miller 1987, Miller 1993), because overstory shading reduces growth and vigor to the extent that they are selected against during selection harvests (Crow et al. 2002).

However, there were a few discrepancies. Species composition in the shelterwood became more heavily dominated by shade-tolerant species than empirical studies in similar stands have shown (Sendak et al. 2003), although many northern hardwoods will regenerate successfully using shelterwood methods (Godman and Tubbs 1973, Crow et al. 2002). Projected cumulative volume yields and mean annual merchantable stand volume production rates in our simulations also were greater than empirical estimates reported in the literature. For example, single-tree selection mean merchantable volume production was projected to be approximately 98 ft^3 $acre^{-1}$ $year^{-1}$ over a 100-year harvest rotation, whereas it varied between approximately 50 and 54 ft^3 $acre^{-1}$ $year^{-1}$ for a variety of selection systems over a 40-year period in Sendak et al. (2003) and was approximately 66 ft^3 $acre^{-1}$ $year^{-1}$ over a 28-year period in Smith and Miller (1987). This discrepancy arises from two sources. First, there are known weaknesses with modeling mortality in many eastern FVS variants, particularly in stands with shade-tolerant species that experience growth stagnation (Arseneault and Saunders 2012). Improving these mortality functions is an active area of research for many of the variants (FVS-Southern [SN]: Radtke et al. 2012; FVS-NE/-Acadian [ACD]: Weiskittel et al. 2012) as more longer-term data become available from Forest Inventory and Analysis plots (Shaw 2012). Second, we simplified volume estimation by assuming that product classes were determined by tree size alone, by ignoring yarding losses of merchantable volume, and by not accounting for loss of productive stand area due to landings and timber extraction networks. These simplifications, in particular, would significantly reduce estimates of volume and yield, making our estimates much more comparable to prior empirical studies.

It is much more difficult, however, to validate the financial results, given the variety of uncertainties inherent in long-term forecasting and the lack economic research on comparable NDBS systems. Several authors have demonstrated that partial harvesting systems, such as selection or irregular shelterwoods, are economically feasible and can earn real rates of return competitive with conventional, even-aged methods (Miller et al. 1995, Howard and Temesgen 1997, Liu et al. 2007), provided they are applied in appropriate conditions and suitable markets for shade-tolerant species exist (Miller 1993). We have no reason to believe, based on the results from our simulations, that the NDBS systems being studied in AFERP would be any different.

Relative Performance of the NDBS Systems

Selection systems have been touted to emulate natural disturbance regimes in much of eastern North America (Bryan 2003). Traditionally applied, selection systems try to mimic creation of individual canopy gaps that form after windthrow, senescence, or other tree-level disturbance agents (Seymour et al. 2002). However, most forests in the Acadian Region are created by a combination of disturbance agents that lead to irregular stand structures, a structure not well emulated by either even-aged or balanced selection systems, but instead irregular shelterwood and selection systems such as AFERP (Raymond et al. 2009). Furthermore, selection systems may homogenize forest structure and composition beyond the patterns present in late-successional or old-growth forests by using strict size-based regulation (Angers et al. 2005, Keeton 2006, Franklin et al. 2007, Bauhus et al. 2009). For example, in this study, a single-tree selection system achieved greater production rates and more sustained yields of merchantable products over time than other naturally regenerated systems, probably because the homogeneous application of the system enabled better redistribution of available growing space to quality trees throughout the stand (Crow et al. 2002, Saunders and Wagner 2008, Bohn et al. 2011).

However, our simulations suggest that expanding-gap harvest systems may be more capable of producing and sustaining greater species diversity across a broader range of tree sizes relative to conventional, uniformly applied, uneven-aged systems (Figure 4). Further, distributing harvests homogeneously throughout the stand, as in the single-tree selection system, rather than within aggregated removals, as in the AFERP systems, resulted in lower cumulative volume losses to mortality (Figure 7) as local competitive pressure on residual trees was alleviated throughout the stand. In practice, merchantable volume lost to mortality would probably be further reduced in these selection systems because frequent harvest entries would presalvage trees of poor health before significant grade reductions occurred (Miller 1993, Goodburn and Lorimer 1998). This suggests that, with strict adherence to a BDq or similar diameter structure, selection systems may be less capable of sustaining certain structural elements associated with late-successional forests such as large defective trees and coarse woody debris (Crow et al. 2002, Angers et al. 2005, Keeton 2006, Kenefic and Nyland 2007).

