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Ecological forestry in an uneven-aged, late-successional forest: Simulated effects of contrasting treatments on structure and yield

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ABSTRACT

Ecological forestry practices are designed to retain species and structural features important for maintaining ecosystem function but which may be deficient in conventionally managed stands. We used the spatially-explicit, individual tree model CANOPY to assess tradeoffs in enhanced ecological attributes vs. reductions in timber yield for a wide variety of treatments in uneven-aged, late-successional northern hardwood forests. Treatments included various combinations of (1) larger retained maximum tree diameters in the post-harvest stand, (2) permanently reserved legacy trees, (3) variable opening sizes, (4) coarse woody debris retention, (5) species harvest restrictions, and (6) occasional moderate-intensity harvests with larger openings ('irregular multi-cohort harvests'). Compared to conventional single-tree selection, reduction in simulated harvest yields varied widely from a 9% decline with 7 reserve trees/ha to a 55% reduction in treatments that retained coarse woody debris along with a maximum residual live-tree diameter of 80 cm. Despite the dominance by shade-tolerant species, simulated declines were similar in magnitude to those predicted or observed for relatively shade-intolerant conifers of the Pacific Northwest. Treatments that protected 'sensitive' species from harvest or raised the maximum residual diameter to 80 cm appeared to have the best balance between fostering ecological values of old-growth forests and moderating the impact on timber yield. These treatments produced stands meeting minimum structural criteria of old-growth forests while causing harvest declines of 27–30% compared to conventional single-tree selection. Coarse woody debris volumes were similar to those produced by the reserve-tree treatments, but the species-protection and 80 cm treatments had higher densities of large trees, and there was less reduction in yield for each large tree retained in the residual stand. Most other treatments maintained mature forest structure or stands that vacillated between mature and borderline old-growth conditions.

1. Introduction

'Ecological forestry' includes treatments in managed forests designed to emulate patterns of species composition and stand structure that develop under natural disturbance regimes. A major objective is to create biological 'legacies' (e.g., live residual trees, dead snags, and fallen logs) and heterogeneous stand structures that may help promote biological diversity, critical ecosystem functions, and resilience to disturbance (Franklin et al., 2007). In some temperate forest regions, more than 20% of the amphibian, bird, and mammal species may rely on cavity trees or decaying logs for nest sites, foraging sites, or escape cover (Evans and Connor, 1979; DeGraaf et al., 1992). Even large living trees without cavities can provide important foraging sites because the thick, furrowed bark provides hiding places for insect prey (Jackson, 1979). Intensively managed forests not only tend to have lower populations of vertebrate species associated with structural elements of old forests, but they also may have reduced populations of fungi, nitrogen-fixing lichens, and other organisms important for ecosystem functions. In the intensively-managed forests of Sweden, about 50% of the threatened forest species, including several hundred species of fungi, depend on dead wood (Stokland and Larsson, 2011). Studies on forest tracts managed for legacy trees and structural complexity suggest that these practices can increase populations of sensitive species relative to conventionally managed forests (Stribling et al., 1990; Mazurek and Zielinski, 2004; Smith et al., 2008; Blomquist and Hunter, 2010), although some controlled experiments suggest that cause-and-effect relations are complex and outcomes can be influenced by various confounding factors (McKenny et al., 2006; Sullivan et al., 2008; Aubry et al., 2009).

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While ecological forestry methods have been applied most commonly in the context of even-aged management (e.g., Hansen et al., 1995; Bergeron et al., 2002), the same principles are readily applicable with some modification to uneven-aged management. For example, raising the maximum diameter of live trees in the residual stand can compensate for the deficiency of large trees often noted in managed uneven-aged stands (McGee et al., 1999; Angers et al., 2005; Keeton, 2006). A small number of trees can be permanently reserved to live out their natural lifespan, or some trees can be girdled or felled and not removed, which can compensate for low levels of coarse woody debris and paucity of soil 'tip-up' mounds. Variable opening sizes and variable harvest intensity can increase species diversity and provide opportunities for less shade-tolerant trees to reach the forest canopy, while more closely mimicking the effects of periodic moderate disturbance (Leak, 1999; Webster and Lorimer, 2005; Hanson and Lorimer, 2007). These moderate–severity events appear to dominate the disturbance regimes in some late-successional forests, inducing irregular population structure that may persist for centuries (Frelich and Lorimer, 1991a; Jenkins, 1995; Woods, 2004).

Several studies, using retrospective approaches and simulation, have investigated the potential for trade-offs in wood production associated with ecological forestry in conifer forests of the western USA. These studies have reported similar findings suggesting a substantial reduction (~25%) in volume of the regenerated cohort with even low reserve-tree densities of 5 trees/ha, with a further but more gradual decline in production as retention levels increase (e.g., Birch and Johnson, 1992; Hansen et al., 1995; Zenner et al., 1998). In theory, yield reductions in uneven-aged stands may not be as dramatic due to the heavy dominance of shade-tolerant tree species. This might especially be the case if production rate per unit area in openings with reserve trees is strongly asymptotic as light intensity increases, so that understory and overstory production varies little across a range of low to moderate residual tree densities. In a field study of two-aged forests of the Pacific Northwest, volume of the relatively intolerant Douglas-fir (*Pseudotsuga menziesii*) was inversely related to residual tree density, while there was no significant trend for the shade-tolerant western hemlock (*Tsuga heterophylla*). It was not clear if the lack of response in hemlock was due to its shade tolerance or the influence of historical factors such as variation in seed source at the time of stand establishment (Zenner et al., 1998).

Ecological forestry goals in uneven-aged, late-successional forests are likely to produce stands of much different structure than in forest regions where stand-replacing fires are common and where these fires often leave only scattered legacy trees. Conventionally managed uneven-aged stands of tolerant species already have dense canopies, and ecological forestry variants are likely to have even higher canopy densities with increased numbers of large trees, interrupted only by relatively small regeneration gaps. Most of the forest matrix is therefore likely to experience high levels of competition, which might reduce production rates even for shade-tolerant species.

Ecological forestry alternatives are currently being implemented in both experimental (Keeton, 2006) and federally managed uneven-aged forests (USDA Forest Service, 2004), but the effects of these treatments on structure and yield will not be evident for decades. The simulation study in this paper was designed as a companion study to a long-term replicated field experiment on the biological and economic effects of ecological forestry in second-growth northern hardwood forests in northern Wisconsin, USA. In this paper, we use the individual tree model CANOPY (Choi et al., 2001, 2007; Hanson et al., 2011) to compare long-term trade-offs between forest structural goals and wood volume production under a wide range of alternative ecological forestry treatments. A major focus is the effectiveness of alternative practices (e.g., reserve-tree vs. maximum diameter standards) as mechanisms for promoting old-growth structural features, desired species composition, and coarse woody debris volumes. Ecological forestry variants of single-tree selection in this study included: (1) raising the maximum diameter retained in the post-harvest stand to levels closer to the maximum size attained in old-growth forests; (2) permanent reserve trees allowed to live out their natural lifespan; (3) a variety of opening sizes for structural diversity; (4) protection of 'sensitive species' that commonly decline in managed stands of the region; (5) retention of downed wood to levels approaching 75% of old-growth values; and (6) irregular multi-cohort harvests based on residual forest patterns created by moderate–severity windstorms of the region. The latter treatments also used various combinations of maximum diameters, reserve trees, and retention of sensitive species.

Because of the numerous dimensions of environmental change likely to occur in coming decades (e.g., climate change, invasive plants and earthworms, exotic insects and diseases), for which effects are poorly known, the simulation results reported in this paper are not intended to be 'forecasts' of the forest condition at some particular future time. Instead, they are best interpreted as representing a 'baseline' trajectory of response to ecological forestry practices expected under the current or otherwise stated environmental conditions. Simulations are projected for a period of 300 years to distinguish more clearly the long-term ramifications of each treatment under the stated conditions and to reduce the effects of initial conditions on the outcome. In addition to providing insights into the dynamics and mechanisms of treatment response, we believe these results will also be useful as a baseline for assessing the magnitude of future impacts caused by climate change and invasive species.

2. Methods

2.1. CANOPY model description

CANOPY (Choi et al., 2001; Hanson et al., 2011) is an individual-tree, spatially explicit model designed to simulate gap dynamics and three-dimensional canopy structure of a large, contiguous forest stand. The model was calibrated with data from >8000 trees in northern hardwood stands across northeastern Wisconsin and western upper Michigan on mesic, relatively fertile sites. Data were obtained from young even-aged and managed uneven-aged stands, as well as unmanaged mature and old-growth stands. CANOPY includes an unusually detailed gap dynamics algorithm, with gap capture predicted from direct simulation of sapling height growth and lateral gap closure determined by variable crown expansion rates of gap border trees. CANOPY also includes many stochastic elements that allow for a wider range of predicted outcomes. Stochastic variation is incorporated into the diameter growth of overstory trees, individual tree mortality, species composition of new sapling recruits, individual tree diameter–height relationships, and rates of snag and log decay.

CANOPY has been subjected to rigorous testing, both with and without silvicultural treatments (Choi et al., 2001, 2007; Hanson et al., 2011). Its predictions of stand growth responses to traditional single-tree selection treatments agree closely with results of independent field experiments in the region in stands with similar species composition and management specifications (Strong et al., 1995; Choi et al., 2007; Halpin, 2009). For example, basal area growth of surviving trees in the single-tree selection field trial was 0.32 $m^2\ ha^{-1}\ yr^{-1}$, compared to 0.35 $m^2\ ha^{-1}\ yr^{-1}$ predicted by CANOPY. Observed and predicted mortality were 0.10 and 0.11 $m^2\ ha^{-1}\ yr^{-1}$, respectively. Simulated natural stand development compared favorably to patterns observed in unmanaged old-growth forests of the Upper Great Lakes region. Density and species composition of new tree recruits over 23 years in a permanent plot study were closely matched by CANOPY predictions using the same initial data set. After several centuries of simulation, basal area and tree densities in various size classes were also near the middle of the observed range of values in old-growth forests of the region (Hanson et al., 2011).

