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ScienceDirect
Forest Ecology and Management 235 (2006) 129–142
Forest Ecology and Management
www.elsevier.com/locate/foreco

Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests

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Received 19 March 2006; received in revised form 2 August 2006; accepted 2 August 2006

Abstract

In the northern hardwood region of North America managing for late-successional forest habitats and functions is an important element of ecosystem management. This study tests the hypothesis that uneven-aged practices can be modified to accelerate rates of late-successional forest development. An approach, termed ''structural complexity enhancement'' (SCE), is compared against conventional uneven-aged systems modified to increase post-harvest structural retention. Experimental treatments, including controls, were applied to 2 ha units and replicated at two multi-aged northern hardwood forests in Vermont, USA.

Structural objectives include vertically differentiated canopies, elevated large snag and downed log densities, variable horizontal density (including small gaps), and re-allocation of basal area to larger diameter classes. The latter objective is achieved, in part, by cutting to a rotated sigmoid diameter distribution. This is generated from a basal area (34 m^2 ha^{-1}) and tree size (90 cm dbh) indicative of old-growth structure. Forest structure data have been collected over 2 years pre-treatment and 3 years post-treatment. Fifty-year simulations of stand development were run in NE-TWIGS and FVS comparing treatment and no treatment scenarios. Simulations also tested the sensitivity of large tree development to prescription parameters. Leaf area index retention was spatially variable but significantly ($P < 0.001$) greater under SCE (91%) compared to conventional treatments (75%). Post-harvest aboveground biomass ($P = 0.041$), total basal area ($P = 0.010$), and stem density ($P = 0.025$) were significantly different among treatments, with SCE generally retaining more structure than conventional treatments. SCE increased coarse woody debris volumes by 140%; there was a 30% increase under conventional treatments. SCE successfully achieved the rotated sigmoid diameter distributions, and sustained these 50 years into the future, resulting in reallocated basal area. Cumulative basal area increments are projected to increase by 3.7 and 5.0 m^2 ha^{-1} compared to no treatment scenarios for SCE and conventional treatments, respectively. Basal areas will be significantly ($P = 0.025$) greater after 50 years in SCE units due to higher residual basal areas. Conventional treatments are projected to produce 10 fewer large trees per hectare (>50 cm dbh) than would have developed without treatment, whereas SCE is likely to recruit five more large trees per hectare than the no treatment scenario. Large tree recruitment rates were related primarily to the form of residual diameter distributions ($P = 0.006$) and, possibly, to maximum diameter limits. Late-successional characteristics in northern-hardwood systems can be promoted through a variety of modified uneven-aged silvicultural approaches based on the results.

Keywords: Old-growth; Late-successional; Northern-hardwoods; Uneven-aged silviculture; Forest structure and development; Sustainable forestry

1. Introduction

Sustainable forestry practices across managed forest landscapes contribute to the maintenance of biological diversity and ecosystem functioning (Lindenmayer and Franklin, 2002). The challenge lies in determining the mix of management approaches – including type, timing, intensity, and spatial configuration of silvicultural treatments – necessary to achieve sustainability objectives. One possibility is to focus on the architecture of individual forest stands and their spatial arrangement, with consideration given to the aggregate representation of multiple structural (or habitat) conditions at landscape scales. Patch and successional dynamics associated with natural disturbance regimes provide a useful guide for designing this type of structure (Keeton, 2005) or disturbance-based (Mitchell et al., 2002; Seymour et al., 2002) approach. A recommendation is to manage for currently under-represented structures and age classes on some portion of the landscape (Franklin et al., 2002; Keeton, 2005). In the northern hardwood region of the eastern U.S. and Canada, this would include managing for late-successional structure, which is vastly under-represented relative to pre-European settlement conditions

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doi:10.1016/j.foreco.2006.08.005

(Mladenoff and Pastor, 1993; Cogbill, 2000; Lorimer, 2001; Lorimer and White, 2003). In this study variants of uneven-aged silviculture are explored as a means for promoting late-successional/old-growth structural characteristics in northern hardwood-conifer forests. Alternate approaches for accelerating stand development rates are tested.

1.1. Why manage for old-growth structure in northern hardwood forests?

In the northeastern United States there has been considerable debate regarding differing proposals for adjusting age class distributions on forested landscapes. Forest structure and composition in pre-European settlement landscapes were spatially and temporally variable due to geophysical heterogeneity, climate variability, and disturbances, both natural and anthropogenic (Foster and Aber, 2004). However, the relative availability of stand structures has changed as a result of 19th century forest clearing, agricultural land-use, land abandonment, subsequent reforestation, and 20th century forest management. In northern hardwood forests, age-class distributions have shifted from a predominance, pre-settlement, of old-growth forests to a present dominance of second growth, 40–80-year old forests (Lorimer and Frelich, 1994; Lorimer, 2001; Lorimer and White, 2003). Lorimer and White (2003) estimate that 70–89% of pre-settlement northern hardwood forests were old-growth (uneven-aged, >150 years old), whereas young forests (up to 15 years old) comprised 1–3% of those systems. Definitions of old-growth northern hardwood-conifer forests generally use a combination of age (ca. >150 years), human disturbance history, and structure (Hunter, 1989; Dunwiddie et al., 1996; Hunter and White, 1997). Today forests with these characteristics occupy less than 0.5% of the region (Davis, 1996). Riparian functions (Keeton et al., in review), habitat values (see reviews in Tyrrell and Crow, 1994b; Keddy and Drummond, 1996; McGee et al., 1999), and carbon sequestration (Harmon et al., 1990; Krankina and Harmon, 1994; Turner and Koerper, 1995; Strong, 1997; Houghton et al., 1999) associated with late-successional forests have declined as a result.

With natural reforestation and successional development on old-fields, the availability of grassland and early-successional forested habitats declined significantly during the 20th century. Early-successional habitats are now re-approaching (Lorimer, 2001) or, in some locales, possibly even below (DeGaaf and Yamasaki, 2003) pre-settlement levels. Patch-cut or large-group selection harvesting methods are sometimes advocated to enhance the relative abundance of early-successional habitats (Hunter et al., 2001; King et al., 2001; Litvaitis, 2001; DeGaaf and Yamasaki, 2003). Similarly, researchers have suggested that a portion of the landscape could be managed for late-successional and old-growth forests (Singer and Lorimer, 1997; Lorimer and White, 2003; Keeton, 2005). These proposals need not be mutually exclusive, but do require differing silvicultural approaches where active manipulations are desired. New or modified approaches are needed to manage for late-stand development characteristics, however, because conventional even- and uneven-aged systems provide only limited availability of these structures (Gore and Patterson, 1985; McGee et al., 1999; Crow et al., 2002; Angers et al., 2005).

1.2. Structural complexity enhancement

Despite theoretical discussions (e.g. Lorimer and Frelich, 1994; Trombulak, 1996), old-growth forest restoration techniques have not been experimentally field-tested in northern hardwood forests. Thus, it remains uncertain whether silvicultural practices can accelerate rates and processes of late-successional forest stand development (Franklin et al., 2002), promote desired structural characteristics, and enhance associated ecosystem functions more than conventional systems. A related, though untested, hypothesis is that active restoration offers advantages over passive (or non-manipulative) restoration as means for recovering old-growth forest conditions. For restorative silviculture to have more than only narrow appeal, it must also provide opportunities for low-intensity timber harvest. This study tests the ability of a variant of uneven-aged systems, termed structural complexity enhancement (SCE), to achieve these objectives (Table 1). In this study, SCE is compared against conventional uneven-aged systems (Leak et al., 1987) modified

Table 1
Structural objectives and the corresponding silvicultural techniques used to promote those attributes in structural complexity enhancement