Size-based stand regulation also requires skilled marking crews and more frequent inventories than would be necessary for systems such as those in the AFERP. Frequent entries and the denser road network provide greater opportunities for invasive species to establish and increased issues with soil erosion in some stands. Harvest products are widely dispersed throughout selection stands, which may result in costlier harvests and greater potential to damage residual structure than either gap-based or even-aged systems (Hassler et al. 2000, Andreassen and Øyen 2002). With skilled logging crews, damage to crop trees and existing regeneration can be minimized in selection systems (Aho et al. 1983, Miller 1993), although gap-based systems concentrate harvest activities in a smaller proportion of the stand and hence lower the *potential* for damage.

This study provides strong evidence that gap-based, NDBS systems are financially competitive with conventional silvicultural approaches in eastern North America. Whereas the AFERP systems could be considered financially suboptimal to selection (Figures 8 and 9), or even shelterwood if more aggressive density control (i.e., thinning) throughout the rotation was used, the criterion of maximizing yields or net present value alone is rarely appropriate when managing for multiple objectives (Klemperer 1996). For example, given that the underlying intent of these NDBS systems is to maintain and preserve biodiversity, greater incidences of mortality could prove beneficial in managing for objectives related to biodiversity and structural complexity, insofar as they pertain to the future availability of coarse woody debris (Crow et al. 2002, Bauhus et al. 2009). Furthermore, the absence of maximum tree size constraints, as in the selection system, combined with long-term retention of trees, notably promoted and sustained large-tree recruitment and a diversity in species composition beyond what was observed in the conventional even- and uneven-aged systems. In fact, the financial competitiveness of these area-based systems may increase over time as a result of their potential to sustain a greater diversity of species groups and tree sizes relative to conventional even- and uneven-aged harvest systems. The relatively high volume of merchantable material that is maintained (Figure 5) could produce a more flexible forest capable of supporting a wider array of harvestable products if market conditions and/or management objectives change in the future. Similarly, the higher species diversity should maintain higher levels of ecosystem services such as carbon storage and wild game production (Gamfeldt et al. 2013).

We recognize that planning and administrative costs may be greater in gap-based, NDBS systems. Further, depending on the equipment used, logging productivity and costs may be negligibly different (Miller et al. 1995) to slightly higher (Andreassen and Øyen 2002, Hartley and Han 2007) than uniformly applied, conventional systems such as clearcutting. However, anecdotally from our experience and those of other foresters in the region who have tried similar approaches (Rick Morrill, pers. comm., Baxter State Park Authority, June 28, 2012), these systems have been favorably received by loggers and have been profitable. More harvest productivity research will be needed to elucidate any differences.

Conclusions

Given the limitations of modeling these complex forests using FVS-NE (Arseneault and Saunders 2012) and the uncertainty inherent in long-term forecasting, our objectives were to simulate these silvicultural systems so that reasonable comparisons of relative performance would be possible. The valuation of these NDBS systems is specific to the initial stand conditions in AFERP and our harvesting, planning horizon, and financial assumptions. Actual returns will probably vary widely based on a variety of factors including differences in harvest and administrative costs among treatments. Consequently, these results are best viewed as relative comparisons among these systems and not as specific estimates of productivity or financial returns. The latter would necessitate more comprehensive and stringent assumptions regarding intrastand variety in growth and regeneration responses, estimates of potential mortality from pathogens and insects, better estimates of costs, and the revenue effects of potential differences in product quality and harvest-induced mortality across treatments.

Nevertheless, our results suggest that NDBS systems will probably be a viable alternative to conventional silvicultural systems as they are capable of generating equal or slightly higher revenues and yields, while meeting a much broader range of structural and compositional objectives than conventional systems. Therefore, these NDBS systems should garner widespread public acceptance by simultaneously maintaining high economic, ecological, and aesthetic values. We suggest that NDBS systems designed to create irregular-aged and spatially variable structures, such as the AFERP treatments, play a much wider role in land management throughout much of eastern North America.

Literature Cited

Aho, P.E., G. Fiddler, and M. Srago. 1983. *Logging damage in thinned young-growth true fir stands in California and recommendations for prevention*. USDA For. Serv., Res. Paper PNW-304, Pacific Northwest Forest and Range Experimental Station, Portland, OR. 8 p.

