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Effects of Management on the Composition and Structure of Northern Hardwood Forests in Upper Michigan

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ABSTRACT. To improve our understanding of how management affects the composition and structure of northern hardwood forests, we compared managed with unmanaged sugar maple (*Acer saccharum* Marsh.) dominated forests. Unmanaged old-growth and unmanaged second-growth forests provided baselines for comparing the effects of even-aged and uneven-aged forest management on selected aspects of biological diversity. Three replications of each condition were located on the Winegar Moraine in Michigan's Upper Peninsula. Old-growth forests were multistoried, dominated by a few, large trees with well-developed crowns extending over a subcanopy stratum 10–15 m in height and an abundance of woody vegetation (mostly sugar maple seedlings) at 2–3 m. This complex stand structure contrasts with the relatively uniform structure of unmanaged second-growth forests with a closed overstory canopy and limited understory development. Forest management, both even- and uneven-aged, created forest structures that were more complex than their unmanaged second-growth baselines, yet managed forests lacked some of the structural complexity characteristic of old-growth. Managed forests had fewer large trees (stem diameter at 1.37 m > 50 cm) and considerably less basal area in dead trees when compared with old-growth. There were fewer tree species in managed forests because commercially important tree species were favored for retention and, when present, early successional species (e.g., *Populus grandidentata* Michx., *Populus tremuloides* Michx.) were harvested. A subcanopy comprised of large shrubs and small trees characteristic of old growth was absent in managed forests, but this structural element may develop with time under management. As expected, thinning the overstory and disturbing the forest floor through tree harvesting promoted understory development in managed forests. Most of the added species, however, were common in the landscape and thus added little to overall species richness. For. Sci. 48(1):129–145.

Key Words: Plant diversity, stand structure, northern hardwoods, *Acer saccharum*, silviculture, Michigan, forest management, old-growth.

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SILVICULTURAL TREATMENTS ARE commonly applied to manipulate the composition and structure of forests with the purpose of producing timber and other forest products. Although the effects of such treatments on tree growth, mortality, and regeneration are well studied, these effects are poorly understood from a more comprehensive ecosystem perspective. As an example, Noss and Cooperrider (1994, p. 190–191) suggest that many forestry practices reduce biological diversity through loss of species richness and loss of structural and functional complexity. There is reason for concern, because losses in diversity may affect ecosystem processes such as net primary productivity and nitrogen dynamics (Tilman et al. 1997, Hooper and Vitousek 1997). However, the effects of management practices on biological diversity are difficult to determine because many interrelated factors affect biological diversity (Hansen et al. 1991, Probst and Crow 1991, Thomas et al. 1999); there are many facets to biological diversity (Franklin 1993, Crow et al. 1994, Roberts and Gilliam 1995); and it is difficult to ascribe causation based on observation alone (Huston 1997).

In the Great Lakes region, both even- and uneven-aged management have been applied to northern hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.). Individual tree selection, an uneven-aged management system, has been used extensively to manage the shade-tolerant sugar maple, while clearcutting and shelterwood, two even-aged systems, have been applied to a lesser extent (Erdmann 1986). When properly applied, the initial treatment for both even- and uneven-aged management involves thinning the stand to decrease canopy density and to increase the abundance of established regeneration in the understory.

Individual tree selection was first developed by foresters to manage mature stands of hardwoods (Eyre and Zillgitt 1953, Arbogast 1957, Crow et al. 1981). When northern hardwoods are managed using individual-tree selection, a stand structure results over time that can be characterized as a reversed J-shaped distribution of tree diameters with many small trees and a few large trees. A widely accepted definition of an uneven-aged forest is one in which there are at least three age-classes of overstory trees intermingled throughout the stand (Smith 1962, p. 13). Individual-tree selection tends to favor the regeneration of shade-tolerant species such as sugar maple (Crow and Metzger 1987).

A forest is considered even-aged if the differences between the oldest and youngest trees in the overstory do not exceed 20% of the rotation length (Smith 1962, p. 13). In contrast to the negative exponential distribution (reversed J-shaped) common to uneven-aged forests, stem density by diameter class in even-aged forests is more normally distributed. When properly applied to northern hardwood forests, clearcutting and shelterwood silvicultural methods often result in a higher proportion of shade intolerant or mid-tolerant hardwood species compared to uneven-aged management (Crow and Metzger 1987).