Structural objective	Silvicultural technique
Vertically differentiated canopy	• Single tree selection using a target diameter distribution • Release advanced regeneration • Regenerate new cohort
Elevated large snag densities Elevated downed woody debris densities and volume	• Girdling of selected medium to large sized, low vigor trees • Felling and leaving trees, or • Pulling over and leaving trees
Variable horizontal density, including small canopy gaps	• Harvest trees clustered around "release trees" • Variable density marking
Re-allocation of basal area to larger diameter classes	• Rotated sigmoid diameter distribution • High target basal area • Maximum target tree size set at 90 cm dbh
Accelerated growth in largest trees	• Full and partial crown release of largest, healthiest trees

to increase post-harvest structural retention and to represent best management practices. Group-selection treatments are modified to approximate the average canopy opening size associated with fine-scale natural disturbance events in New England, based on the findings of Seymour et al. (2002).Research over almost three decades has described the characteristics and dynamics of old-growth northern hardwood and mixed northern hardwood-conifer forests across a range of geographic settings and disturbance histories (e.g. Whitney, 1984; Gore and Patterson, 1985; Foster, 1988; Hunter, 1989; Woods and Cogbill, 1994; Tyrrell and Crow, 1994a,b; Dahir and Lorimer, 1996; Hunter and White, 1997; Goodburn and Lorimer, 1998, 1999; McGee et al., 1999; Hale et al., 1999; McLachlan et al., 2000; Ziegler, 2000; Crow et al., 2002; Angers et al., 2005; Keeton et al., in review). Structural objectives for SCE are derived from this body of research. They include vertically differentiated canopies, elevated large snag and downed log volumes and densities, variable horizontal density (including canopy gaps), and re-allocation of basal area to larger diameter classes (Table 1). The latter objective is achieved, in part, using an unconventional guiding curve based on a rotated sigmoid target diameter distribution.

Rotated sigmoid diameter distributions have been widely discussed in the theoretical literature (e.g. Goff and West, 1975; Nyland, 1998; O'Hara, 1998; Leak, 2002) but their silvicultural utility has not been field tested. Sigmoidal form is one of several possible distributions in eastern old-growth forests (Meyer and Stevenson, 1943; Lorimer, 1980; Goodburn and Lorimer, 1999). These vary with disturbance history, species composition, and competitive dynamics (Goff and West, 1975; Leak, 1996, 2002). It is uncertain whether sigmoidal diameter distributions can be sustained silviculturally versus reverting to a negative exponential form. The latter would be expected if density-dependent mortality (or self-thinning) proves constant across all size classes (O'Hara, 1998). This study tests the hypothesis that the rotated sigmoid distribution offers advantages for late-successional structural management because it allocates more growing space and basal area to larger size classes. I predict this distribution is sustainable in terms of recruitment, growth, and mortality. If so, it would support O'Hara's (1998, 2001) assertion that there are naturally occurring alternatives to the negative exponential or "reverse-J" curve used in uneven-aged silviculture.

2. Methods

2.1. Experimental design

The study was conducted at the Mount Mansfield State Forest (MMSF, 44°30′23.03″N; 72°50′11.24″W) and at the University of Vermont's Jericho Research Forest (JRF, 44°26′43.70″N; 72°59′44.15″W). The former is located on the western slopes and the latter resides in the foothills of the northern Green Mountain Range in Vermont, USA. Elevations range from 470 to 660 m (MMSF) and from 200 to 250 m (JRF) above sea level. Soils are primarily Peru extremely stony loams (MMSF) and Adams and Windsor loamy sands or sandy loams (JRF). Study areas are northern hardwood-conifer forests; dominant canopy trees are approximately 70–100 years old. Tree demography is distinctly multi-aged due to regeneration resulting from four to six documented management entries since the early 20th century. Multi-aged structure was confirmed by extensive pre-treatment tree coring across size classes. Dominant overstory species include *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Betula alleghaniensis* (yellow birch). *Tsuga canadensis* (eastern hemlock) is also co-dominant at JRF. There are minor components of *Picea rubens* (red spruce) at MMSF and *Acer rubrum* (red maple) and *Quercus rubra* (red oak) at JRF.

There were three experimental manipulations randomly assigned to treatment units. Treatment units were 2 ha in size and separated by 50 m (minimum) unlogged buffers to minimize cross contamination of treatment effects. The first two manipulations were conventional uneven-aged systems (single-tree selection and group-selection) modified to increase post-harvest structural retention. The modifications were based on a target residual basal area of 18.4 $m^2 ha^{-1}$, maximum diameter of 60 cm, and q-factor (the ratio of the number of trees in each successively larger size class) of 1.3. The group selection treatment was based on the same BDq prescription but applied through spatially aggregated harvesting. Individual groups were placed to: (a) be well-distributed, (b) emcompass the range of tree diameters needed to achieve the prescription, and (c) release advanced regeneration. Group-selection cutting patches averaged approximately 0.05 ha in size which resulted in eight to nine groups per treatment unit. Slash and unmerchantable upper tree boles were retained by the conventional treatments, but there were no additional requirements for coarse woody debris (CWD) retention.

The third treatment was SCE. The guiding curve, based on a rotated sigmoid target diameter distribution, was applied as a non-constant q-factor: 2.0 in the smallest sizes classes, 1.1 for medium-sized trees, and 1.3 in the largest size classes. The guiding curve was also derived from a target basal area (34 $m^2 ha^{-1}$) and maximum diameter at breast height (90 cm) indicative of old-growth structure. As a target, these parameters define the form of the desired future diameter distribution. Superimposing the target on pre-harvest diameter distributions results in cutting to a residual basal area below both the target and pre-harvest basal area. This is because target large tree classes are unoccupied (i.e. pre- and immediately post-harvest), pending future large tree recruitment. However, the prescription also resulted in retention of all trees >60 cm dbh. Full (three- or four-sided) and partial (two-sided) crown release were employed to accelerate growth in larger trees. To generate site-appropriate CWD enhancement prescriptions, the differences between literature-derived targets and pre-harvest volumes and densities were determined by unit. Snags were created by girdling diseased, dying, or poorly formed trees. Pre-treatment densities of low vigor trees were sufficient such that girdling of healthy trees was not necessary to achieve snag prescriptions. On one SCE unit at each of the two study areas, downed logs were created by pulling (skidder and cable) or pushing (mechanized tree shear) trees over, rather than felling, to create pits and exposed root wads. Natural tip-ups were observed at these sites and deemed likely to occur due to shallow bedrock and/or moderately to very mesic soils.

Each of the first two treatments (uneven-aged) was replicated twice at MMSF; the third (SCE) was replicated four times, twice at each of the two study areas. Two un-manipulated control units were located at each study area. Experimental manipulations (i.e. logging) were conducted on frozen ground in winter (January–February) of 2003. All treatments included retention of American beech exhibiting resistance to beech bark disease (*Nectria coccinea*). Scattered mature red spruce were retained as seed trees to encourage recolonization where this species was historically more abundant.

2.2. Data collection

Each treatment unit contains five, randomly placed, 0.1 ha permanent sampling plots. These are positioned at least 15 m inside of unit boundaries, and collectively represent 25% of each unit's area. Within each plot, all live and dead trees >5 cm dbh and >1.37 m tall were permanently tagged, measured, and recorded by species, diameter, height, and vigor/decay stage (1–7). Tree heights were measured using an Impulse 200 laser range finder. Canopy closure was measured with a spherical densitometer at 13 systematically placed points nested within each overstory plot (n = 65 per unit). Plot and tree positions were geo-referenced using a Trimble Pro XRS Global Positioning System. We also used the GPS to map the perimeter of group selection cutting patches. Downed log (logs > 10 cm diameter) volume by decay class (1–5) was estimated using a line-intercept method (two 31.62 m transects per plot) following Shivers and Borders (1996). Log densities were inventoried across 0.1 ha plots. Snag and downed log decay classes followed Sollins et al. (1987). Leaf area index (LAI) at ground level was measured at five points in each plot (n = 25 per unit) using a Li-Cor 2000 Plant Canopy Analyzer. LAI values were post-processed to calibrate "below canopy" measurements against ambient "above canopy" light measurements taken by a remotely placed Li-Cor meter. Tip-up mounds were inventoried across each unit and measured in three dimensions. Two dominant canopy trees per plot were cored at breast height to allow subsequent laboratory determination of tree age. Two years of pre-treatment and 3 years of post-treatment data collection have been completed. Two sample plots (one SCE unit and one single-tree selection unit) escaped treatment due to inoperable or wet terrain. Data from these plots were not included in analyses of post-treatment data.