2.2. Overview of CANOPY model components

The following description summarizes the main features from the latest version of CANOPY (v. 2.1) relevant for understanding the simulations in this paper. Further details, equations, validation tests, and sensitivity analyses are included in Hanson (2009) and Hanson et al. (2011).

2.2.1. Competition, growth, and mortality

A plot competition metric based on empirical stand density charts (Tubbs, 1977) expresses plot basal area as a percentage of a regional baseline level for stands with the same mean tree diameter (analogous to self-thinning diagrams; Osawa and Sugita, 1989; Westoby, 1984). A grid of non-overlapping 10×10 m cells is superimposed on the stand, and a competition term is computed for the 900 m^2 zone surrounding each cell. This competition term is used to estimate effects of crowding on diameter growth and mortality for each tree in the cell. For gap saplings and understory trees, gap area and the aggregate crown area of saplings are used to predict the effect of competition on height growth. Gap area is calculated as an irregular polygon defined by the distances from the subject tree's stem to the edge of each border tree's crown.

Diameter growth rates of overstory trees vary with habitat type, species, subject tree diameter, and the competition level on each 900 m^2 subplot. Stochastic variation is incorporated by adding the predicted diameter increment to the product of the mean squared error from regression analysis and a random deviate between -1 and 1 drawn from a standard normal distribution.

Annual probabilities of mortality for each species are logistic functions of diameter and plot competition level, and are applied stochastically based on a random number draw. In some of the calibration data, unusually high mortality was observed for yellow birch (*Betula alleghaniensis*) as a result of the severe 1988 drought. In all treatments in this paper, a non-drought scenario was simulated by using mortality equations with the 1988 measurement interval excluded.

2.2.2. Recruitment

CANOPY predicts the annual recruitment of new 2–6 cm saplings entering each 10×10 m cell. The number and species of new recruits are functions of habitat type, species composition of the surrounding overstory, plot competition level, and current sapling abundance. Species of low shade tolerance make up a higher proportion of the sapling recruits at low stocking levels than at high stocking based on relationships in the calibration data set (Fig. 2 in Hanson et al. (2011)). However, for any specified set of conditions, stochastic variation is introduced by comparing a random number draw with the expected proportions of each species in that local environment. Eastern hemlock (*Tsuga canadensis*) recruitment is heavily dependent on the level of deer browse, but only recruitment equations from low-browse study sites are utilized for treatments in this paper.

2.2.3. Coarse woody debris dynamics

The CWD module first determines if a newly dead tree is a snag or a log. At yearly intervals, it estimates the annual decay of each snag, determines when it falls to become a log, and estimates log decay. This module utilizes equations of woody debris dynamics reported in the literature for northern hardwood forests of the Great Lakes region. Equations and conditional probabilities that predict a newly dead tree becoming either a snag or a log, rate of snag decay, and snag fall were calibrated by Vanderwel et al. (2006) in northern hardwoods of southern Ontario. Decay rates of hemlock logs were estimated using conditional probability tables from Tyrrell and Crow (1994a) in hemlock-hardwood forests of upper Michigan. Decay rates of sugar maple (*Acer saccharum*) logs (also applied to all other hardwood species) are based on conditional probability tables from Hale and Pastor (1998) in northern hardwoods of Minnesota. Annual probabilities of tree fall, snag fall, snag decay, and log decay specified from the equations or tables are implemented stochastically within CANOPY using a random number draw.

In the model, the median longevity of a snag is <10 years for most species and tree sizes. The median longevity for logs is 34 years for hardwoods and 64 years for hemlock. In the original studies, log decay rates were calibrated for trees 20–45 cm dbh, but in the model, probabilities are applied to all tree sizes due to a lack of data on decay rates for smaller and larger trees. Data are also insufficient to estimate volume reductions directly as logs decay, and so available data on the rate of decrease in wood density of fallen logs (Tyrrell and Crow, 1994a; Hale and Pastor, 1998) were used as a preliminary substitute. The CWD predictions are therefore considered tentative until further calibration data are available.

2.3. Stand template used in CANOPY simulations

Because long-term simulations on large, mapped tracts in CANOPY are time consuming, a representative mapped northern hardwood stand on the Argonne Experimental Forest in northern Wisconsin was used as a starting condition for simulations. This second-growth, even-aged stand is about 100 years old and is heavily dominated by sugar maple, with lesser amounts of hemlock and other species. The stand was selected because it includes approximately equal proportions of the three most common and widely distributed northern hardwood habitat types in the region (Kotar et al., 2002): *Acer-Osmorhiza-Caulophyllum* (AOCa; the most productive of the three types), *Acer-Tsuga-Dryopteris* (ATD), and *Acer-Tsuga-Maianthemum* (ATM; the least productive). The species, dbh, and coordinate of each tree >2 cm dbh were recorded on a 1-ha section of the stand, along with the crown radii of each tree in the four cardinal directions. Initial snag and downed log diameters, decay classes, and species were estimated from an inventory recorded in the Argonne Experimental Forest (USDA Forest Service, 2005). The 1-ha section was replicated in a grid of nine 1-ha 'tiles' to form a 9-ha stand large enough to accommodate the various silvicultural treatments. The tiles were rotated in random orientations to avoid repeating spatial patterns in the initial stand condition. In long-term simulations, the initial composition and structure of the template stand have diminished influence as these attributes become shaped more heavily by prevailing conditions in the regional calibration data set and by stochastic variation built into the model.

2.4. Simulated silvicultural treatments

Ten replicates of an unmanaged control (no treatment), a conventional single-tree selection treatment, and various combinations of the structural retention treatments were simulated for a period of 300 years (Table 1).

2.4.1. Standard single-tree selection

Simulations of selection silvicultural systems were implemented using the *BDq* method (Marquis, 1978), the most common

Table 1
Single-tree selection *BDq* specifications for ecological forestry treatments simulated by the CANOPY model. All single-tree selection treatments were performed on 20 year cutting cycles. Ten replicates of each treatment were simulated for 300 years.

Treatment	Basal area (B; m^2 ha^{-1})	Max dbh (D; cm)	q-ratio (q)	Notes
Maximum diameter				
60 cm dbh	20	60	1.3	60 cm maximum dbh treatment is traditional ('standard')
70 cm dbh	23	70	1.2	in northern hardwoods
80 cm dbh	23	80	1.2	
Group selection (250 and 450 m^2 gaps)				
60 cm max dbh	20	60	1.3	Six 250 m^2 groups and three 450 m^2 groups created on 9 ha
70 cm max dbh	23	70	1.2	in each treatment
80 cm max dbh	23	80	1.2	
Reserve trees (60 cm max dbh)				
7 reserve trees/ha	20	60	1.3	Reserve trees not harvested. New reserve trees randomly selected
15 reserve trees/ha	20	60	1.3	from 30 to 50 cm dbh size class
22 reserve trees/ha	20	60	1.3	
CWD creation (+ group selection)				
60 cm max dbh	20	60	1.3	CWD target 75 m^3 ha^{-1} of downed logs, ~75% of log volume
70 cm max dbh	23	70	1.2	in old-growth northern hardwoods
80 cm max dbh	23	80	1.2	
Species harvest restrictions (70 cm max dbh)				
Retain all hem and YB/or half allowable cut	23	70	1.2	All hemlock and yellow birch trees, or half allowable cut,
Same + group selection	23	70	1.2	reserved from harvest
Multi-cohort harvests				
60 cm max dbh for selection harvests	20	60	1.3	Two multi-cohort harvests applied in each 300 year simulation:
70 cm max dbh for selection harvests	23	70	1.2	the first in year 2 and the second ~year 150. Five selection harvests
80 cm max dbh for selection harvests	23	80	1.2	on 20 year cutting cycles followed each multi-cohort harvest. *BDq*
7 reserve trees/ha (80 cm max dbh)	23	80	1.2	method used for selection harvests but not multi-cohort harvests
15 reserve trees/ha (80 cm max dbh)	23	80	1.2	
22 reserve trees/ha (80 cm max dbh)	23	80	1.2	
Retain all hem and YB (70 cm max dbh)	23	70	1.2	

method applied in managed, uneven-aged stands in the region. Prior to harvests, a target residual basal area (B) and a maximum diameter (D) were selected, along with the q-ratio (the ratio of the number of trees in one 5 cm size class to the number of trees in the next larger size class). The standard selection treatment simulated in CANOPY had a target residual basal area of 20 m^2 ha^{-1}, a maximum residual dbh of 60 cm, and a q of 1.3 (Tubbs, 1977). From these parameters, a target residual diameter distribution was calculated, and surplus trees in each size class above the residual curve were harvested, as were trees larger than the maximum diameter. Harvesting ceased when the basal area of the stand reached the specified target residual basal area. As is presently common in federally managed forests of the region, selection harvests were repeated on a 20-year cutting cycle (Mark Theisen, Chequamegon-Nicolet National Forest, *personal communication*).

2.4.2. Maximum diameter

Ecological forestry variants of single-tree selection included two treatments in which the maximum retained diameter was raised from 60 cm dbh to 70 and 80 cm. To ensure an adequate number of large trees, the target residual basal area was raised to 23 m^2 ha^{-1}, and the q-ratio was lowered to 1.2 for both treatments.