The objective of our study was to compare the structural complexity and species richness in forest ecosystems dominated by sugar maple under traditional management regimes (even- and uneven-aged) to the complexity and richness found in forests that were unmanaged (second-growth and old-growth). Complexity refers to variation in the distribution of biomass, both living and dead, in the forest, while richness refers to the number of plant species, including tree, shrub, and herbaceous species. We tested the null hypotheses (H_0) that management practices have no effect on the structural complexity, composition, or species richness of northern hardwood forests growing in similar environments.

Methods

Site Description

The study was established in northern hardwood forests located in Michigan's Upper Peninsula on the Ottawa National Forest, Watersmeet and Iron River Ranger Districts (Figure 1). All study sites were located within Albert's (1995) Sub-Subsection IX.3.2, which is the Winegar Moraine, a prominent glacial feature located in the western portion of the Upper Peninsula and extending southwestward into northern Wisconsin. This regional ecosystem is characterized by acidic, rocky, sandy loam, or loamy sand soils derived from iron-rich Precambrian bedrock. The Winegar Moraine was formed by the Ontonogan Lobe of the late Wisconsin glaciation and is a rolling, sandy and loamy terminal moraine complex with strongly collapsed hill and swale topography and a large number of embedded wetlands.

To further minimize variation in the physical environment, all study sites were limited to ecosystems mapped primarily as Ecological Landtype Phase (ELTP) 38B or 38C within Sub-Subsection IX.3.2 (Albert 1995). Both ELTPs are characterized by moderately well-drained sandy loam and loamy sand, but differ in degree of slope. ELTP 38B has nearly level to gently sloping moraines (1 to 6%), while ELTP 38C has gently to strongly sloping moraines (6 to 18%). A fragipan, often occurring 45–90 cm below the surface in ELTP 38, may significantly influence soil moisture, especially following snowmelt when soils are likely to be saturated. (Jim Jordan, pers. comm.). All study areas were heavily dominated by sugar maple, with lesser amounts of yellow birch (*Betula alleghaniensis* Britton), American basswood (*Tilia americana* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr), red maple (*Acer rubrum* L.), and eastern hophornbeam (*Ostrya virginiana* [Mill.] K. Koch).

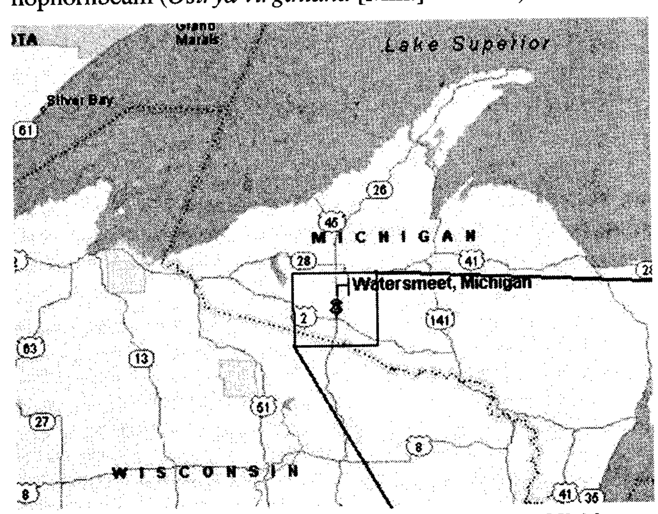


Figure 1. Locations of study sites in western Upper Michigan.

Study Design and Field Measurements

Study areas were selected to provide three replicates each of two treatments, even-aged and uneven-aged management, and two controls, unmanaged second-growth and unmanaged old-growth. The size of the 12 study areas ranged from 10 to 90 ha. To ensure statistically independent replicates (Hurlbert 1984), sites were separated by a minimum of 1,000 m, but in most cases, several kilometers or more separated the study sites. Within each site, a line grid was established along cardinal directions at 40 m intervals with the intersections of the grid serving as reference points to guide movement within the site and for establishing plots and sample points.