During treatment implementation, harvested logs were sorted by product grade or type and treatment unit at the landing. Logs were then transported and tracked independently by unit through to scaling at the processing mill. In this way harvest volumes (based on mill receipts rather than inventory data) could be determined by treatment. Volumes reported here are based on a conversion factor of 4.53 m^3 per 1000 board feet.

2.3. Data analysis

Pre- and post-harvest sample data were input into the Northeast Decision Model (NED-2) (Twery et al., 2005), which was used to generate a suite of stand structure metrics. These included aboveground biomass estimates based on species-specific allometric equations developed by Jenkins et al. (2003). Structural metrics were compared pre- to post-harvest and among treatments using a before/after/control/impact design (Krebs, 1999). Tukey-tests were used for the former while analysis of variance and post hoc Bonferroni (CWD data) or least significant difference (LSD, overstory data) multiple comparisons were used for the latter. Homogeneity of variance was tested using F-tests for both pre- and post-harvest data. "Site" was not modeled as a random effect due to low sample size and incomplete replication of treatments across sites. The error term in one-way ANOVAs was thus mean square error. Multiple comparisons were used to validate the assumption of consistency in structural parameters among similarly treated units, including controls, at different sites. In addition, spatial autocorrelation tests (Ripley, 1981) using the Moran coefficient were performed on key response variables. Response data were sorted by treatment and made spatially explicit using geo-referenced plot positions. Spatial autocorrelation results were cross-checked against empirical variograms produced using S-Plus software. Pre- to post-harvest shifts in downed woody debris decay class distributions were assessed using the Kolmogorov–Smirnov two-sample goodness of fit test.

A focused assessment of diameter distribution (5-cm diameter classes) responses was conducted to determine whether SCE successfully shifted diameter distributions, immediately post-harvest, towards the target rotated sigmoid form. Pre- and post-harvest and target distributions were log transformed to enhance sigmoidal tendencies (Leak, 2002). Residual distributions were smoothed using a Friedman smoothing run in S-Plus software. Differences between transformed residual and target cumulative frequency distributions were assessed using Kolmogorov–Smirnov two-sample goodness of fit tests. Residual distributions were created using real (sample) data for smaller diameter classes (<70 cm dbh) and hypothetical (e.g. future potential) values for larger diameter classes (>70 cm dbh). The latter borrowed values from the target distribution. Statistical tests evaluated whether residual distributions achieved that portion of the target distribution possible given the pre-harvest structure.

NED-2 output was used for simulation modeling of stand development using two models: the northeastern U.S. variant (NE-FVS; Bush, 1995) of the USDA Forest Service's Forest Vegetation Simulator (Dixon, 2003) and NE-TWIGS (Hilt and Teck, 1989). The NE-FVS modeling structure is based on NE-TWIGS, which is an individual tree-based, distance-independent stand growth simulator. The models are empirical, with coefficients fitted from repeated measurements in permanent sampling plots encompassing more than 90,000 trees (Bankowski et al., 1996). In validation tests, NE-TWIGS has proven somewhat more reliable at estimating growth in uneven-aged stands compared to even-aged stands (Bankowski et al., 1996). Mortality and large-tree growth functions operate slightly differently in NE-FVS and calculations are made every 10 years, rather on the annual time step employed in NE-TWIGS. Site $index_{50}$ (a required input parameter) was held constant and set to 19.8 m for sugar maple, representing a moderately productive site.

Fifty-year projections of stand development were run for each treatment unit, including controls. To compare relative restorative potential, only stand development resulting from initial treatment (rather than periodic re-cuttings) was modeled (see Section 4.3). For manipulated units, both no treatment (based on pre-harvest sample data) and treatment (based on post-harvest sample data) scenarios were simulated. Mean projected diameter distributions by treatment were evaluated to determine whether either rotated sigmoid (SCE) or negative exponential (conventional uneven-aged) were sustained over time. Projected basal area distributions were generated to determine the corresponding effect on basal area re-allocation. To evaluate projected growth responses, I calculated cumulative basal area increment (CBAI) for each simulation run at 5-year intervals. To normalize treatment scenarios against site/unit-specific rates of stand development that could be expected without treatment, I calculated differences in CBAI between "no-treatment" and "treatment" scenarios at each time step. The Kolmogorov–Smirnov two-sample goodness of fit test was used to test for differences between treatment groups along mean CBAI time series. The log-likelihood ratio goodness of fit test (*G* test) was used to examine total CBAI developed after 50 years; response ratios (treatment versus no treatment) were compared against a null ratio (no treatment effect). Simulation modeling also generated predictions regarding the number of large trees (two classes: >50 and >60 cm dbh) that might develop after 50 years.

Additional simulations were run to determine the sensitivity of projected large tree densities and basal area allocations to prescriptive diameter distributions and maximum diameter limits. These simulated stand development for each of the four SCE units when cut to: (1) a negative exponential (*q*-factor = 1.3) distribution with no maximum diameter limit (i.e. set to 90 cm to generate the distribution), (2) a negative exponential distribution with a maximum diameter of 60 cm, and (3) a rotated sigmoid distribution with a maximum diameter of 60 cm. When combined with the actual SCE treatment (rotated sigmoid, no maximum diameter limit), this resulted in a factorial design with two levels of each independent variable. Simulated cuts were conducted by deleting (random selection by tree tag #) or adding (random selection of harvested trees by tag #) the number of trees required (by diameter class) to change post-harvest diameter distributions to the desired form. Additions and deletions were evenly distributed across plots. Where pre-harvest distributions were in deficit for particular size classes, as with actual treatment, post-harvest densities were not modified. Thus, the sensitivity analysis evaluated alternate post-harvest distributions that could be created given real pre-treatment structure. Residual basal area was held constant. Simulation results were evaluated using two-way Analysis of Variance.

Single-tree selection and group selection treatments were classified as one group ("conventional uneven-aged") for analyses of simulation output (e.g. calculations of mean projections by treatment) and other statistical tests. This was appropriate because: (1) there were no significant differences among uneven-aged units in residual structure when data were aggregated to the unit scale; and (2) quantitative prescriptions were the same for both, the only difference being dispersed versus aggregated harvesting. This difference was not relevant since neither NED-2 output nor the simulations were spatially explicit. Spatial attributes of group selection cutting patches and correspondence with sampling plots were analyzed in a geographic information system.

3. Results

3.1. Pre-harvest structure

Pre-treatment structure was not significantly different ($\alpha = 0.05$) among treatment units based on ANOVA results. This held for basal area, aboveground biomass, stem density, and all other variables tested (Table 2). Variance in structure among units assigned to the same treatment was not statistically significant ($\alpha = 0.05$). These results suggest there is a statistically valid basis for comparisons of both pre- to post-harvest changes and with respect to differences in residual structure among treatment units.