2.4.3. Group selection

In simulated group selection treatments, the aggregate area of groups harvested per cutting cycle was ~3% of the stand area. Six openings with areas of 250 m^2 and three openings of 450 m^2 were harvested in the 9 ha stand followed by single-tree selection in the forest matrix. Candidate group selection locations were selected at random, subject to restrictions. The automated harvester preferentially placed groups in areas of high basal area ($\geqslant$20 m^2 ha^{-1}), avoided overlap with group openings from previous harvest entries, and provided a buffer zone equal to a subject group's radius between all group openings made in the same harvest entry (Halpin, 2009). *BDq* parameters spanned the same range as in the three single-tree selection treatments.

2.4.4. Reserve trees

Permanent reserve trees were retained at densities of 7–22 trees/ha, similar to specifications on some federally managed uneven-aged forests in the region (USDA Forest Service, 2004). Residual stand parameters were otherwise identical to standard single-tree selection. To replace those lost to natural mortality, living trees between 30 and 50 cm dbh were selected as new reserve trees at each harvest entry. Trees smaller than the 60 cm dbh maximum in the residual stand were considered part of the residual basal area for calculations of the allowable cut using the *BDq* method, but larger trees were not. Actual residual basal areas in reserve tree treatments may therefore exceed the residual basal area target for the overall stand.

2.4.5. Species harvest restrictions

Hemlock and yellow birch are often underrepresented in managed northern hardwood stands, and so treatments were applied to promote the recovery of these species by reserving all hemlock and yellow birch from harvest or by removing only half of the calculated allowable cut for these species.

2.4.6. Coarse woody debris retention

In this simulated single-tree/group selection treatment, some trees marked for harvest were girdled or felled to create dead wood. Half of the retained coarse woody debris was left in the form of snags and half as downed logs. Downed coarse woody debris volumes for conventionally-managed uneven-aged hardwoods in the region average about 60% of levels found in old growth (Goodburn and Lorimer, 1998). Target levels of downed logs for ecological forestry treatments were therefore selected to be at an intermediate level of about 75% of old-growth values, or 75 m^3 ha^{-1} for trees >20 cm dbh. If log volume was below this level, up to 10 live trees/ha >40 cm dbh were converted to snags and logs. Limits were placed on the number of large trees retained for CWD in stands with few large trees in order to minimize yield reductions. If trees >40 cm dbh retained for CWD made up more than 50% of all trees marked for harvest, up to 13 smaller trees/ha (25–40 cm dbh) were substituted for CWD retention. Total CWD included both snags and logs and could exceed 75 m^3 ha^{-1}.

2.4.7. Irregular multi-cohort harvests

The harvest pattern of the irregular multi-cohort treatment was based on evidence from effects of moderate–severity windstorms in the region (Hanson and Lorimer, 2007). Harvested areas included patches of undisturbed forest, zones with 10–30% basal area removal, as well as large group and patch openings. Fifteen percent of the stand area (1.35 ha) was allocated to each of three harvest intensity levels (10%, 20%, and 30% basal area removal), for a total of 4.05 ha or 45% of the stand area. Also included on the 9 ha tract were six group openings each with areas of 1000 m^2 and three larger openings with areas of 2000, 4000, and 5000 m^2. A temporary shelterwood overstory, with basal area of 14 m^2 ha^{-1}, was retained within each of the group openings to enhance hemlock and yellow birch regeneration and to hinder raspberry (*Rubus* spp.) dominance. The shelterwood overstory was reduced to 2 m^2 ha^{-1} 10 years after the primary harvest. In total, however, no more than 40% of the original stand basal area was removed.

Two multi-cohort harvests were performed in each 300 year simulation, the first in year 2 and the second in year 150. After each of the multi-cohort harvests, five cutting cycles of single-tree selection harvests at 20-year intervals were initiated once stand basal area had recovered to 27 m^2 ha^{-1}, a level close to the minimum required for a viable timber sale (Mark Theisen, Chequamegon-Nicolet National Forest, *personal communication*). *BDq* parameters spanned the range used in other single-tree selection treatments. Prior to the second multi-cohort harvest, the stand basal area was allowed to recover to 30 m^2 ha^{-1} to help restore mature-old forest characteristics.

2.5. Analytical methods

Tree volume was calculated using the equation of Gevorkiantz and Olsen (1955), which estimates cubic stem volume from dbh and total height.

Stand characteristics at years 60 and 300 were analyzed with one-way ANOVAs and Tukey's HSD tests for multiple comparisons (with a family-wise error rate of 0.05). Some summary values of stand characteristics were log- or square-root transformed to meet the assumption of homogeneity of variance. Chi-square goodness of fit tests as well as two-sample Kolmogorov–Smirnov tests were performed to examine differences in tree diameter frequency distributions between the mean of 10 replicates of the managed stands vs. the target determined by the *BDq* selection system. Following each of the first five selection harvests in the standard selection and the multi-cohort treatments, tree diameters >25 cm were binned in 5 cm size classes and compared to the number of trees in each size class of the target distribution. All statistical analyses were calculated in the R statistical package, version 2.0.9 (R Foundation for Statistical Computing, Vienna, Austria).

Simulated stands were examined to determine if they met the minimum criteria of old growth based on structural definitions developed in a set of 70 unmanaged stands in upper Michigan (Frelich and Lorimer, 1991b). The classification rules were based on the proportion of the aggregate exposed crown area occupied by mature and large trees, but the present study uses proportional equivalents based on basal area (Hanson and Lorimer, 2007). Old-growth stands have basal areas of at least 20 m^2 ha^{-1} in trees >26 cm dbh and >45% of the total stand basal area in trees >46 cm dbh. The 46 cm dbh size class corresponds to a mean age of ⩾150 years in most species (Tyrrell and Crow, 1994b; Lorimer and Frelich, 1998).

3. Results

3.1. Variation in harvested wood volume among treatments

All ecological forestry treatments reduced harvest yields relative to standard single-tree selection, but the magnitude of the response at the end of the simulation ranged from a fairly modest 9% reduction for 7 reserve trees/ha to a 55% reduction for treatments that combined coarse woody debris retention with an 80 cm maximum dbh (Table 2). In some cases, quite different approaches to ecological forestry had broadly similar outcomes. For example, raising the maximum diameter in the residual stand to 70 cm had similar effects on yield reduction, natural mortality rates, and coarse woody debris volume as reserving 15 trees/ha to live out their natural lifespan. Effects of raising the maximum diameter to 80 cm were similar to those of reserving 22 trees/ha (Fig. 1 and Tables 2 and 3). Protecting hemlock and yellow birch from harvest also had similar effects to raising the maximum diameter to 80 cm except that it produced more CWD.

Initial responses in the first 60 years were not always representative of long-term trends. In the first few cutting cycles, the reserve tree treatments with densities of 7–22 trees/ha produced harvest volumes within 92–98% of those generated by standard single-tree selection (Table 2). In later harvests, though, yields steeply declined and leveled off at an average reduction of 9%, 17%, and 26% per cutting cycle with reserve densities of 7, 15, and 22 trees/ha, respectively (Fig. 1). In contrast, yields from treatments with maximum diameters of 70 and 80 cm, which were 15–24% below the standard single-tree selection harvest in the first cutting cycle, remained fairly constant over the 300-year time span (Fig. 1). Purposeful retention of trees for coarse woody debris (selected from trees that would otherwise be harvested) caused immediate reductions in yield—an 18–20% decrease by year 60 compared to selection treatments with the same maximum diameter (Table 2). Yields decreased an additional 16–17% by year 300. In all treatments, harvest volumes in the first 60 years were higher than subsequently because of the relatively high initial volume in a previously unmanaged stand (Table 2).

Treatments that mainly manipulated opening sizes (group selection and multi-cohort) but retained a 60 cm maximum dbh had little effect on cumulative harvested volumes. Following each relatively heavy multi-cohort harvest, however, stands in subsequent decades contained fewer trees large enough for sawtimber compared to stands managed only by single-tree selection. After a multi-cohort harvest, 56% (SD ±3%) of total yield in the subsequent two single-tree selection harvests with a 70 cm maximum dbh was composed of sawtimber trees, compared to 71% (SD ±2%) in stands treated solely by single-tree selection with the same maximum diameter.

"Recoverable volume" represents the wood volume potentially available if management objectives shifted from an ecological forestry method back to either conventional single-tree selection or even-aged methods. Based on this metric, much of the loss in harvest volume for ecological forestry treatments, at least over a moderate planning horizon of 60 years, was still 'held in reserve' in the form of greater standing live volume compared to standard selection. After three cutting cycles in year 60, treatments with maximum diameters of 70 and 80 cm retained 19–28% more residual volume than the standard selection harvest (Table 2). If this surplus residual volume were to be harvested at that point and averaged in with harvests over the previous 60 years, cumulative yield would be reduced only by 5–8% relative to standard selection. The reduction would be even less if the comparison is based on the

Table 2
Predicted mean productivity attributes of the stand following ecological forestry treatments.[*,†]