Andreassen, K., and B.H. Øyen. 2002. Economic consequences of three silvicultural methods in uneven-aged mature coastal spruce forests of central Norway. *Forestry* 75:483–488.

Angers, V.A., C. Messier, M. Beaudet, and A. Leduc. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manage.* 217:275–293.

Arseneault, J.E., and M.R. Saunders. 2012. Incorporating canopy gap-induced growth responses into spatially implicit growth model projections. *Ecol. Model.* 237–238:120-131.

Arseneault, J.E., M.R. Saunders, R.S. Seymour, and R.G. Wagner. 2011. First decadal response to treatment in a disturbance-based silviculture experiment in Maine. *For. Ecol. Manage.* 262:404–412.

Banal, S., D.J. Marceau, and A. Bouchard. 2007. Sapling responses to variations in gap densities and spatial configurations modeled using SORTIE. *Ecol. Model.* 206:41–53.

Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258:525–537.

Bergeron, Y., D. Cyr, C.R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, E. Lauzon, et al. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: Implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Can. J. For. Res.* 36:2737–2744.

Bohn, K.K., R.D. Nyland, and R.D. Yanai. 2011. Comparing selection system and diameter-limit cutting in uneven-aged northern hardwoods using computer simulation. *Can. J. For. Res.* 41:963–973.

Briggs, R.D. 1994. *Site classification field guide*. MAFES Misc. Publ. 724, Univ. of Maine, Orono, ME. 15 p.

Brissette, J.C. 1996. Effects of intensity and frequency of harvesting on abundance, stocking, and composition of natural regeneration in the Acadian forest of eastern North America. *Silva Fenn.* 30:301–314.

Bryan, R.B. 2003. *Long-term impacts of timber harvesting on stand structure in northern hardwood and spruce-fir forests: Implications for biodiversity and timber production.* Maine Audubon, Falmouth, ME. 27 p.

Burns, R.M., and B.H. Honkala (tech. coords.). 1990. *Silvics of North America: Vols. 1 and 2. Conifers and hardwoods*. USDA For. Serv., Agriculture Handbook 654, Washington, DC. 877 p.

Coates, D.K., C.D. Canham, M. Beaudet, D.L. Sachs, and C.M. Messier. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manage.* 186:297–310.

Crookston, N.L., and G.E. Dixon. 2005. The Forest Vegetation Simulator: A review of its structure, content, and applications. *Comput. Electron. Agr.* 49:60–80.

Crookston, N.L., D.L. Gammel, S. Rebain, D. Robinson, and C. Keyser. 2005. *Users guide to the database extension to the Forest Vegetation Simulator,* version 2.0. January 2011 revision. USDA For. Serv., Internal Rep., Forest Management Service Center, Fort Collins, CO. 56 p.

Crow, T.R., D.S. Buckley, E.A. Nauertz, and J.C. Zasada. 2002. Effects of management of the composition and structure of northern hardwood forests in Upper Michigan. *For. Sci.* 48:129–145.

Dixon, G.E., and C.E. Keyser (comps.). 2008. *Northeast (NE) variant overview test version—Forest Vegetation Simulator*. February 2011 revision. USDA For. Serv., Internal Rep., Forest Management Service Center, Fort Collins, CO. 42 p.

Franklin, J.F. 1993. Preserving biodiversity: Species, ecosystems or landscapes? *Ecol. Appl.* 3:202–205.

Franklin, J.F., R.J. Mitchell, and B.J. Palik. 2007. *Natural disturbance and stand development principles for ecological forestry.* USDA For. Serv., Gen. Tech. Rep. NRS-19, Northern Research Station, Newtown Square, PA. 44 p.

Fraver, S., and A.S. White. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16:597–610.

Gamfeldt, L., T. Snall, R. Bagchi, M. Jonsson, L. Gustafsson, P. Kjellander, M.C. Ruiz-Jaen, et al. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun*. 4:1340. 8 p. doi: 10.1038/ncomms2328.

Godman, R.M., and C.H. Tubbs. 1973. *Establishing even-age northern hardwood regeneration by the shelterwood method—A preliminary guide.* USDA For. Serv., Res. Pap. NC-99, North Central Forest Experiment Station, St. Paul, MN.12 p.