3.2. Timber harvest volume

Timber harvest volumes varied by treatment and unit. Single-tree selection averaged 34.7 (minimum = 30.5, maximum = 39.0) $m^3\,ha^{-1}$ in volume harvested. The average volume harvested from group selection units was 20.0 (minimum = 19.9, maximum = 20.2) $m^3\,ha^{-1}$, and averaged

Table 2
Pre- to post-treatment changes in response data for key structural response variables

	Controls		SCE		Conventional	
	Mean	S.E.[a]	Mean	S.E.[a]	Mean	S.E.[a]
Aboveground biomass[b] (kg ha^{-1})						
Pre-harvest	10026.2	1016.1	11313.0	985.4	11163.6	570.8
Post-harvest	10165.4	1087.1	8646.3	808.7	6398.1	691.7
Percent change	1.4		−23.6		−42.7	
Basal area[b] ($m^2\,ha^{-1}$)						
Pre-harvest	31.4	2.0	35.6	3.2	32.2	1.0
Post-harvest	31.4	1.8	26.5	3.2	18.6	1.6
Percent change	0.2		−25.6		−42.3	
Canopy cover (%)						
Pre-harvest	92	4	95	2	96	2
Post-harvest	92	4	77	3	69	2
Percent change	0		−19		−28	
Stem density[b] (trees ha^{-1})						
Pre-harvest	982.0	98.7	1044.0	4.5	958.5	107.0
Post-harvest	934.5	84.6	750.0	41.2	564.1	95.6
Percent change	−4.8		−28.2		−41.1	
Downed log volume ($m^3\,ha^{-1}$)						
Pre-harvest	42.0	5.3	41.2	7.7	38.2	3.1
Post-harvest	43.1	4.2	91.6	11.4	49.0	2.2
Percent change	4.0		140.0		30.0	

Means and errors are assessed among treatment units ($n = 4$).
[a] ±1S.E. of the mean.
[b] Live and dead trees >5 cm dbh.

16.4 (minimum = 11.6, maximum = 20.7) $m^3\ ha^{-1}$in SCE units. Variation among units sharing similar treatment was due, primarily, to differences in timber quality (e.g. stem defect and form); this determined allocation to sawlog and veneer grade (i.e. board foot) production versus cordwood (i.e. firewood) production. Harvest volumes for SCE do not include trees allocated to CWD, which were included in the total number of stems cut to achieve the target diameter distribution. SCE produced 53% of the average saw/veneer log volume harvested by conventional uneven-aged treatments.

Normalizing the data to reflect differences in pre-treatment (or available) volume yields a slightly different perspective. In SCE units 19% of the pre-harvest merchantable volume (85.8 $m^3\ ha^{-1}$) was removed on average. Considering pre-harvest merchantable volume in single-tree (96.9 $m^3\ ha^{-1}$) and group selection (62.9 $m^3\ ha^{-1}$) units, 36 and 32% of the available volume was cut, respectively. From this perspective, SCE resulted in a harvesting intensity about 57% of that incurred by the conventional treatments.

3.3. Residual stand structure

All of the experimental treatments maintained high levels of residual structure, although there were distinct differences. There were no significant differences ($\alpha = 0.05$) in post-harvest structure between similarly treated units based on F-tests of variance. There was no significant ($\alpha = 0.05$) spatial autocorrelation among plots sorted by treatment. This result was confirmed by empirical variograms. These results suggest that similar treatments produced consistent effects with respect to horizontal structure and spatial heterogeneity. In group selection units on average, 30% of the area in cutting patches coincided with sampling plots and 32% of total plot area was in cut patches. Of the total area in these units 35% was cut on average. Thus cut areas were slightly under-sampled and post-harvest structure was slightly over-estimated for the group selection treatment.

There were significant differences ($P < 0.001$) in treatment effects on leaf area index (LAI). LAI values decreased pre- to post-harvest from 6.27 to 5.05 (single-tree selection) and from 6.49 to 4.79 (group selection). This represented reductions of 20 and 30% respectively. LAI reductions were lowest in SCE units (9%), falling from 5.75 to 5.15. Changes (pre- to post-harvest) in LAI were significantly more spatially variable for both SCE ($P = 0.031$) and group-selection ($P = 0.010$) compared to single-tree selection. Variability in LAI change was not significantly different between SCE and group-selection units ($P = 0.296$). These results reflect the high degree of horizontal structural variability associated with aggregated harvesting in group-selection. In SCE units, smaller (<0.05 ha on average) gaps and canopy openings were created through variable density marking and clustered harvesting around crown-release trees. LAI in control units increased from 5.33 to 5.35 over the course of this study; this change was not statistically significant.

Both SCE and conventional uneven-aged treatments resulted in structural changes pre- to post-harvest (Table 2), but these were statistically significant only for the conventional treatments ($P < 0.001$). Stand structure did not change significantly in control units during the course of this study. Post-harvest aboveground biomass ($P = 0.041$), total basal area ($P = 0.010$), and stem density ($P = 0.025$) were significantly different among treatments based on ANOVA and post hoc comparisons. Conventional treatments resulted in significantly lower aboveground biomass ($P = 0.014$), total basal area ($P = 0.003$), and stem density ($P = 0.008$) in comparison to control units. SCE did not result in statistically significant contrasts with controls. Residual basal area ($P = 0.037$) was significantly greater in SCE units compared to conventional uneven-aged units; post-harvest biomass ($P = 0.104$) and stem density ($P = 0.124$) were not significantly different between these treatments.

There were no statistically significant differences ($P > 0.05$) between residual and target distributions for any of the SCE units based on comparisons of log transformed diameter distributions (Fig. 1). This suggests that SCE was successful at shifting residual diameter distributions towards the target rotated sigmoid form. The smallest trees (5–10 cm dbh) were undercut by all the treatments due to normal operational limitations (see Nyland, 1998).

3.4. Canopy structure

Post-harvest canopy closure was significantly ($P < 0.01$) greater for SCE (mean 77%) and group-selection (mean 73%) compared to single-tree selection (mean 64%); SCE and group selection were not significantly different in this respect. Aggregate canopy closure remained relatively high following group-selection because 70–80% of each unit retained full pre-harvest structure. However, spatial variability in canopy closure was also greatest across group-selection units. In SCE units, variable density marking achieved a similar though less pronounced effect.

3.5. Crown release

Clustered harvesting in SCE units resulted in crown release around 45 dominant and co-dominant trees per hectare on average. The average pre-treatment number of large trees (not released) was 20 ha^{-1}, so our future target of 55 large (>50 cm dbh) trees per hectare was exceeded when these densities are combined. The excess provides a ‘‘margin of safety’’ to accommodate canopy mortality. Canopy trees were released across a range of diameter classes (>25 cm dbh); the majority (79%) were fully, rather than partially, crown released.

3.6. Coarse woody debris enhancement

The treatments had distinctly different effects on CWD availability, both in terms of standing dead trees and downed logs. SCE prescriptions increased CWD densities by 10 boles (>30 cm dbh) per hectare on average for snags and 12 boles (>30 cm dbh) per hectare on average for downed logs. Post harvest dead tree basal area was 39% greater in SCE compared to conventional treatments, although this was not statistically significant ($P = 0.092$) based on multiple comparison results.