The richness of plant species was investigated by sampling species present in 1/12 ha circular (16.28 m radius) overstory plots, 1/20 ha circular (12.62 m radius) shrub and small tree plots, and 100 m^2 (10 × 10 m) understory plots. In each site, ten 1/12 ha plots were located by randomly selecting north-south and east-west coordinates within the line grid. In each plot, we measured diameter at breast height (dbh, 1.37 m) for both live and dead trees. On three of the ten plots, stem height of tree species ≥ 1.5 cm dbh was also measured. Based on these measurements, the following were calculated: presence (species lists), frequency by species, diameter distributions for trees ≥ 1.5 cm dbh, mean vertical height to top of upper canopy, and mean vertical height to top of subcanopy when present. A relative importance value (IV) was calculated for each tree species by summing the relative density and relative dominance (based on basal area) and dividing by two [modified from Cottom and Curtis (1956)]. We predicted aboveground biomass for trees from stand basal area and mean stand height using a regression equation from Crow (1978).

We recorded species, stem height, and basal stem diameter for shrub and tree species ≥ 1 m in height but < 1.5 cm dbh on the 1/20 ha plot nested within each 1/12 ha plot. From these measurements, species presence, frequency of species, mean height, and stem frequency by 40 cm height classes were determined.

Tree and shrub species < 1 m in height and herbaceous species were recorded in three 100 m^2 plots located randomly in each site. The size of this plot was based on plant species–area relationships examined by determining the cumulative number of species present in nested 1, 4, 16, 32, 60, 130, 200, and 300 m^2 circular plots. To measure presence and percent cover, the 10 × 10 m plot was subdivided into four 5 × 5 m subplots, with percent cover recorded by species in one randomly drawn subplot and a species list compiled in each subplot. The 10 × 10 m plots were sampled in late spring and again in mid-summer and early fall to capture total species diversity throughout the growing season.

Canopy structure was investigated by establishing a 10 × 30 m transect established along a randomly selected azimuth at a fixed point within each treatment and control, and by sketching canopy profiles and mapping crown projections. Sketches were prepared to scale in the field using telescoping height poles and clinometers to determine tree heights and crown dimensions. Sketches were checked for accuracy by comparison with photographs. Crown projections were mapped by sighting the edges of crowns along a vertically extended height pole and plotting the location of various points along crown edges on a 10 cm grid established on the ground with transect tapes.

Management History

All managed stands were last entered for harvesting from 1 to 3 yr prior to the establishment of our study in 1994 (Table 1). To the extent possible, sites were selected that had been managed for similar periods of time. Regardless of the management approach, an important objective in managing northern hardwoods is the sustained production of high quality veneer and sawlogs (Erdmann 1986).

Table 1. A summary of the management history for each study site. All sites were located on the Watersmeet and Iron River Districts, Ottawa National Forest, in Michigan's Upper Peninsula.

Treatment	Replicate	Management history
Even-aged	1	A crop-tree release was conducted in 1979. Thirty-two hectares of the study area were thinned in 1981. The remaining 16 ha were thinned in 1993.
Even-aged	2	Thinned in 1993 to ≈ 25 m^2 ha^{-1} basal area in trees >30 cm dbh. The site index is 19.8 m at age 50 for sugar maple.
Even-aged	3	Thinned in 1995 to ≈ 18 m^2 ha^{-1} of basal area in trees >30 cm dbh. Site index is 19.5 m at age 50 for sugar maple.
Uneven-aged	1	An individual-tree selection harvest occurred on part of the study area in 1992 and on the remaining area in 1994.
Uneven-aged	2	There have been several individual-tree selection harvests in this stand with the last entry occurring in 1992.
Uneven-aged	3	Same as replicate 2.
Unmanaged second-growth	1	This stand had a limited timber stand improvement treatment conducted in 1977. Disturbance to the forest was minimal.
Unmanaged second-growth	2	Uncut since estimated year of stand origin in 1920 (based on National Forest Vegetative Management Stand Records). Stand basal area is 28 m^2 ha^{-1}.
Unmanaged second-growth	3	Uncut since estimated year of stand origin in 1915. Total stand basal area is 25 m^2 ha^{-1}.
Old growth	1	Uncut. Located immediately adjacent to the north boundary of the Sylvania wilderness Area on the Ottawa National Forest. Estimated date of origin is 1800.
Old growth	2	Uncut. Located on the east side of the Sylvania Wilderness Area. Estimated date of origin is 1774
Old growth	3	Uncut. Located within the Sylvania Wilderness Area. Estimated date of origin is 1750.