Treatment	Harvest volume (m^3 ha^{-1} yr^{-1})		Natural mortality (m^3 ha^{-1} yr^{-1})		Residual volume (m^3 ha^{-1})		Recoverable volume[‡] (m^3 ha^{-1} yr^{-1})	
	Year 60	Year 300	Year 60	Year 300	Year 60	Year 300	Year 60	Year 300
Control (no treatment)	–	–	3.31^{a}	4.23^{a}	460^{a}	432^{a}	7.66^{f}	7.20^{ab}
Maximum diameter								
60 cm dbh	6.08^{a}	4.03^{a}	1.62^{e}	0.88^{j}	197^{k}	194^{jk}	9.36^{a}	7.27^{a}
70 cm dbh	5.17^{d}	3.38^{c}	1.82^{cd}	1.22^{hi}	234^{fg}	231^{gh}	9.08^{b}	7.24^{a}
80 cm dbh	4.63^{h}	2.89^{d}	2.00^{b}	1.53^{ef}	253^{d}	246^{e}	8.85^{c}	6.99^{c}
Group selection (250 and 450 m^2 gaps)								
60 cm max dbh	6.04^{a}	4.01^{a}	1.64^{e}	0.94^{j}	198^{jk}	194^{k}	9.34^{a}	7.24^{a}
70 cm max dbh	5.12^{de}	3.31^{c}	1.82^{cd}	1.30^{gh}	235^{fg}	231^{gh}	9.04^{bc}	7.16^{b}
80 cm max dbh	4.14^{h}	2.87^{de}	2.03^{b}	1.61^{de}	253^{d}	246^{e}	8.83^{c}	6.96^{c}
Reserve trees (60 cm max dbh)								
7 reserve trees/ha	5.94^{ab}	3.65^{b}	1.63^{e}	1.14^{i}	202^{j}	212^{ij}	9.30^{a}	7.19^{ab}
15 reserve trees/ha	5.83^{b}	3.35^{c}	1.67^{de}	1.35^{gh}	207^{i}	229^{hi}	9.28^{a}	7.16^{b}
22 reserve trees/ha	5.64^{c}	3.00^{d}	1.69^{de}	1.60^{de}	216^{h}	242^{ef}	9.24^{a}	7.03^{c}
CWD creation (+ group selection)[¶]								
60 cm max dbh	4.98^{ef}	2.65^{fg}	1.56^{e}	0.92^{hi}	198^{k}	194^{k}	8.27^{d}	5.84^{d}
70 cm max dbh	4.14^{j}	2.13^{h}	1.84^{c}	1.28^{h}	236^{f}	230^{gh}	8.07^{e}	5.93^{d}
80 cm max dbh	3.74^{k}	1.83^{i}	2.04^{b}	1.57^{ef}	253^{d}	245^{e}	7.95^{e}	5.87^{d}
Species harvest restrictions (70 cm max dbh)								
Retain all hem and YB	4.86^{fg}	2.80^{ef}	1.89^{bc}	1.76^{cd}	256^{d}	256^{cd}	9.12^{ab}	7.07^{c}
Retain all hem and YB + group selection	4.98^{ef}	2.70^{ef}	1.92^{bc}	1.46^{fg}	247^{e}	256^{cd}	9.09^{ab}	6.97^{c}
Retain half hem and YB allowable cut	5.21^{cd}	3.29^{d}	1.84^{c}	1.28^{h}	234^{fg}	231^{gh}	9.11^{b}	7.14^{c}
Retain half hem and YB allowable cut + gs	5.22^{cd}	3.35^{c}	1.87^{c}	1.27^{h}	236^{fg}	230^{gh}	9.16^{b}	7.19^{ab}
Multi-cohort harvests								
60 cm max dbh for selection harvests	5.31^{c}	3.94^{a}	1.60^{e}	1.25^{h}	231^{g}	199^{jk}	9.49^{a}	7.26^{a}
70 cm max dbh for selection harvests	4.87^{fg}	3.34^{c}	1.65^{de}	1.51^{ef}	266^{c}	234^{fg}	9.31^{a}	7.24^{a}
80 cm max dbh for selection harvests	4.38^{i}	2.94^{d}	1.81^{cd}	1.80^{bc}	281^{b}	252^{d}	9.06^{b}	7.14^{c}
7 reserve trees/ha (80 cm max dbh)	4.34^{i}	2.85^{de}	1.84^{c}	1.79^{bc}	281^{b}	255^{cd}	9.01^{bc}	7.11^{c}
15 reserve trees/ha (80 cm max dbh)	4.36^{i}	2.65^{fg}	1.75^{d}	1.91^{bc}	283^{b}	257^{cd}	9.08^{b}	6.93^{c}
22 reserve trees/ha (80 cm max dbh)	4.32^{i}	2.48^{g}	1.78^{cd}	1.93^{b}	283^{b}	260^{bc}	9.04^{bc}	6.81^{c}
Retain all hem and YB (70 cm max dbh)	4.80^{g}	2.52^{g}	1.79^{cd}	1.77^{cd}	278^{b}	267^{ab}	9.44^{a}	6.97^{c}

[*] Values with same letters in each column not significantly different (Tukey's HSD test, family-wise error rate of $\alpha = 0.05$). Mean untransformed standard deviation for data columns 1–8: 0.09, 0.10, 0.09, 0.11, 2.70, 3.00, 0.09, 0.10; transformed variables were used for significance tests.
[†] Residual volumes (m^3 ha^{-1}) are based on mean standing volumes in years 60 and 300. The volumetric rates shown (m^3 ha^{-1} yr^{-1}) are based on means of the three cutting cycles prior to years 60 and 300.
[‡] Recoverable volume = (total harvested volume + residual volume)/(measurement interval; i.e., 60 years in this table).
[¶] In the first three harvests, wood volumes retained for CWD creation were 1.14, 0.99, and 0.85 m^3 ha^{-1} yr^{-1} for the 60, 70, and 80 cm maximum diameters, respectively; in the final three harvests, retained wood volumes were 1.43, 1.26, and 1.12 m^3 ha^{-1} yr^{-1}, respectively.

final 60 years or if the entire stand volume were utilized (Table 2). Similar trends occurred in the reserve tree treatments, where recoverable volumes with 22 reserve trees/ha were only 1–6% below that of the standard selection harvest.

3.2. Simulated structural characteristics and similarities to old growth

3.2.1. Size distributions and the abundance of large trees

Under the low-browse scenarios simulated here, all selection treatments converted the initial unimodal size distribution to the negative exponential target distribution by the second harvest (simulation year 40 and total stand age of 140 years; chi-square test: $\chi^2 = 3.4$, df = 8, $P = 0.9$; K–S test: $d = 0.11$, $P = 1$). Size distributions in all multi-cohort treatments approached the negative exponential form 40 years later, in simulation year 80 and a total stand age of 180 years (chi-square for the 70 cm max diameter treatment: $\chi^2 = 5.7$, df = 8, $P = 0.68$; K–S test: $d = 0.22$, $P = 0.99$). Multi-cohort harvests delayed the development of a negative exponential size distribution by removing trees relatively uniformly among size classes. However, the new cohort of trees recruited after the relatively heavy multi-cohort harvest did not develop into a persistent irregular size distribution, as is often present in old-growth stands of the region (e.g., Tyrrell and Crow, 1994b). A major reason was that most of the excess pole trees (<25 cm dbh) were removed in subsequent single-tree selection harvests before they could advance into larger diameter classes.

The 22 ecological forestry treatments had highly variable effects on the degree to which the size distribution of live trees satisfied old-growth structural criteria. The initial stand contained almost 40% of the total basal area in trees >46 cm dbh, and with no treatment reached old-growth status in <15 years (115 years after the original commercial harvest ca. 1905). Most harvest treatments, though, merely maintained mature forest structure or vacillated between mature and borderline old-growth structure. Trials with 70 cm maximum diameters maintained ~44% of total stand basal area in trees >46 cm dbh (Table 3), close to the minimum threshold of 45% in the old-growth structural classification. In reserve-tree treatments with a 60 cm maximum diameter, no more than 38% of stand basal area consisted of large trees (Table 3). Treatments with 80 cm maximum diameters, as well as those that protected all hemlock and yellow birch, were the only ones to consistently promote negative exponential size distributions with large trees similar to those in the later stages of old-growth development (Fig. 2).

3.2.2. Accumulation of coarse woody debris

Coarse woody debris levels in the control treatment (no harvest) were more than double the abundance predicted for most of the ecological forestry treatments. Due to natural mortality, the volume of CWD in the control steadily increased to a maximum of ~190 m^3 ha^{-1} in year 165, and then declined to ~160 m^3 ha^{-1} in year 300 (Fig. 3). In the standard selection treatment, dead wood volume increased to 77 m^3 ha^{-1} following the first harvest, then declined to 44 m^3 ha^{-1} by year 300. The purposeful retention of coarse woody debris in selection trials produced the most CWD volume among the ecological forestry treatments, but the

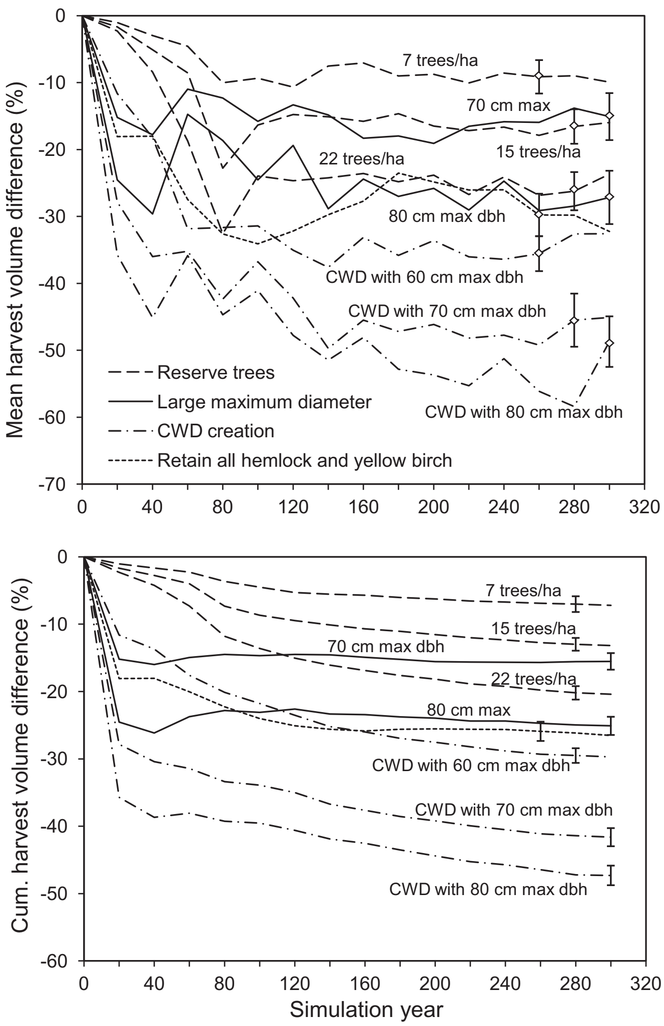

Fig. 1. Percent difference in harvested volume of ecological forestry treatments relative to standard single-tree selection with a 60 cm maximum retained diameter. Maximum retained dbh was 60 cm in reserve-tree treatments and 70 cm in species retention treatments. Top graph: % mean volume differences in each 20-year cutting cycle. Error bars indicate mean 95% confidence interval of the difference in mean harvested volume over the 300-year simulations. Bottom graph: % cumulative volume difference of alternative treatments through time. Error bars indicate 95% confidence interval of the difference in mean cumulative volume in year 300. Confidence intervals shown were calculated from untransformed data; transformed data were used in significance tests.

treatment retaining all hemlock and yellow birch approached similar levels by simulation year 150 (Fig. 3). Reserve-tree treatments did not result in significant increases in snag and downed log volume in the first 60 years, but in later decades, CWD volume was 20–50% higher than in standard selection (Table 3 and Fig. 4).