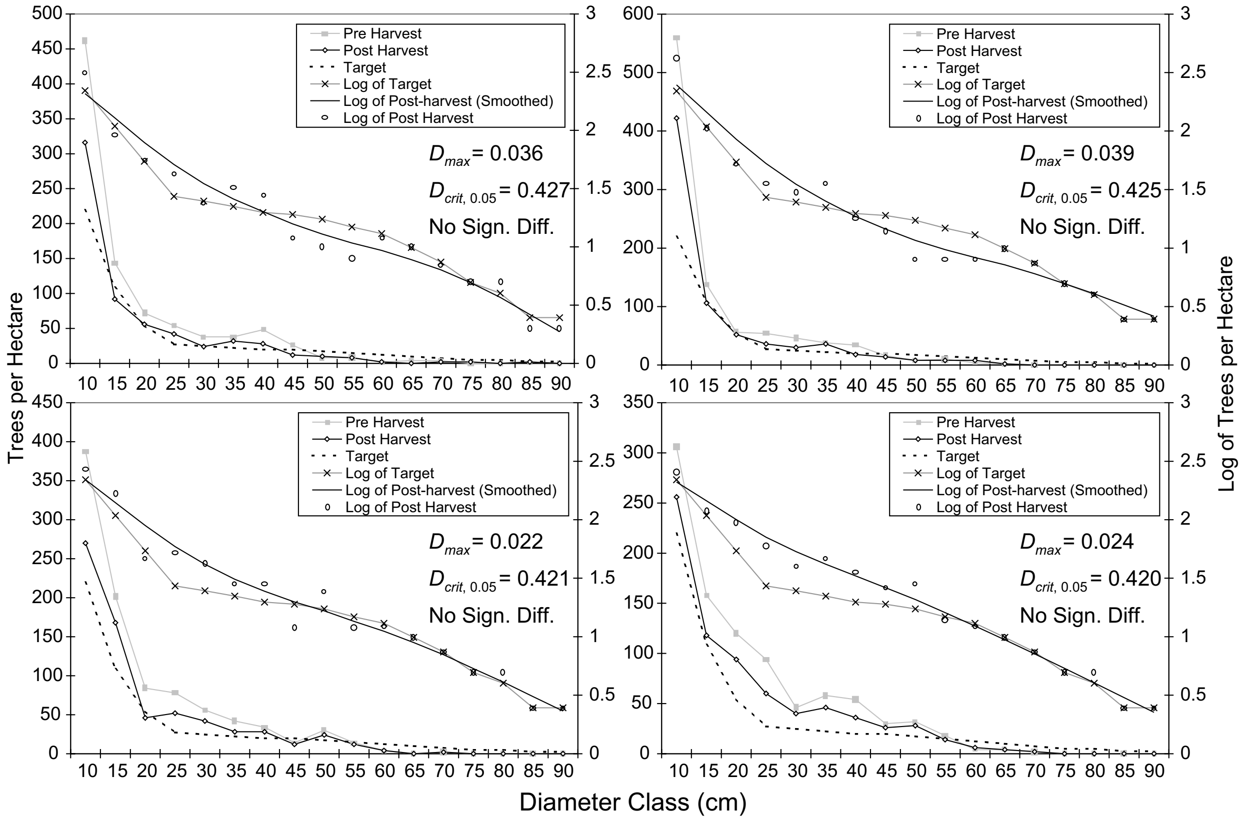

Fig. 1. Pre-harvest, post-harvest, and target diameter distributions (cm dbh) for the four SCE units, two at Mt. Mansfield (above) and two at the University of Vermont's Jericho Research Forest (below). Log transformed post-harvest and target distributions are compared (top portion of graphs) using the Kolmogorov–Smirnov two-sample goodness of fit test. There were no statistically significant differences. Thus, the post-harvest distributions achieved the target rotated sigmoid distribution.

Post-harvest dead basal area was significantly greater when SCE units were compared to controls ($P = 0.036$); conventional units showed no significant differences with controls.

There were statistically significant differences ($P = 0.002$) among treatments with respect to effects on downed log volume (Fig. 2). SCE increased downed log volumes by 140% on average. Volumes increased from 41 m^3 ha^{-1} pre-harvest to 92 m^3 ha^{-1} post-harvest. Mean downed log volume increased 30% in the uneven-aged units, changing from 38 m^3 ha^{-1} pre-harvest to 49 m^3 ha^{-1} post-harvest, although this effect was not statistically significant relative to the controls. There were slight (4% mean) increases in two of the four control units caused by windthrow. Background recruitment rates were thus not sufficient to explain SCE treatment effects. Analyses of downed log decay class distributions in SCE units showed, as expected, significant ($P < 0.05$) shifts towards less decayed logs due large inputs of felled trees (Fig. 3).

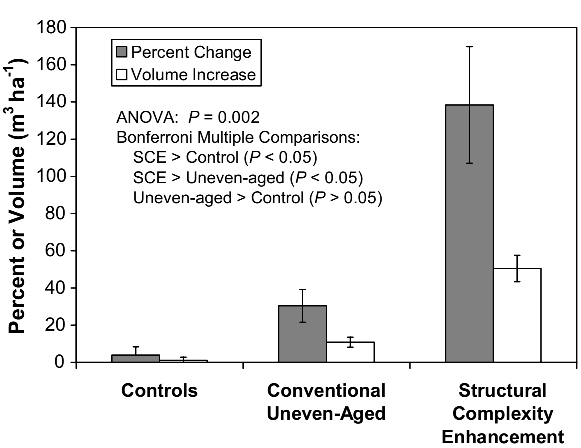

Fig. 2. Downed log response to treatments. Shown are percent change from pre-harvest levels and absolute change in volume (m^3 ha^{-1}). Error bars are ±1S.E. of the mean.

Of 48 attempts (24 per study area) at pulling (Mt. Mansfield) or pushing (Jericho) trees over, 45 were successful at creating large (mean of 14 m^3) exposed root wads and pits (mean of approximation 7 m^3). Success rates were influenced by the relatively shallow depth to bed rock (0.5–1.2 m mean) at sites where this was attempted. Tip-up mounds were significantly larger ($p < 0.01$) at Mount Mansfield, which was probably related to the greater loam and moisture content of soils at that site.

3.7. Projected stand development

3.7.1. Basal area and aboveground biomass development

In comparison to NE-TWIGS, FVS (northeastern variant) tended to produce more conservative estimates of growth increment and large tree recruitment due to the differences in model operation previously mentioned. Simulations in

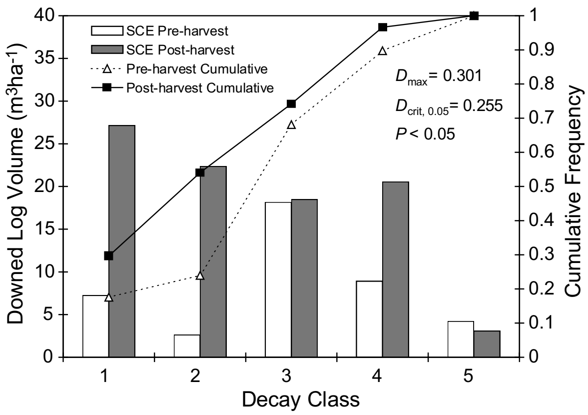

Fig. 3. Mean pre and post-treatment downed log (>10 cm) decay class distributions for SCE units. Cumulative frequency distributions were significantly different based on Kolmogorov–Smirnov two-sample goodness of fit tests. Decay class (DC) 1 is least decomposed while DC 5 is most decomposed. Note the large input of fresh logs (DC 1) following treatment. Post-harvest increase in DC 4 is related to recruitment from DC 3 and inputs of several large, well-decayed upper limbs from declining trees.

NE-TWIGS of stand development following SCE project, on average, that basal areas will approach 34 $m^2 ha^{-1}$ after 50 years (Fig. 4, top). This is 24% (or 8 $m^2 ha^{-1}$) greater than the mean for the conventional uneven-aged units. Projected basal area for SCE also exceeds the mean predicted for control units

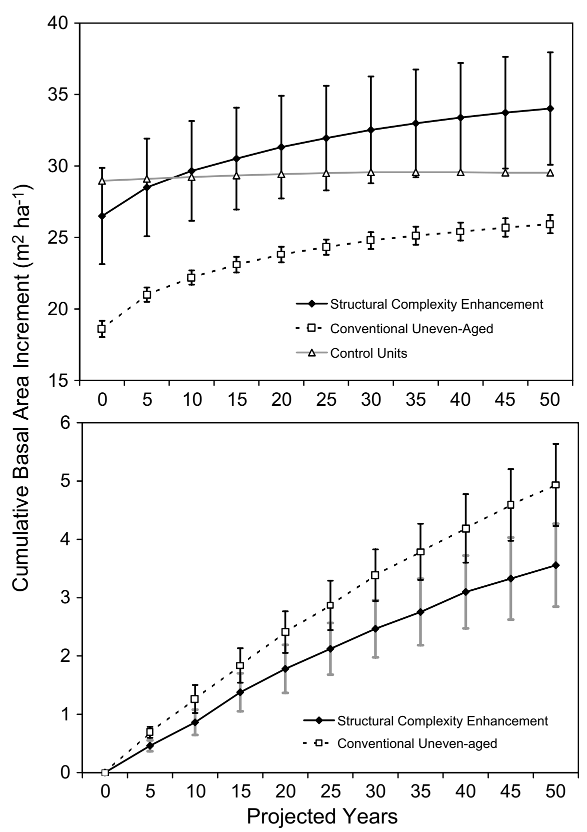

Fig. 4. Results of NE-TWIGS stand development modeling. Shown are 50-year projections of post-treatment cumulative basal area (live tree) production (top) and normalized scenarios (post-harvest minus pre-harvest cumulative basal area increment, bottom). Error bars are ±1S.E. of the mean.