This goal is obtained by controlling tree density (a component of structural complexity) at almost every stage of tree and stand development.

The cutting prescription for each of our study areas was obtained from records maintained by the Ottawa National Forest. For uneven-aged management, the guides applied called for reductions in stand basal area to 7.5 –8.0 $m^2 ha^{-1}$ in trees ≥12 cm dbh using individual tree selection. The first priority was to harvest trees that were considered high risk (i.e., likely to be lost to mortality before the next entry) along with those that have obvious defects that reduce their timber quality. Harvesting small groups of trees to create canopy gaps was recommended in order to promote tree regeneration. Uneven-aged management was applied when stands had a significant component of trees in sawtimber size-classes (≥17 cm dbh).

For even-aged management, Erdmann's (1987) guide for small sawlog-size forests dominated by sugar maple was generally followed. In this treatment, forests were thinned to about 90% crown cover, with the goal of leaving 150 to 180 dominant and codominant crop trees per ha. In the thinning operation, high risk, cull, and subcanopy trees were harvested to meet the goal of 90% crown cover. Under even-aged management, several thinnings precede the final harvest—a clearcutting. Only the initial thinning had been conducted in two of the three even-aged treatment areas (Table 1).

Other guidelines that affect composition and structure were applied uniformly across the study areas. In both even- and uneven-aged treatments, eastern hemlock and northern white cedar (*Thuja occidentalis* L.) were retained when present. An average of five to ten den trees per ha was recommended for retention in managed stands as wildlife habitat. Finally, sugar maple and yellow birch ≥50 cm dbh were generally harvested under both management systems. The guidelines used in our study for both even- and uneven-aged management are similar to those applied widely to northern hardwood forests throughout the Great Lakes region.

Statistical Analysis and Data Visualization

One-way and nested analyses of variance (ANOVA) models were used to evaluate differences in species richness, stem density, and basal area. Tests for normality were applied, and either square root or $\log_{10}$ transformations were used when necessary to meet the assumption of normality. If significant differences were found among treatments, Tukey's Honestly Significant Differences (HSD) test was applied for comparisons among means.

Using PC-ORD software (McCune and Mefford 1999), we applied Detrended Correspondence Analysis (DCA) to investigate the underlying structure of the presence/absence data recorded for tree and shrub species <1 m in height and herbaceous species in the 100 m^2 plots located in each site. DCA is an eigenanalysis ordination technique based on reciprocal averaging or correspondence analysis (Hill and Gauch 1980). Measurements recorded in the early fall of 1998 provide the basis for the ordinations.

We used Tukey's (1977) box plot to compare the age structure of trees among the treatments and baselines. This graphical method is ideal for comparing the distributions of groups of measurements (Cleveland and McGill 1985, Cleveland 1993). Each box plot summarizes the age distribution of trees in one treatment or baseline. The vertical line segment inside the box represents the 50th percentile or median age, while the left and right boxes represent the 25th and 75th percentiles, respectively. The distance between these two values, the interquartile range, is a measure of the spread of the distribution. The "whiskers" attached to the box represent "adjacent values." The upper adjacent value is the largest observation ≤ the 75th percentile plus t, and the lower adjacent value is the smallest observation ≥ the 25th percentile minus t, where t is 1.5 times the 75th percentile minus the 25th percentile, i.e., the interquartile range (Tukey 1977). Outliers, which are observations beyond the adjacent values, are plotted individually.

Age Structure

To characterize the age structure of the stands, we extracted increment bores at dbh from 20 sugar maple within each study area. Sampling was restricted to intermediate, codominant, and dominant stems ≥10 cm dbh. Trees were selected from throughout the site to obtain a sample representative of the study area and samples were selected in proportion to the frequency of stems in 5 cm diameter classes up to maximum diameters of 55 to 60 cm on sites with mature trees. Species other than sugar maple were sampled less intensively. Cores were mounted after extraction on grooved boards and sanded before counting annual rings using a stereo-zoom microscope.

Unmanaged forests represented contrasting age structures (Figure 2). As expected, the old-growth forests were all-aged, with trees ranging from 51 to 273 yr of age, and with dominant trees in the overstory generally exceeding 175 yr. In contrast, the age structure was more uniform in the unmanaged second-growth, with the middle quartiles ranging between 50 and 70 yr, and with a few trees > 150 yr.