For treatments that also actively created CWD in addition to raising maximum residual live-tree diameters, fewer live trees needed to be girdled or felled to reach the CWD target because of higher natural mortality. But timber yield under CWD retention with an 80 cm maximum live-tree diameter was 25–31% lower than in CWD retention with a 60 cm maximum dbh, and yet it resulted in no significant increase in dead wood volume. By the end of the simulation, approximately 35% of harvestable volume (volume of 'surplus trees' above the residual size distribution) was retained as coarse woody debris in these three CWD retention treatments.

Effects of treatments on the volume of medium to large dead trees (>40 cm dbh) followed a pattern similar to total coarse woody debris abundance. By year 60, dead-tree volume was not higher in reserve-tree treatments than in the standard selection trial (Fig. 4). Among the ecological forestry treatments, medium to large dead trees were most abundant in trials of coarse woody debris retention with large maximum diameters. These were followed by treatments restricting the harvest of hemlock and yellow birch and other treatments with 80 cm maximum diameter. These treatments with large maximum diameters or species harvest restrictions, along with the control, were the only trials in which >50% of the total dead wood volume was comprised of very large dead trees (>60 cm dbh; Fig. 4).

Multi-cohort trials produced coarse woody debris volumes similar to those in other treatments with the same maximum diameters except for peak CWD volumes in about simulation year 150 (Fig. 3). The peaks correspond to increased tree mortality as stand basal area recovered to the minimum level required to perform a multi-cohort harvest. In these treatments, the mean time for the stand to regain the required basal area of 30 $m^2\ ha^{-1}$ before initiating a multi-cohort harvest was 34 years (SD ±1) in the 60 cm maximum diameter treatment, 34 (±2) in the 70 cm treatment, and 36 (±3) years in the 80 cm trial. Following multi-cohort harvests, the 60, 70, and 80 cm maximum diameter treatments required 23 (±1), 26 (±1), and 30 (±2) years, respectively, for the stand basal area to recover from the post-harvest residual (20–23 $m^2\ ha^{-1}$) to a level of 27 $m^2\ ha^{-1}$ needed to re-initiate single-tree selection harvests.

3.3. Species compositional trends

With the exception of treatments that protected all hemlock and yellow birch, the ecological forestry treatments produced minimal variation of species composition on this site. In the control treatment, sugar maple remained heavily dominant, hemlock declined to about half of its initial level (to 7% relative basal area), and yellow birch remained at low levels (1–1.5%). Compared to the control, all treatments resulted in more yellow birch but also less hemlock in most cases (Table 3 and Fig. 5). In nearly all trials, sugar maple comprised >80% of stand basal area by year 60 and >90% by year 300 (Table 3). Group selection openings and multi-cohort harvests generally increased the relative abundance of yellow birch by 1–2 percentage points and had little effect on hemlock compared to treatments with no groups. Treatments with large maximum diameters retained higher proportions of hemlock than most other treatments in the short term, but eventually hemlock declined to similarly low levels (Table 3).

Retention of all hemlock and yellow birch in selection, group selection, and multi-cohort treatments greatly enhanced the prominence of the two species, and both species were more abundant in these scenarios than in the unmanaged control. In the first few decades, hemlock abundance increased rapidly as only sugar maple and other less abundant species were harvested, but more than 100 years elapsed before yellow birch exceeded 5% of the total stand basal area (Fig. 5). In treatments that removed only half of the allowable cut of hemlock and yellow birch, hemlock did not decline as much as in most other treatments, although it was only 60–75% as abundant as in the untreated control by year 300. Yellow birch, however, was substantially more abundant than in the control and most other treatments, including conventional single tree-group selection (Table 3).

4. Discussion

4.1. Mechanisms of structural retention effects on species composition and yield

Despite the high shade tolerance and late-successional status of most of the component species, yield reductions under ecological

Table 3
Predicted stand structural characteristics following ecological forestry treatments.[*,†]

Treatment	%BA >46 cm dbh		CWD volume (m^3 ha^{-1})		Species abundance (% basal area)					
	Year 60	Year 300	Year 60	Year 300	Year 60			Year 300		
					SM	Hem	YB	SM	Hem	YB
Control (no treatment)	64.4[a]	58.5[a]	138[a]	161[a]	74.5[h]	16.0[c]	1.0[g]	89.5[d]	7.3[c]	1.4[i]
Maximum diameter										
60 cm dbh	26.1[i]	26.8[k]	64[g]	44[h]	82.5[bc]	7.0[hi]	1.7[def]	93.3[a]	0.8[f]	3.7[efhg]
70 cm dbh	43.9[g]	44.4[fg]	74[d]	55[g]	81.4[cdef]	9.3[ef]	1.5[ef]	93.1[ab]	0.8[ef]	4.1[de]
80 cm dbh	49.5[e]	50.3[de]	81[c]	67[f]	80.6[efg]	10.3[de]	1.8[def]	93.1[ab]	1.1[def]	3.8[efhg]
Group selection (250 and 450 m^2 gaps)										
60 cm max dbh	29.6[i]	26.6[k]	64[g]	46[h]	82.4[bc]	6.8[i]	2.2[c]	92.1[c]	0.7[f]	4.7[cd]
70 cm max dbh	44.6[f]	43.5[g]	73[de]	58[g]	80.4[efg]	8.9[fg]	1.8[cde]	91.5[cd]	0.9[def]	5.4[c]
80 cm max dbh	48.9[e]	51.3[de]	82[c]	70[ef]	79.8[fg]	10.5[de]	2.0[cd]	91.9[c]	1.5[d]	4.8[cd]
Reserve trees (60 cm max dbh)										
7 reserve trees/ha	29.9[i]	31.0[j]	63[g]	53[g]	82.6[bc]	7.2[hi]	1.8[cde]	93.5[a]	1.0[def]	3.2[fgh]
15 reserve trees/ha	33.2[h]	35.2[i]	66[fg]	58[g]	82.0[bcde]	8.3[fgh]	1.8[cde]	93.8[a]	1.1[def]	3.0[gh]
22 reserve trees/ha	35.9[h]	37.8[h]	66[efg]	66[f]	80.6[efg]	9.4[def]	1.8[cde]	93.4[a]	1.4[de]	3.0[gh]
CWD creation (+ group selection)										
60 cm max dbh	29.5[i]	26.6[k]	107[b]	102[bc]	81.9[bcde]	7.0[hi]	2.2[c]	91.5[c]	0.7[f]	5.0[cd]
70 cm max dbh	45.4[f]	43.8[fg]	111[b]	110[b]	80.7[defg]	9.3[ef]	1.7[def]	91.9[c]	0.9[ef]	5.2[c]
80 cm max dbh	48.9[e]	50.9[de]	113[b]	112[b]	79.4[g]	10.8[d]	2.1[cd]	91.5[cd]	1.1[def]	5.3[c]
Species harvest restrictions (70 cm max dbh)										
Retain all hem and YB	50.9[d]	51.0[de]	78[cd]	87[d]	62.4[i]	27.6[a]	3.3[b]	58.0[ef]	24.4[b]	15.9[b]
Retain all hem and YB + group selection	50.9[d]	51.8[cd]	82[c]	90[d]	61.6[i]	28.4[a]	3.6[b]	48.1[f]	28.6[a]	21.8[a]
Retain half hem and YB allowable cut	47.2[ef]	45.1[fg]	82[c]	52[g]	70.0[h]	18.3[b]	1.1[g]	85.2[d]	4.4[c]	8.3[bc]
Retain half hem and YB + group selection	46.8[ef]	43.8[g]	83[c]	54[g]	69.9[h]	18.5[b]	1.4[f]	80.8[ef]	5.5[c]	11.6[b]
Multi-cohort harvests										
60 cm max dbh for selection harvests	43.7[g]	27.1[k]	65[g]	45[h]	84.4[a]	4.4[j]	3.4[b]	91.2[c]	0.8[f]	5.4[c]
70 cm max dbh for selection harvests	54.9[c]	45.0[fg]	73[def]	58[g]	83.1[ab]	6.7[i]	2.9[b]	91.6[c]	0.9[def]	5.2[c]
80 cm max dbh for selection harvests	58.4[b]	50.1[e]	81[cd]	68[ef]	81.9[bcde]	8.3[fgh]	2.9[b]	91.7[c]	1.1[def]	4.9[cd]
7 reserve trees/ha (80 cm max dbh)	59.2[b]	51.7[de]	82[c]	67[f]	82.3[bcde]	7.7[ghi]	3.1[b]	92.0[c]	1.0[def]	4.8[cd]
15 reserve trees/ha (80 cm max dbh)	59.4[b]	53.3[bc]	79[cd]	73[ef]	81.9[bcde]	8.2[fgh]	3.2[b]	92.2[bc]	1.1[def]	4.8[cd]
22 reserve trees/ha (80 cm max dbh)	59.6[b]	54.3[bc]	79[cd]	75[ef]	81.6[bcde]	8.9[fg]	3.0[b]	92.1[c]	1.2[def]	4.8[cd]
Retain all hem and YB (70 cm max dbh)	55.5[c]	51.0[de]	79[cd]	95[cd]	61.9[i]	25.5[a]	5.7[a]	49.0[f]	26.9[ab]	22.6[a]