by 13% (or 4.5 $m^2 ha^{-1}$). Conventional units were projected to have basal areas still 12% (or 3.6 $m^2 ha^{-1}$) below the control units after 50 years of development. Projected basal area was more variable (Fig. 4, top) among SCE units (±2.9 $m^2 ha^{-1}$) compared to conventional units (±0.6 $m^2 ha^{-1}$). Stand development projections differed slightly depending on choice of model. While the magnitude of difference among treatments was consistent in FVS projections, CBAI and end-of-run basal area were 12–18% lower, except for control units in which CBAI was flat and thus consistent under both models.

Projected tree growth rates did not differ statistically between treatment scenarios, as measured by CBAI and evaluated using goodness of fit tests ($D_{max} = 0.007$, critical value of $D_{0.05} = 0.307$). When projected development with treatment is normalized, to reflect the amount of development (specific to each unit) that would have been expected with no treatment, the simulations indicate that CBAI will be slightly faster under conventional systems (Fig. 4, bottom). However, this difference was not statistically significant ($D_{max} = 0.005$, critical value of $D_{0.05} = 0.183$). Both SCE ($P < 0.05$) and conventional treatments ($P < 0.01$) are projected to significantly accelerate tree growth rates above that expected with no treatment based on both NE-TWIGS and FVS modeling. Projected CBAI after 50 years was 2.7 $m^2 ha^{-1}$ (no treatment) compared to 6.4 $m^2 ha^{-1}$ (with treatment), on average, in SCE units. For conventional units projected CBAI increased from 0.34 $m^2 ha^{-1}$ (no treatment) to 5.3 $m^2 ha^{-1}$ (with treatment). Therefore, differences in basal area development are largely attributable to treatment effects on residual basal. Both conventional and SCE treatments accelerate basal area increment, but SCE leaves more residual basal area and thus ultimately results in higher basal areas.

Neither SCE nor conventional treatments resulted in projected basal areas that exceeded those projected for the corresponding units under a ‘‘no treatment’’ scenario. However, basal area in SCE units recovered to within 89% of the no-treatment scenario, whereas conventional units recovered to within 77% on average. This difference was statistically significant ($P = 0.025$).

Aboveground biomass is predicted to increase over the next 50 years in all of the experimental units, including controls, based on the FVS simulations and NED-2 biomass calculations. Living biomass increases 70.5, 66.1, and 73.6% on average for SCE, uneven-aged, and control units respectively under a ‘‘no treatment’’ scenario. It increases 90.7 and 105.2% following SCE and uneven-aged treatment, but starts from a post-harvest level that is 18.3 and 35.9% lower than pre-treatment respectively. Consequently, neither treatments achieve the biomass they would have without treatment. However, after 50 years SCE results in aboveground biomass that is 91.4% of that projected under no treatment, while the conventional treatments result in 79.1% of the no treatment potential. Biomass production annual increment is accelerated 5.1% for SCE and 1.9% for conventional treatments based on normalizing treatment against no treatment scenarios.

Table 3
Two-way ANOVA results exploring projection sensitivity to diameter distribution (rotated sigmoid vs. negative exponential) and use of maximum diameter limit (60 cm dbh limit vs. no limit)

Factor	Difference from no treatment scenario for:	MS	F	P
Maximum diameter limit	Large tree density	29.675	0.770	0.398
	Large tree basal area	6.428	1.826	0.202
Diameter distribution	Large tree density	436.706	11.327	*0.006*
	Large tree basal area	36.552	10.384	*0.007*
Diameter distribution × max	Large tree density	2.933	0.076	0.787
Diameter limit (interaction)	Large tree basal area	0.495	0.141	0.714

Results shown are for SCE units ($n = 4$) at both study areas. The tests evaluated the difference in large tree (>50 cm dbh) density and basal area projected 50 years following treatment compared to an equal period of development with no treatment for the same experimental unit. Italicized values are statistically significant ($\alpha = 0.05$).

3.7.2. Large tree recruitment

Rates of large tree recruitment are likely to be faster under SCE compared to no treatment scenarios. In SCE units, there will be an average of five more large trees (>50 cm dbh) per hectare than there would have been without treatment after 50 years, based on FVS projections. There will be 10 fewer large trees per hectare on average in the conventional units than would have developed in the absence of timber harvesting. SCE results in an increase of four very large trees (>60 cm dbh) per hectare, while conventional treatments produce three fewer very large trees per hectare than would have been recruited without treatment.

The sensitivity analysis showed no significant interaction between residual diameter distribution and maximum diameter limit (Table 3). Choice of target diameter distribution, however, had a significant effect on large tree (>50 cm dbh) density ($P = 0.006$) and basal area ($P = 0.007$) recruitment. Maximum diameter limit also affected projected densities and basal areas (Table 4), but these differences were not statistically significant (Table 3). Increases in projected large tree densities (over that projected for no treatment) after 50 years were highest when both the rotated sigmoid and a very high (or no) maximum diameter limit were employed (actual treatment). Adding a diameter limit of 60 cm to the rotated sigmoid prescription reduced large tree recruitment to three stems per hectare more than would have developed with no treatment.

Simulated negative exponential distributions employed with no diameter limit resulted in an intermediate level of large tree recruitment, but nevertheless had fewer large trees than would have developed with no treatment (Table 4). Large tree densities were lowest for the combination of a negative exponential distribution and a maximum diameter limit (Table 4). This held true as an average and for three of the four units evaluated. However, one unit (Mt Mansfield) showed large tree recruitment under this scenario comparable to the actual treatment due to: (1) a competitive response to the removal of one very large tree, and (2) a general pre-harvest deficit of trees >45 cm dbh. The latter limited the potential to create substantial differences in post-harvest structures through simulated treatments.

3.7.3. Projected diameter and basal area distributions

Projections suggest that a rotated sigmoid diameter distribution will sustain itself over 50 years in SCE units (Fig. 5). Projected and target (i.e. desired future) rotated sigmoid distributions were not significantly different ($D_{max} = 0.058$, critical value of $D_{0.05} = 0.430$). This held as long as densities in smallest two diameter classes (stems <15 cm dbh) were held constant. This was appropriate because both NE-TWIGS and FVS lack a seedling recruitment model (there is only limited regeneration through stump spouting). Pronounced regeneration deficiencies thus develop rapidly in model projections. This explains the low densities evident in the smallest size classes in Fig. 5. Uneven-aged units appear to maintain the negative exponential distributions initially prescribed. However, they have significantly less recruitment into larger size classes compared to the projected distributions for SCE (Fig. 5).

Differences in projected diameter distributions and large tree recruitment explain related changes in basal area distributions. Compared to stand development under a ''no treatment'' scenario, SCE results in significant reallocation of basal area

Table 4
Results of the sensitivity analysis exploring projected differences after 50 years of stand development between alternate treatment scenarios for SCE units ($n = 4$)

Treatment		Structural response	
Residual diameter distribution	Use of maximum diameter limit	Large tree density (stems/ha)	Large tree basal area (m^2/ha)
Rotated sigmoid	No	+5	+2
Rotated sigmoid	Yes	+3	+1
Negative exponential	No	−5	−1
Negative exponential	Yes	−8	−3

Values shown for large tree (>50 cm dbh) densities and basal areas are the mean change with treatment relative to development projected under no treatment (passive management) for the same units.