Goodburn, J.M., and C.G. Lorimer. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Can. J. For. Res.* 28:427–438.

Hartley, D.S., and H.S. Han. 2007. Effects of alternative silvicultural treatments on cable harvesting productivity and cost in western Washington. *West. J. Appl. For.* 22:204-212.

Hassler, C.C., S.T. Grushecky, and C.B. LeDoux. 2000. The effects of group selection harvest size on logging productivity. *North. J. Appl. For.* 17:51–56.

Howard, A.F., and H. Temesgen. 1997. Potential financial returns from alternative silvicultural prescriptions in second-growth stands of coastal British Columbia. *Can. J. For. Res.* 27: 1483–1495.

Hunter, M.L., G.L. Jacobson, and T. Webb. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conserv. Biol.* 2:375–385.

Irland, L.C. 2000. Ice storm and forest impacts. *Sci. Total Environ.* 262:231–242.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manage.* 235:129–142.

Kenefic, L.S., and R.D. Nyland. 2007. Cavity trees, snags, and selection cutting: A northern hardwood case study. *North. J. Appl. For.* 24: 192–196.

Klemperer, W.D. 1996. *Forest resource economics and finance.* McGraw-Hill, New York. 551 p.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9:1179–1188.

Larsen, J.B., and A.B. Nielsen. 2007. Nature-based forest management—Where are we going? Elaborating forest development types in and with practice. *For. Ecol. Manage.* 238: 107–117.

Leak, W.B. 1964. An expression of diameter distribution of unbalanced uneven-aged stands and forests. *For. Sci*. 10:39–50.

Leak, W.B. 2003. Best density and structure for uneven-aged northern hardwood management in New England. *North. J. Appl. For.* 20: 43–44.

Leak, W.B., and P.E. Sendak. 2002. Changes in species, grade, and structure over 48 years in a managed New England northern hardwood stand. *North. J. Appl. For.* 19:25–27.

Liu, C., J.C. Ruel, and S.Y. Zhang. 2007. Immediate impacts of partial cutting strategies on stand characteristics and value. *For. Ecol. Manage.* 250:148–155.

Long, J.N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. *For. Ecol. Manage.* 257: 1868–1873.

Maine Forest Service. 1996–2009. *Stumpage price reports*. Available online at www.maine.gov/doc/mfs/pubs/annpubs.htm#stump; last accessed Dec. 8, 2012.

Menard, A., P. Dube, A. Bouchard, and D.J. Marceau. 2002. Release episodes at the periphery of gaps: A modeling assessment of gap impact extent. *Can. J. For. Res.* 32:1651-1661.

Miller, G.W. 1993. *Financial aspects of partial cutting practices in central Appalachian hardwoods*. USDA For. Serv., Res. Paper NE-673, Northeastern Forest Experiment Station, Radnor, PA. 16 p.

Miller, G.W., T.M. Schuler, and H.C. Smith. 1995. *Method for applying group selection in central Appalachian hardwoods*. USDA For. Serv., Res. Paper NE-696, Northeastern Forest Experiment Station, Radnor, PA. 11 p.

North, M.P., and W.S. Keeton. 2008. Emulating natural disturbance regimes: An emerging approach for sustainable forest management. P. 341–372 in *Patterns and processes in forest landscapes—Multiple use and sustainable management*, Lafortezza, R., J. Chen, G. Sanesi, and T.R. Crow (eds.). Springer, Houten, The Netherlands.

Olson, M.G., and R.G. Wagner. 2010. Long-term composition dynamics of Acadian mixedwood stands under different silvicultural regimes. *Can. J. For. Res.* 40:1993–2002.

Puettmann, K.J., A.W. D'Amato, U. Kohnie, and J. Bauhus. 2009. Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings. *Can. J. For. Res.* 39:2437–2449.

Puettmann, K.J., K.D. Coates, and C. Messier. 2009. *A critique of silviculture: Managing for complexity*. Island Press, Washington, DC. 190 p.

R Development Core Team. 2011. *R: A language and environment for statistical computing*, version 2.11.1. R Foundation for Statistical Computing, Vienna, Austria. Available online at www.R-project.org; last accessed Dec. 8, 2012.