[*] Values with same letters in each column not significantly different (Tukey's HSD test, family-wise error rate of $\alpha = 0.05$). Mean untransformed standard deviation for data columns 1–10: 0.83, 0.78, 3.50, 3.61, 0.93, 0.77, 0.31, 0.91, 0.31, 0.62.
[†] Table entries are based on mean values in years 60 and 300.

forestry methods in northern hardwoods were not substantially less pronounced than for less tolerant species such as Douglas-fir in the Pacific Northwest. In both ecosystems, yield reductions of about 25% could be expected after relatively modest increases in the number or volume of residual trees (Hansen et al., 1995; Rose and Muir, 1997). In northern hardwoods, for example, a 26% increase in residual stand volume over a conventional selection harvest resulted in a 28% decline in net production due to increased mortality and slower tree growth (residual volume about 57% that of an old-growth stand; 80 cm max dbh treatment in Table 2). Over a limited planning horizon such as 60 years, most of this volume loss is potentially 'recoverable' if management objectives switched back to conventional selection harvests. But over a span of hundreds of years, recoverable volume becomes only a small fraction of the yield reduction (e.g., 9% over a span of 500 years for the preceding example). The conclusion that net production for shade-tolerant species is reduced, and mortality increased, as residual volume increases is consistent with trends observed in independent field studies. For example, in a 50-year replicated experiment in second-growth northern hardwoods, the untreated control had 227% higher mortality and 58% lower net production than stands managed by standard single-tree selection (Strong, 2005).

In spite of the yield reductions, however, all treatments generated more than the minimum harvest volume usually required for economically viable timber sales to private contractors on federally-managed hardwoods in the region (>4.6 m^2 ha^{-1} of basal area removed in each cutting cycle; Mark Thiesen, Chequamegon-Nicolet National Forest, *personal communication*). Only the selection harvest with retention of CWD in conjunction with a maximum residual diameter of 80 cm dbh produced yields lower than the minimum required on a 20 year cutting cycle, and only by a small amount (each of the final three harvests removed an average of 4.4 m^2 ha^{-1}).

Simply raising the maximum retained diameter in selection harvests increased mortality volume in forest stands in the last three cutting cycles by 39–74% compared to standard single-tree selection. Size-mortality trends in mesic temperate forests are frequently U-shaped, with a steep increase in mortality rates for trees >65 cm dbh (Busing and Wu, 1990; Lorimer et al., 2001; Fraver et al., 2008; Salk et al., 2011). Thus, treatments that raised the maximum diameter led to an increase in the abundance of trees with high risks of death, reducing harvest volumes but raising CWD levels. Increased mortality rates accounted for 52–57% of the volume reduction in the last three cutting cycles relative to standard selection (i.e., difference in mortality volume divided by difference in harvested volume; Table 2). Although larger maximum diameters only reduced stand-level volume growth of surviving trees by 6–10%, 38% of the overall harvest reduction was attributable to slower growth of surviving trees, and 10% or less to a slower rate of new recruitment into the smaller size classes (Table 4).

Unlike the treatments with large maximum diameters, reserve-tree treatments had only a small effect on harvest volume, CWD volume, and large tree abundance until the third or fourth harvest (after 60–80 years of management). The reason is that reserved trees do not affect forest structure and yield, relative to standard selection harvests, until they grow beyond the specified maximum diameter for the other trees in the residual stand. In unmanaged northern hardwoods, the approximate mean size of canopy trees at the time of death is 50 cm (Lorimer et al., 2001). Because of the high natural mortality of large trees, the model predicts that the long-term mean number of reserve trees >60 cm dbh would

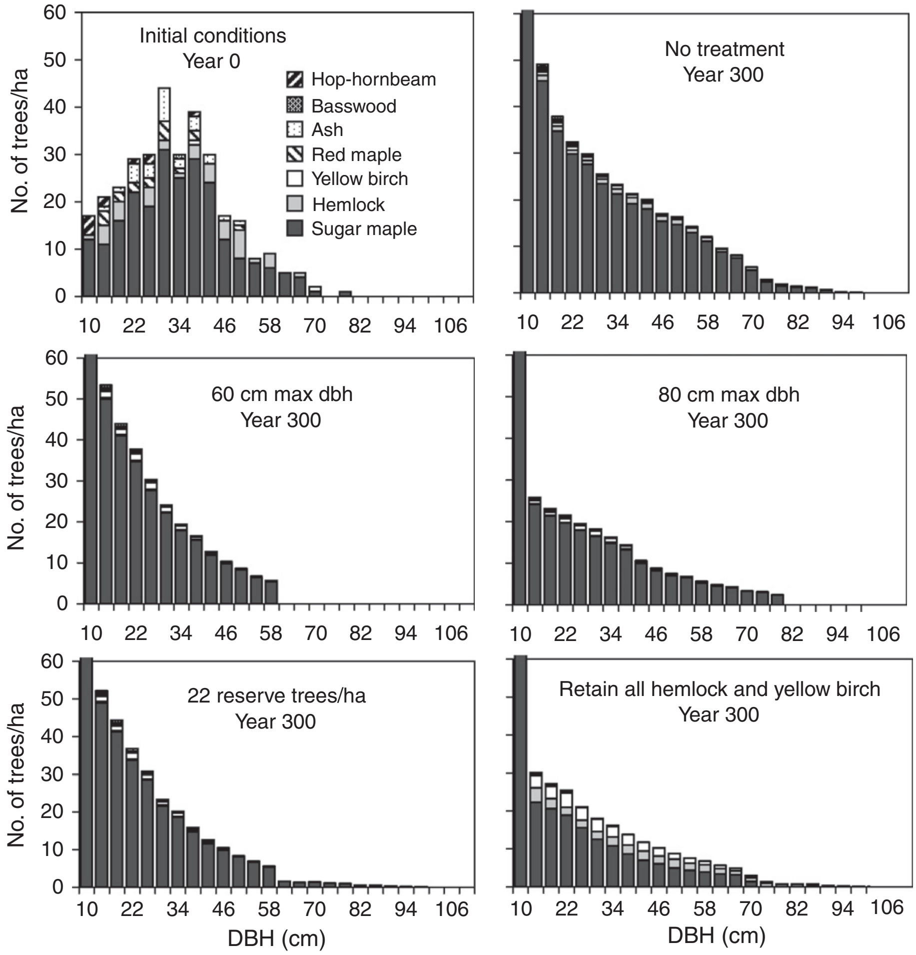

Fig. 2. Diameter distribution of the initial forest stand and mean distributions in year 300 with no treatment, standard single-tree selection harvest with 60 cm maximum dbh, and three ecological forestry treatments. Each treatment was simulated on a 9 ha forest stand and replicated 10 times. *X*-axis labels are size-class midpoints. Scientific names of minor species: hop-hornbeam (*Ostrya virginiana*), basswood (*Tilia americana*), ash (*Fraxinus* spp.), red maple (*Acer rubrum*).

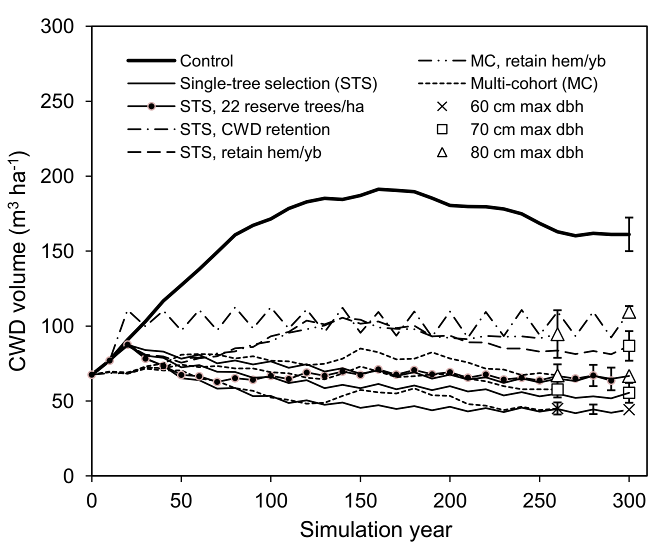

Fig. 3. Mean coarse woody debris volume (snags and logs) in selected treatments through time. In each of the multi-cohort trials, the final single-tree selection harvest occurred between simulation years 260 and 270. Error bars indicate mean 95% confidence intervals of CWD volume over the 300-year simulations. Confidence intervals shown here were calculated from untransformed data.

be equal to less than half (~40%) of the originally prescribed reserve-tree density. Redefining reserve trees to include only those larger than the maximum retained diameter, rather than the prescribed 7, 15, and 22 trees/ha, results in 'realized' reserve tree densities of 3, 6, and 9 trees/ha, respectively. Reductions in harvested volume of 9–26% under these scenarios are similar to those reported in even-aged stands of Douglas-fir with low densities of reserve trees (Hansen et al., 1995; Zenner et al., 1998).