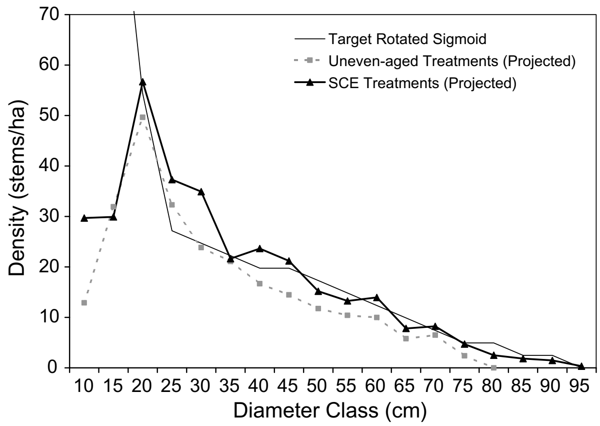

Fig. 5. Projected diameter distributions (cm, dbh) for 50 years into the future based on FVS simulations. Mean distributions developed after structural complexity enhancement (SCE) and conventional uneven-aged treatments are compared against the target or desired future condition prescribed for SCE. Note the close fit with the target shown by SCE, and the disparity evident for the conventional treatment.

into the largest size classes (e.g. >50 cm dbh). This includes a shift of basal area into the very largest size classes (>85 cm dbh) that experience no basal area recruitment under the "no treatment" scenario (Fig. 6, top). The uneven-aged

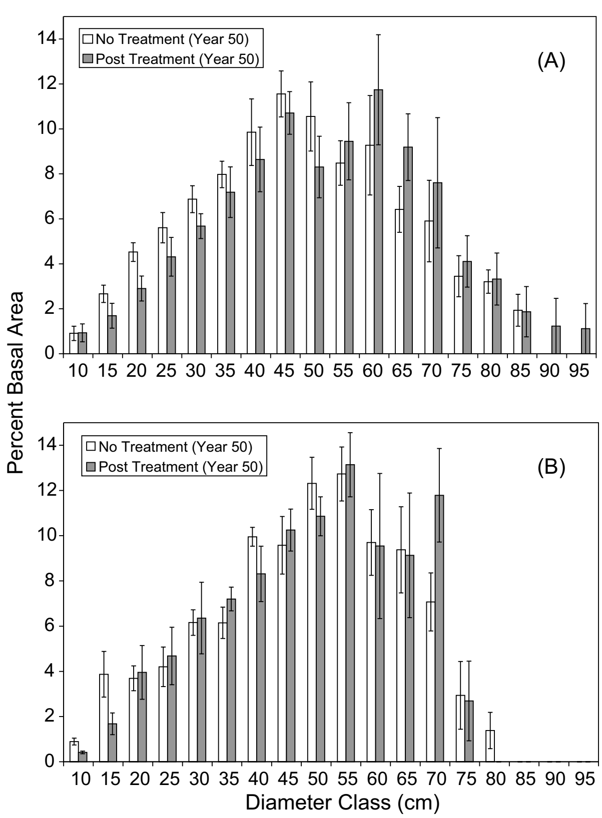

Fig. 6. Projected live tree basal area distributions for 50 years into the future based on FVS simulations of stand development. Mean distributions are shown for SCE units: (A) and conventional uneven-aged units and (B) projected both with and without treatment. No treatment scenarios are specific to treatment unit (i.e. development that would have occurred without treatment in a given unit); they are not based on data from control plots. Thus, the "no treatment" scenarios differ by treatment unit/type. Error bars are ±1S.E. of the mean.

treatments – modified to include a low q-factor and relatively high maximum diameter – also resulted in some reallocation of basal to larger size classes (Fig. 6, bottom). However, this reallocation was substantially lower than for SCE and did not include recruitment into size classes larger than the projected "no treatment" distribution. In fact, the "no treatment" simulations showed basal area development into the 75–80 cm diameter class, whereas this was lacking for the corresponding units subjected to uneven-aged treatments (Fig. 6, bottom).

4. Discussion

Uneven-aged silvicultural techniques can be modified to promote development of old-growth structural characteristics in northern hardwood and mixed northern hardwood-conifer forests. Both the uneven-aged and SCE approaches tested maintain high post-harvest levels of some structural attributes, such as stem density and canopy cover. However, SCE maintains or supplements CWD volume, basal area, aboveground biomass, large tree recruitment, and other structural attributes to a greater degree. Higher post-harvest LAI under SCE signals greater retention of foliage bearing tree crowns, representing an important element of vertical complexity (Parker et al., 2004). In addition, SCE results in a rotated sigmoid diameter distribution that appears self-maintaining at least over 50 years, and consequently reallocates growing space and aboveground structure into larger size classes. This contributes to increased density of large trees, a higher foliage biomass, and increased canopy complexity. The treatments are likely to develop differently with respect to horizontal complexity or patchiness. This inference is supported by the observed spatial variability in LAI and canopy closure created by group selection (most variable and contrasting) and SCE (moderately variable). The finding of more spatially uniform structure maintained by single-tree selection (least variable) is supported by previous research (Kenefic and Nyland, 2000; Crow et al., 2002).

4.1. Accelerating rates of stand development

Accelerated tree growth can be expected after both SCE and conventional uneven-aged treatments according to simulation projections. Conventional treatments retain less basal area and, thus, result in moderately greater projected basal area increments. This finding is consistent with previous research on growth responses to stocking density and growing space availability (Leak et al., 1987). A shortcoming in the stand development projections is that neither NE-TWIGS nor the FVS model is spatially explicit. Individual tree growth rates reflect competition only as a function of the total stand stocking in trees of equivalent or greater diameter (Bush, 1995). The models do not, therefore, capture the effects of crown release on selected dominant trees as employed in SCE. Crown release has been found to partially arrest or dampen declining growth rates in older, dominant northern hardwoods, leading to rates of large tree development that are 50–100% faster compared to no release scenarios (Singer and Lorimer, 1997). Despite this limitation, the projections suggest that SCE does promote large tree recruitment. Large tree recruitment will be significantly impaired under conventional treatments. The results of the sensitivity analysis suggest this is due to both maximum diameter limits and negative exponential diameter distributions that, collectively, provide lower large tree recruitment potential. This holds even when the basal area prescription is the same as under SCE.

Projected basal area and aboveground biomass are greater after 50 years of development under SCE (in comparison to conventional treatments) due, primarily, to elevated post-harvest structural retention. Substantial increases in rates of production over that likely without treatment also contribute to these changes. However, while structural development in SCE units is projected to surpass controls units, none of treatments are likely to result in basal areas or aboveground biomass exceeding levels that would have developed without treatment. This provides a strong argument for passive restoration, rather than silvicultural manipulation, as an approach for ultimately developing greater levels of structural complexity associated with these parameters. However, that conclusion does not account for the accelerated rates of large tree recruitment, reallocation of basal area, and associated structural complexity projected for SCE. In this respect, active silvicultural manipulation may offer some advantages.

It is also clear that the conventional uneven-aged approaches were less effective at retaining and promoting some aspects of late-successional/old-growth structural development. Periodic harvests under a more standard entry cycle (e.g. 20 years) would further limit basal area development and, if practiced with a diameter limit, large tree density (Bryan, 2003). The results do show that conventional approaches can be modified to reallocate basal area to some degree and provide a relatively high degree of biomass and vertical complexity. That single-tree selection in northern hardwoods has the potential to maintain vertical complexity is supported by previous research (Kenefic and Nyland, 2000). However, uneven-aged practices that employ maximum diameter limits impair and, in fact, reduce large tree recruitment potential based on the results reported here. In comparison, SCE ultimately results in greater levels of structural complexity across a range of parameters. Therefore, SCE offers a useful alternative for landowners interested in both low-intensity harvesting and promotion of old-growth characteristics.