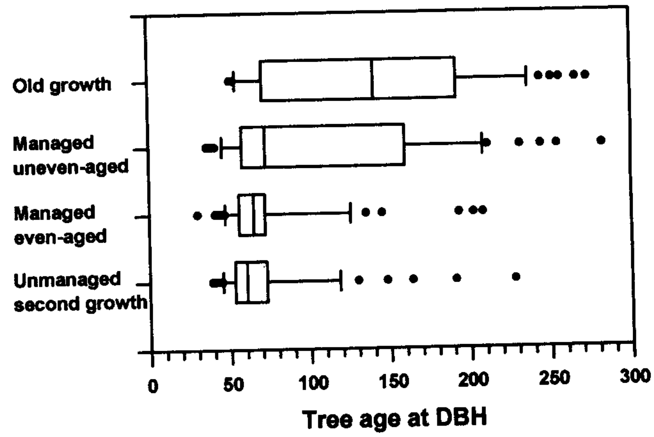


Figure 2. A comparison of the stand age structure among the treatments and baselines using Tukey's (1977) box plots. The box represents the distribution of ages within the first two quartiles along with median age, i.e., the vertical line within the box. "Adjacent values" are represented by the "wiskers" attached to the boxes, and outliers are plotted as points. A more complete description can be found in the Methods. N = 60 for each box plot (20 trees × 3 replications).

The median age for trees sampled in the managed even-aged forest was 65 yr, and the common range as defined by the 25 and 75% quartiles was 56 and 72, respectively, compared to a median age of 61 yr and a common range of 53 and 73 for unmanaged second-growth. Both the managed even-aged and unmanaged second-growth can be described as two-aged forests; they contained a few older trees shown as outliers in the box plots that represent residual trees remaining from the previous stand (Figure 2). Likewise, the comparisons between the age structure for old-growth and managed uneven-aged suggests similarities. For example, the maximum and minimum tree ages are comparable, as is the common range as defined by the quartiles. However, the median tree age for the managed uneven-aged forests (73 yr) was half that for unmanaged old-growth (141 yr).

Based on age structures, unmanaged second-growth was used as the comparative baseline for the even-aged treatment, and unmanaged old-growth was used as the baseline for the uneven-aged treatment.

Results

Composition

Sugar maple dominated both the overstory and understory of these forests (Table 2). Importance values for sugar maple ranged from 66.1 (maximum of 100) in the managed even-aged to 80.7 for the managed uneven-aged (Table 2). Eastern hemlock and yellow birch had the next highest importance values among the common tree species, with 12.9 for eastern hemlock in the old growth and 11.2 for yellow birch in the unmanaged second-growth. Although yellow birch, eastern hophornbeam, American basswood, and eastern hemlock had relatively high percent occurrences in most treatments and baselines, none approached the 100% occurrences recorded for sugar maple (Table 2).

Compared to the old-growth baselines, managed uneven-aged northern hardwoods had fewer tree species (11 compared to 16), slightly greater average importance values for sugar maple (80.7 compared to 70.7), and lacked the assemblage of large shrubs and small trees with stems in the ≥1.5 cm size class that included leatherwood (*Dirca palustris* L.), mountain maple (*Acer spicatum* Lam.), alternate-leaf dogwood (*Cornus alternifolia* L.f.), and hazel (*Corylus cornuta* Marsh.) (Table 2). The basal area of managed uneven-aged forests averaged 23.4 m^2 ha^{-1} ± 1.2 (± SD) compared to 34.0 m^2 ha^{-1} ± 3.6 for old-growth, a difference of 32%. When the amount of variation is expressed as a percentage of the mean basal area (i.e., the coefficient of variation), old-growth had more variation (10.3 vs. 5.2%) associated with the estimate of mean basal area than the managed uneven-aged forest.