Yield reductions attributable to reserve trees can be linked to both their occupancy of 'unutilized' growing space and their competitive effects on nearby trees (Rose and Muir, 1997). An estimate of the space occupied by reserve trees was obtained by multiplying the density of 'realized' reserve trees (3, 6, or 9 trees/ha) by their mean exposed crown area (140 m^2). To adjust yields to account for the unavailable growing space, harvested volumes of the three reserve-tree treatments were then divided by the proportion of the stand area available to harvestable trees (i.e., 1 – proportion of space occupied by reserve trees). In all reserve-tree treatments, slightly less than half of the total reduction in harvested volume, relative to standard selection harvests, was attributable directly to the canopy space preempted by reserve trees.

A second independent estimate of the reduction in yield due to space occupancy can be obtained from the mortality volume of reserve trees. After several hundred years, the reserve trees have reached quasi-equilibrium density; mortality volume of 'realized' reserve trees is approximately equal to the sum of the volume growth of the surviving reserve trees and volume of trees newly recruited into the 'realized' reserve-tree population. Dead realized

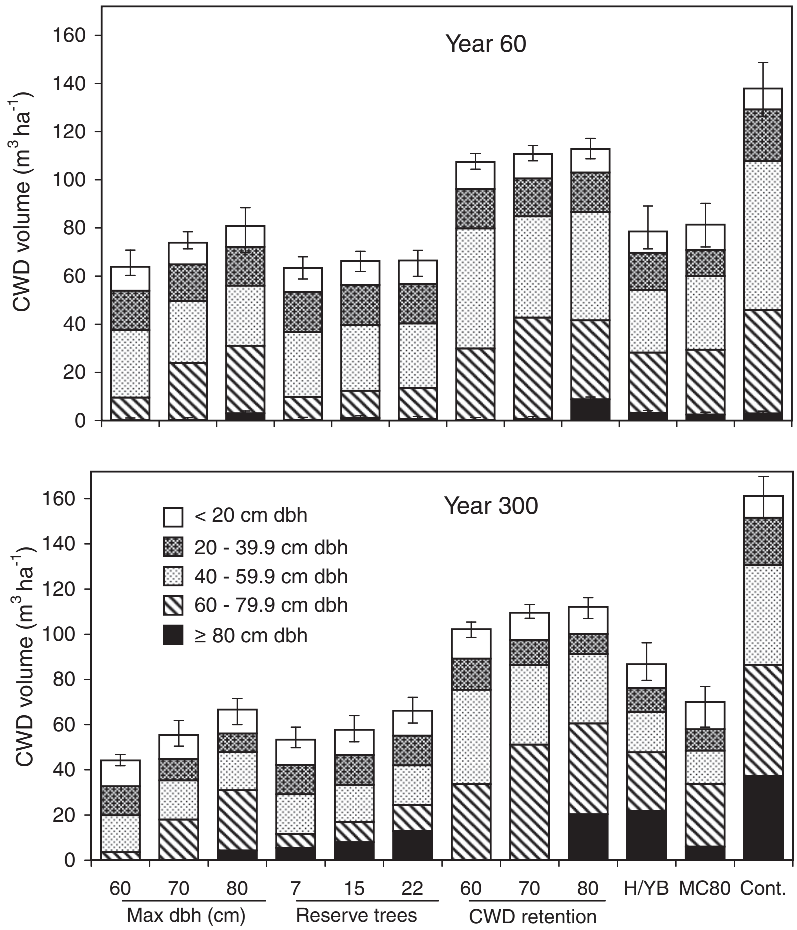

Fig. 4. Predicted volume of coarse woody debris (snags and logs) produced in each of five broad size classes following 60 (top graph), and 300 (bottom graph) years of ecological forestry treatments. Vertical lines on histogram bars represent maximum and minimum volumes (m^3 ha^{-1}) of total CWD simulated in 10 replications of each treatment. Abbreviations: H/YB, all hemlock and yellow birch reserved from harvest; MC80, multi-cohort treatment + single-tree selection harvests with 80 cm maximum diameters; Cont., control.

reserve trees contributed means of 0.18, 0.34, and 0.51 m^3 ha^{-1} yr^{-1} of dead wood volume with 3, 6, and 9 realized reserve trees/ha. This likewise accounts for approximately 50% of the total yield reduction (mortality volume of dead realized reserve trees divided by the difference in harvested volume of the treatments). The remaining reduction in yield was again due to crowding effects from higher residual basal areas; reserve trees >60 cm dbh increased residual basal areas by 1.5–3.8 m^2 ha^{-1}, depending on their density. Compared to standard single-tree selection, the reserve trees caused a reduction in survivor volume growth of the non-reserve 'matrix' trees of 3–9%, a 14–30% reduction in ingrowth volume, and a 9–24% increase in mortality volume (Table 4).

4.2. Comparisons of model predictions with field observations

While direct comparisons with long-term ecological forestry trials are not available, simulated results can be compared to a local, independent single-tree selection field trial on similar sites on the Argonne Experimental Forest but not used in the calibration of CANOPY. Observed mean harvest volume in the Argonne stand was 4.27 m^3 ha^{-1} yr^{-1} for the three most recent cutting cycles (Strong, 2005), compared to the long-term mean of 4.03 m^3 ha^{-1} yr^{-1} simulated by the CANOPY model for a stand with the same target diameter distribution (<6% difference; Table 2). Observed mortality rates in the field trial were 0.82 m^3 ha^{-1} yr^{-1} compared to long-term means of 0.88 m^3 ha^{-1} yr^{-1} in simulated treatments. Residual stand volumes were similar following the field and simulated selection trials, with 204 m^3 ha^{-1} on the Argonne Experimental Forest and 195 m^3 ha^{-1} in simulated stands (Table 2). The predicted 36% reduction in yield of the first harvest in the 80 cm maximum diameter–CWD retention treatment compares with a 43% reduction in a Vermont northern hardwood stand with similar specifications (Keeton, 2006).

The simulated log and snag volume of 44 m^3 ha^{-1} in standard selection harvests compares with 46 m^3 ha^{-1} measured by Goodburn and Lorimer (1998) in northern hardwood selection stands (harvest tops and branches excluded since branch volumes are not simulated in CANOPY). The final (year 300) predicted coarse woody debris volumes in the control treatment of 160 m^3 ha^{-1} are similar to downed wood volumes of 139 and 166 m^3 ha^{-1} observed in old-growth northern hardwood forests of New Hampshire (Carbonneau, 1986; McGee et al., 1999) but are higher than the total coarse woody debris volume of 127 m^3 ha^{-1} reported in old-growth northern hardwoods of upper Michigan (Goodburn and Lorimer, 1998). The higher site quality of the Argonne stand in the current study may account for some of the difference; Spetich et al. (1999) noted an almost linear trend between site productivity and total CWD volume in other old-growth forests of the Midwest. However, model CWD predictions are tentative and can likely be improved by obtaining direct estimates of wood volume reduction due to decay, rather than the current approximations based on reductions in wood density.

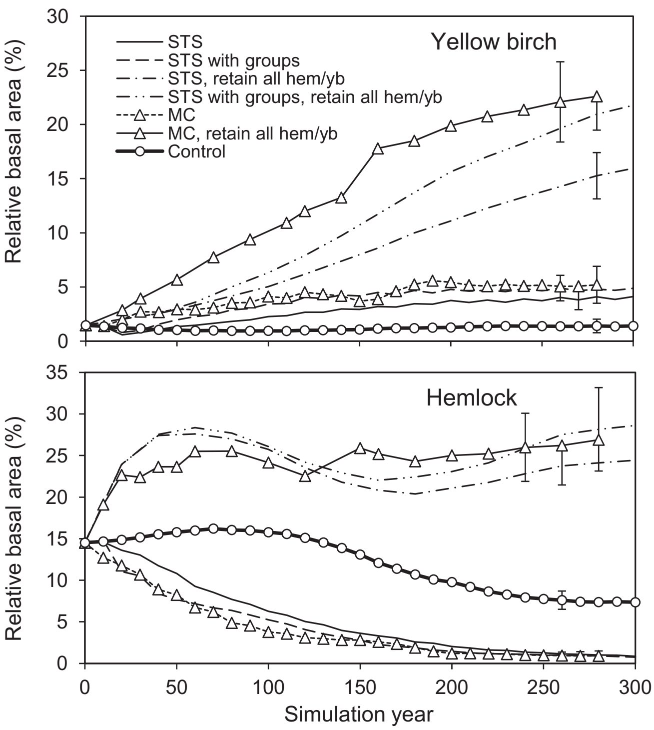

Fig. 5. Predicted species proportions over time under ecological forestry treatments. All single-tree selection treatments shown here have maximum dbh of 70 cm. STS, single-tree selection treatments; MC, multi-cohort treatments. The final single-tree selection harvest in multi-cohort treatments was in simulation year 270. Error bars indicate mean 95% confidence intervals of species proportions over the 300-year simulations. Confidence intervals shown here were calculated from untransformed data.

The actual trajectory of treated stands in the future will likely gradually diverge over time from simulated results because of changes in environmental factors such as global climate, invasive species, and natural disturbances. Natural disturbances can be expected to reduce the large-tree component in some stands, although 60–70% of the northern hardwood landscape prior to European settlement in this region met the stated minimum structural criteria for old-growth stands in spite of frequent natural disturbances (Frelich and Lorimer, 1991a,b; Schulte and Mladenoff, 2005). Imminent changes in global climate and invasive species will likely have much more drastic impacts. These will present daunting challenges for modelers, as data are currently limited and interactions among factors poorly known. For example, hemp-nettle (*Galeopsis tetrahit*), a recently arrived exotic plant in northern Wisconsin, now dominates many of the forest openings in the companion field study to this project and has unknown implications for future regeneration patterns. Exotic earthworms may also make it difficult for seedling regeneration of sugar maple and other species by removing much of the litter and duff layers (Corio et al., 2009); interactions are complex and depend on many factors such as the species of worms present and their relative biomass (Bohlen et al., 2004). The fact that 30 years ago, few ecologists anticipated the potential impacts of these invasives—or the decimation of major tree species such as eastern hemlock and ashes (*Fraxinus* spp.) by exotic insects—raises a cautionary note about the ability of models to forecast actual future stand conditions in an era of global change. Until the mechanisms and interactions are better understood, it may be necessary to periodically recalibrate forest models with permanent plot data to reflect these emerging influences on species composition, structure, and yield.