4.2. Coarse woody debris dynamics and tip-up mounds

Coarse woody debris, both standing and downed, plays a critical role in northern-hardwood systems as habitat and in other ecosystem processes (Hunter, 1999). Techniques employed in SCE were successful at creating the tip-up mounds (i.e. root wads) common to late-successional northern hardwood forests (Crow et al., 2002). Similar techniques have been employed at the Harvard Forest, MA to simulate hurricane effects (Carlton and Bazzaz, 1998), but this study is among the first to experimentally manipulate tip-mound density as part of commercial or restorative timber harvest. Tip-up mounds provide unique microsite habitat characteristics and influence soil nutrient processes (Beatty and Stone, 1986; Liechty et al., 1992; Crow et al., 2002). It remains uncertain whether the treatments will affect long-term mound recruitment dynamics.

SCE proved effective at enhancing CWD densities and volumes above the immediately post-harvest levels associated with slash and crowns left by the conventional treatments. Post-harvest densities of downed logs and snags (>30 cm dbh), including treatment additions, were substantially greater than minimum levels suggested by some previous guidelines (e.g. Elliott, 1988) but were consistent with more recent recommendations (e.g. TNC, 2001). Downed log volumes achieved 88% of the level recommended by McGee et al. (1999) to approximate old-growth characteristics. They were about 50–100% greater than volumes reported in mature northern hardwoods managed under selection systems elsewhere (Goodburn and Lorimer, 1998; Hale et al., 1999; McGee et al., 1999).

It remains uncertain whether silviculturally elevated CWD will persist until natural log recruitment rates increase, or, alternatively, whether CWD enhancement in mature stands has only transient or short-term management applications. As silviculturally enhanced CWD decays it will become more biologically available in habitat and nutrient processes (Gore and Patterson, 1985; Tyrrell and Crow, 1994a; Goodburn and Lorimer, 1998). Terrestrial salamander (McKenny et al., 2006) and soil invertebrate (Donald R. Tobi, unpublished data) populations are responding positively to increased downed log densities in the treatment units.

Treatment effects on future snag and downed log recruitment are also uncertain, especially given the potential for episodic recruitment associated with natural disturbance events (Ziegler, 2002). If practiced with periodic harvest re-entries, all of the treatments could result in subsequent CWD inputs and maintenance of a range of decay classes (Kenefic and Nyland, 2000), although the net effect on CWD volume is likely to be more limited under conventional systems (McGee et al., 1999). In this study, silviculturally created snags and downed logs were culled from the total number of trees harvested to achieve target diameter distributions, and thus did not result in additional removals of low-vigor trees beyond that associated with conventional harvests. Nevertheless, preferential cutting of low-vigor trees under any harvest system is likely to result in a near-term reduction in CWD recruitment. Over the longer-term, however, increased densities of large trees associated with SCE may also accelerate recruitment of large snags and logs.

4.3. Applications for structural complexity enhancement

SCE has a variety of useful applications, ranging from old-growth restoration, to riparian management, to low-intensity timber management. These will depend greatly on economic feasibility under a variety of operational scale, site quality, product, and market conditions (Niese and Strong, 1992), which is the subject of an on-going investigation (Keeton and Troy, 2006). SCE could be employed to varying degrees depending on the specific application. For instance, where timber production is emphasized, a subset of SCE elements might be used. Other elements, such as CWD enhancement, might be avoided or employed at a lesser intensity. In this scenario, multiple stand entries would be expected, but late-successional structural development would be lower compared to full SCE implementation. Such an approach, however, would allow forest managers to build some degree of old-growth associated structure into actively managed stands, while maintaining greater timber management flexibility. This study evaluated a 50-year growing period (no additional harvests) in order to evaluate longer-term stand development potential resulting from initial treatment alone. This was appropriate because: (a) the primary research question pertained to the restorative potential of alternate treatments, and (b) the growth and yield models lacked adequate regeneration sub-models, such that simulations could only project growth for the initial population of trees. However, a 20–25-year entry cycle is certainly a plausible option for SCE where low intensity timber production is a management objective. This conclusion is supported by the similar growth trends between all treatments evaluated, including uneven-aged treatments typically scheduled on this (or a more frequent) entry cycle in northern hardwoods.

Intermediate applications of SCE could be employed where ecologically sensitive management is required within riparian areas. Managing for forest structural complexity along freshwater streams would be useful where the associated influences on in-stream aquatic habitat conditions are desired (Keeton et al., in review). In protected areas, the full compliment of techniques employed in SCE provide options for late-successional forest restoration. Managers might conduct harvest entries once or twice, thereafter relying on accelerated successional processes. The degree of implementation and the number of stand entries will thus vary by application.

4.4. *Silvicultural flexibility in managing stand structure*

Late-successional/old-growth characteristics in northern-hardwood conifer systems can be promoted through a variety of silvicultural approaches, including those investigated in this and other studies (e.g. Singer and Lorimer, 1997; Bryan, 2003). Uneven-aged systems provide some (e.g. vertically complex canopies), but not all (e.g. large live and dead trees) late-successional structural characteristics or provide them to a more limited extent based on the results reported here. Prescriptions can be modified to retain more post-harvest structure, for instance by specifying a greater residual basal area, larger maximum diameter, and/or lower q-factor. However, maximum diameter limits significantly impair the potential for large tree recruitment based on the results. Similar findings have been reported for diameter-limit cutting (as opposed to selection system) in uneven-aged stands (Nyland, 2005).

Cutting to alternative diameter distributions provides another way to manipulate stand structure for a range of objectives, including old-growth structural development. The results show that SCE's variable q-factor marking approach can be used to successfully achieve a rotated sigmoid diameter distribution. In addition, the results indicate that this distribution is sustainable in terms of growth and recruitment across size classes. Density-dependent mortality in middle size classes does not appear to self-thin a stand to a negative exponential distribution, at least over the time frame investigated in this study. This may be due to reduced (or non-constant) mortality rates in these size classes (O'Hara, 1998; Goodburn and Lorimer, 1999; Zenner, 2005).

Like any silvicultural prescription, use of the rotated sigmoid will reflect stand management objectives. The distribution would not necessarily develop in a particular stand through natural mortality alone. Diameter distributions in old-growth northern-hardwood forests vary considerably (Goodburn and Lorimer, 1999). Both rotated sigmoid and negative exponential distributions are possible, depending on disturbance history and stand development pathway (Goff and West, 1975; Manion and Griffin, 2001; Leak, 2002). For silviculturists, the rotated sigmoid offers the flexibility to manage for stand structures in which basal area distributions are shifted towards medium and larger size classes. They would also maintain sufficient densities of smaller stems to ensure recruitment across all size classes. This would provide benefits associated with larger dimension timber, large tree habitat functions, and carbon storage associated with greater biomass.

5. Conclusion

Foresters can manage for late-successional/old-growth structure where desired in northern hardwood-conifer ecosystems. Active silvicultural manipulations, such as SCE, as well as passive approaches provide alternatives for achieving this objective. There are multiple options for retaining high levels of post-harvest structure and for promoting accelerated rates of stand development. These include unconventional prescriptive diameter distributions, such as guiding curves based on a rotated sigmoid distribution, combined with higher levels of residual basal area, very large (or no) maximum diameters, and/or crown release. Managing for late-successional forest characteristics can be actively employed as an element of structure-based forestry and ecosystem management.

Acknowledgements

This research was supported by grants from the USDA CSREES National Research Initiative, the Vermont Monitoring Cooperative, the Northeastern States Research Cooperative, and the USDA McIntire-Stennis Forest Research Program. Nine anonymous reviewers provided helpful comments on manuscript drafts. The author is grateful to Donald R. Tobi for assistance throughout this project. Dr. Austin Troy assisted in collecting and processing timber harvest volume data. Assistance with NED software was provided by Dr. Mark Twery. Jonathan Trigaux provided computer administration support. Alan Howard provided statistical consulting. A special thanks goes to the outstanding field crews at the University of Vermont.

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