Radtke, P.J., N.D. Herring, D.L. Loftis, and C.H. Keyser. 2012. Evaluating Forest Vegetation Simulator predictions for southern Appalachian upland hardwoods with a modified mortality model. *South. J. Appl. For.* 36: 61–70.

Ray, D.G., M.R. Saunders, and R.S. Seymour. 2009. Recent changes to the Northeast variant of the Forest Vegetation Simulator and some basic strategies for improving model outputs. *North. J. Appl. For.* 26:31–34.

Raymond, P., S. Bedard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *J. For.* 107:405–413.

Saunders, M.R., and R.G. Wagner. 2008. Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. *Can. J. For. Res.* 38:498–517.

Saunders, M.R., R.S. Seymour, and R.G. Wagner. 2013. The Acadian Forest Ecosystem Research Program: An example of disturbance-based silviculture in the Northeast. In *The Penobscot Experimental Forest: 60 years of research, education and demonstration*, Kenefic, L.S., and J.C. Brissette (comps.). USDA For. Serv., Gen. Tech. Rep. In press.

Sendak, P.E., J.C. Brissette, and R.M. Frank. 2003. Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. *Can. J. For. Res.* 33:2116–2128.

Seymour, R.S. 2005. Integrating disturbance parameters into conventional silvicultural systems: Experience from the Acadian forest of northeastern North America. P. 41–48 in *Balancing ecosystem values: Innovative experiments for sustainable forestry*, Peterson, C.E., and D.A. Maguire (eds.). USDA For. Serv., Gen. Tech. Rep. PNW-635, Pacific Northwest Research Station, Portland, OR.

Seymour, R.S., J. Guldin, D. Marshall, and B. Palik. 2006. Large-scale, long-term silvicultural experiments in the United States: Historical overview and contemporary examples. *Allg. For. Jagdztg.* 177:104–112.

Seymour, R.S., and M.L. Hunter Jr. 1999. Principles of ecological forestry. P. 22–61 in *Maintaining biodiversity in forest ecosystems*, Hunter, M.L. Jr. (ed.). Cambridge University Press, Cambridge, UK.

Seymour, R.S., A.S. White, and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155:357–367.

Shaw, J.D. 2012. A framework for validation and model improvement using Forest Inventory Analysis data. In *Fourth Forest Vegetation Simulator (FVS) conference* (program), April 17–19, Fort Collins, CO. Available online at www.fs.fed.us/fmsc/fvs/fvs_conference.shtml; last accessed Mar. 17, 2013.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. *For. Ecol. Manage.* 115:101–111.

Smith, H.C., and G.W. Miller. 1987. Managing Appalachian hardwood stands using four regeneration practices—34-year results. *North. J. Appl. For.* 4:180–185.

Stokes, V., G. Kerr, and D. Ireland. 2009. Seedling height and the impact of harvesting operations on advance regeneration of conifer species in upland Britain. *Forestry* 82:185–198.

Turcotte, R.M., T.R. Elliott, M.A. Fajvan, Y.-L. Park, D.A. Snider, and P.C. Tobin. 2012. Effects of ice storm damage on hardwood survival and growth in Ohio. *North. J. Appl. For.* 29:53–59.

Wagner, J.E., and P.E. Sendak. 2005. The annual increase of Northeastern regional timber stumpage prices: 1961 to 2002. *For. Prod. J.* 55:36–45.

Weiskittel, A., J. Kershaw, and M. Russell. 2012. Development and evaluation of the Acadian variant of the Forest Vegetation Simulator. In *The Fourth Forest Vegetation Simulator Conference* (program), April 17–19, Fort Collins, CO. Available online at www.fs.fed.us/fmsc/fvs/fvs_conference.shtml; last accessed Mar. 17, 2013.

Wickham, H. 2007. Reshaping data with the reshape package. *J. Stat. Softw.* 21:1–20.

Wickham, H. 2009. *ggplot2: Elegant graphics for data analysis*. Springer, New York. 224 p.

Wickham, H. 2011. *plyr: Tools for splitting, applying and combining data,* version 1.4. Available online at cran.r-project.org/web/packages/plyr/index.html; last accessed Mar. 17, 2013.

Zenner, E.K., Y.L. Dickinson, and J.E. Peck. 2013. Recovery of forest structure and composition to harvesting in different strata of mixed even-aged central Appalachian hardwoods. *Ann. For. Sci.* 70:151–159.