4.3. Relative merits of alternative treatments for balancing ecological and production concerns

Although all of the ecological forestry alternatives involved tradeoffs in lowered timber production vs. gains in old-growth structural features, two general approaches—reserving sensitive species and raising the maximum diameter—stand out as having a relatively high ratio of 'benefits to cost.' The treatment that reserved all hemlock and yellow birch fostered the development of stands that met the minimum structural criteria of old growth and by year 300 had CWD volumes about double those of standard single-tree selection. It also substantially increased the proportion of hemlock and yellow birch over time relative to the control, resulting in the highest species diversity (evenness component; Fig. 2). The corresponding 18–33% decline in harvest volume compared to standard selection was less pronounced than in the CWD treatments and multi-cohort treatments with the higher reserve-tree density. Single-tree selection with a raised 80 cm maximum diameter also fostered stands that exceeded minimum old-growth structural criteria, and the level of harvest decline was similar to the treatment reserving all hemlock and yellow birch. CWD volume was about 50% higher than under standard selection in the last three cutting cycles. But as in standard selection, hemlock declined drastically relative to the control.

Treatments that only removed half of the allowable cut of hemlock and yellow birch were intermediate in both positive ecological gains and reductions in harvest volume relative to standard selection. Stands had borderline old-growth structure, greater species equitability, and modest gains in CWD.

In treatments that protected all hemlock and yellow birch, the harvest burden was shifted almost exclusively to sugar maple. As hemlock and yellow birch became more abundant, each harvest removed an even greater proportion of sugar maple from the stand. By the end of the simulation, almost 50% of the forest stand was comprised of the two protected species. In this paper, however, all treatments were simulated with CANOPY's 'low browse' setting for hemlock recruitment and the 'no drought' scenario for yellow birch mortality. Hemlock recruitment in many areas is currently inhibited by excessive deer browsing (Rooney et al., 2000; Witt and Webster, 2010), and periodic severe droughts can cause high mortality of large yellow birch (Prey et al., 1988; Erdmann, 1990; Lorimer et al., 2001). Actual long-term abundances of these two species in many areas are therefore likely to be lower than predicted under conditions presumed in these simulations.

Examination of the underlying calibration data elucidated some of the likely mechanisms of hemlock decline predicted under most of the silvicultural treatments. There is a great deal of scatter in the calibration data showing the relationship between the proportion of hemlock saplings in the regeneration pool and stand variables like stand basal area and relative basal area of hemlock. However, 60% relative overstory basal area of hemlock and a stand density that is 80% of regional averages for managed stands (Tubbs, 1977) appear to be critical threshold values, below which abundance of hemlock saplings declines rapidly. While standard single-tree selection and most ecological forestry treatments maintain stand densities above these thresholds, examination of individual 900 m^2 subplots showed that competition level often dipped well below these threshold values at the subplot level. This outcome was exacerbated by the algorithm of the automated harvester that preferentially reduced locally dense patches of forest and removed the allowable cut of large trees first, of which hemlock was often the most prominent. A possible long-term reduction in hemlock even under conservative silvicultural treatments may warrant further field study. Our results tentatively suggest that if patches of hemlock are entered for harvest, foresters should mark

Table 4
Predicted demographics ($m^3\ ha^{-1}\ yr^{-1}$) of 'matrix trees' (i.e., non-reserve trees) in selected treatments of simulated single-tree selection harvests over the final 60 years of simulation.

Treatment	Survivor growth[a]	Ingrowth[b]	Mortality[c]	Loss to reserves[d]	Exp. harvest[e]	CANOPY harvest
60 cm max dbh	4.12	0.80	0.88	0.00	4.04	4.03
70 cm max dbh	3.87	0.74	1.22	0.00	3.39	3.38
80 cm max dbh	3.69	0.76	1.53	0.00	2.92	2.89
7 reserves/ha	3.99	0.69	0.96	0.06	3.66	3.65
15 reserves/ha	3.89	0.64	1.01	0.14	3.38	3.35
22 reserves/ha	3.76	0.56	1.09	0.24	2.98	3.00

[a] Survivor growth: volume growth of living trees present at both the beginning and end of the measurement period.
[b] Ingrowth: mean annual wood volume of trees that grew into the 11.7 cm minimum dbh of harvestable trees.
[c] Mortality: mean annual wood volume of trees that died during the final 60 years of simulation treatments.
[d] Loss to reserves: mean annual wood volume of living trees >60 cm dbh transferred to reserve tree population.
[e] Expected harvest = survivor growth + ingrowth − mortality − loss to reserves.

these patches very lightly and not reduce the proportion of hemlock in the residual stand.

Occasional irregular, multi-cohort harvests generated little to no decrease in harvest yields relative to selection treatments with the same maximum diameter (Table 2). However, the increased horizontal heterogeneity with variable opening sizes may be helpful in providing habitat conditions for a range of fauna and flora uncommon in stands managed by conventional uneven-aged methods (e.g., Kohn and Eckstein, 1987; Annand and Thompson, 1997; Costello et al., 2000), including moderately shade tolerant tree species such as yellow birch (Webster and Lorimer, 2005; Hanson and Lorimer, 2007).

In CANOPY simulations, however, the spatially variable multi-cohort harvests in this stand did not result in tree species composition much different than in the group selection treatments (Fig. 5). The minimal response of the midtolerant yellow birch to openings as large as 0.5 ha is likely attributable to the fact that more than 2/3 of the stand area is on habitat types (AOCa and ATD) not conducive to yellow birch establishment and growth. These habitat types are typically heavily dominated by sugar maple (Kotar et al., 2002; Bakken and Cook, 1998). Yellow birch abundance is expected to be much greater following multi-cohort harvests on ATM habitats, where it can comprise 40% of the trees in gaps >400 m^2 (Webster and Lorimer, 2005; Halpin, 2009).

Reserve-tree retention was generally less efficient overall in meeting ecological goals and minimizing yield reductions than the other treatments above, at least in restoring old-growth characteristics. Even the highest level of reserve trees did not result in CWD volumes any greater than the 80 cm maximum diameter treatment (where no trees were permanently reserved from cutting), nor did it meet minimum old-growth structural standards for live trees. Of the two ecological forestry treatments with the explicit goal of increasing the number of large trees, raising the maximum residual diameter appeared to be more efficient at minimizing reductions in yield. Maximum diameter treatments of 70 cm and 80 cm dbh produced residual stands with an average of 13 and 22 trees/ha >60 cm dbh, respectively, compared to only 3–9 trees/ha >60 cm dbh retained by the three reserve-tree treatments. For the maximum diameter treatments, this equates to ~1.0–1.5% reduction in yield for each tree >60 cm dbh, given the long-term mean reduction per cutting cycle of 16–28% for the 70 and 80 cm dbh trials (Fig. 1). Reserve-tree treatments, on the other hand, resulted in reductions of 2.5–3% for each 'realized' reserve tree, almost double that of the maximum diameter trials. The difference between the two treatments appears to be due to the utilization of all available growing space by harvestable trees in maximum diameter treatments, unlike reserve-tree treatments. The combination of coarse woody debris retention with the 80 cm maximum diameter treatment produced yield reductions of approximately 2.3–2.7% per large tree (50–60% reduction in harvested volume with 22 trees/ha >60 cm dbh), very similar to predicted reductions in reserve-tree treatments.

There has been a recent trend for master plans on US national forests to set up 'zones' within a forest type with different ecological and timber management goals. For example, in the Chequamegon-Nicolet National Forest in Wisconsin, some northern hardwood tracts are designated for standard single-tree selection with a maximum 60 cm residual diameter. Other zones are designated to maintain 'interior' forest conditions using criteria such as retention of reserve trees, increased maximum tree sizes, and retention of sensitive species (USDA Forest Service, 2004). The ecological forestry options examined in our study appear to vary widely in both ecological benefits and corresponding harvest reductions, which offer managers much flexibility in selecting management regimes for different objectives. Lower densities of reserve trees can accomplish some ecological goals with minimal yield reductions, but the present study also suggests that reserve trees alone are not always the most effective or efficient means of fostering old-growth structural features.

Retention of reserve trees in uneven-aged stands ideally requires that a crew mark reserve trees by some permanent means (e.g., metal tree tags) and continually replenish the reserve tree population at each entry. Another option is to leave reserve trees unmarked but re-designate a new set of reserve trees every time the stand is marked for harvest (the current procedure on national forests in northern Wisconsin). Alternatively, this study suggests that raising the maximum diameter of the residual stand and protecting some individuals of long-lived or sensitive species may be a more effective and presumably less costly way of allowing some trees to live out their natural lifespan because it requires no separate marking/inventory procedures. It is also a more readily verifiable system since unmarked reserve trees below 60 cm dbh are impossible to identify, whereas it is fairly easy to verify that sensitive species have been retained and that a stand has a specified residual diameter distribution and maximum tree size. Ecologically, this approach would help maintain a diverse species composition and promote similar levels of CWD and tip-up mounds as in reserve-tree retention, given the similar natural mortality rates under these two approaches (Table 2). Yet our results suggest that residual stands with an increased maximum diameter would also result in much greater numbers of large trees and a forest structure more closely resembling old growth than under the existing reserve-tree guidelines, but without causing further decreases in harvest yields.

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