Despite the lower dominance of sugar maple, managed even-aged had fewer woody species ≥1.5 cm dbh than the second-growth baseline (13 compared to 16). Two early successional species, bigtooth aspen (*Populus grandidentata* Michx.) and quaking aspen (*Populus tremuloides* Michx.), were still present in small numbers in the unmanaged second-growth, but they were absent from managed forests. Differences in richness of woody species ≥1.5 cm dbh, however, were not statistically significant between managed and unmanaged forests (one-way ANOVA, $F_{3,7} = 0.64$, $P = 0.615$, model $R^2 = 21\%$). The mean basal area for the unmanaged second-growth forest was 31.0 m^2 ha^{-1} ± 3.0 (±SD) compared to 24.3 m^2 ha^{-1} ± 0.6 for the managed even-aged forest, a 22% reduction in basal area. The coefficients of variation for estimates of mean basal area were 9.7% for unmanaged second-growth and 2.5% for even-aged forests.

As measured by species richness, the diversity of shrubs and trees ≥1 m in height and <1.5 cm dbh did not differ significantly between managed and unmanaged forests (one-way ANOVA, $F_{3,8} = 0.40$, $P = 0.758$, model $R^2 =$ 13%). However, species abundance, and to some extent, composition did vary among these forests (Table 3). Within this size class, sugar maple averaged 92% of the stems in the old-growth, 18% in the unmanaged second-growth, 31% in the managed even-aged, and 36% in the managed uneven-aged forests. Two species—black cherry (*Prunus serotina* Ehrh.) and American elder (*Sambucus canadensis* L.)—were locally abundant in managed forests, while other shrubs and small trees—balsam fir, beaked hazel, eastern hophornbeam, and leatherwood—were common to both managed and unmanaged forests (Table 3). Hemlock and yellow birch were largely absent from this size class in both managed and unmanaged forests.

Based on species-area curves, the richness of understory plants in managed forests was slightly greater than for unmanaged forests (Figure 3). The range for number of species sampled at 300 m^2 in the uneven-aged treatment ranged from 35 to 69 (Figure 3c) compared to 14 to 63 for the old-growth baseline (Figure 3a), while the even-aged treatment varied from 41 to 59 species (Figure 3d) compared to 25 to 47 for the second-growth baseline (Figure 3b). The obvious outlier in Figure 3c resulted when the sample plots intersected a logging road in one replication of the uneven-aged managed forest.

Similar trends in richness of understory vegetation between managed and unmanaged forests were evident from sampling herbaceous species and woody plants <1 m in height in the 10 × 10 m plots during the late spring, summer, and early fall of 1997 (Figures 4a, b, and c). Similar trends were found for the three sampling dates in 1998 and 1999. Regardless of sampling period and sampling year, the total number of vascular plant species in managed forests exceeded those for unmanaged forests. These differences, however, were not always statistically significant ($P < 0.05$) (Figure 4). Although introduced species represented a small proportion of the understory flora in these forests, significantly greater proportions were found in managed forests compared to unmanaged forests (Figure 4). Species commonly associated with disturbance areas in our managed study areas included burdock (*Arctium minus* Schk.), golden rocket (*Barbarea vulgaris* R.Br.), bull thistle (*Cirsium vulgare* [Savi] Tenore.), timothy (*Phleum pratense* L.), plantain (*Plantago major* L.), bitter dock (*Rumex obtusifolius* L.), and common dandelion (*Taraxacum officinale* Weber).

Table 2. Means and standard deviations for percent occurrence and importance values (IV) for tree species in managed and unmanaged sugar maple-dominated forests. Values are based on measurements taken in 1/12 ha plots (N = 30); IV = (relative density + relative dominance)/2 for a maximum value of 100. All woody plants with stem diameters ≥1.5 cm were measured.

	Unmanaged				Managed			
	Old growth		Second growth		Uneven-aged		Even-aged	
Species	Percent occurrence	Importance value	Percent occurrence	Importance value	Percent ocurrence	Importance value	Percent occurrence	Importance value
Abies balsamifera	20	0.3 ± 0.1	43	4.8 ± 4.8	—	—	23	3.5 ± 2.9
Acer rubrum	20	0.6 ± 0.7	50	5.3 ± 3.8	10	0.1 ± 0.0	60	9.7 ± 2.8
A. saccharum	100	70.7 ± 10.9	100	73.0 ± 6.0	100	80.7 ± 2.7	100	66.1 ± 10.1
A. spicatum	3	0.0 ± 0.0	—	—	—	—	—	—
Alnus rugosa	—	—	3	0.0 ± 0.0	—	—	—	—
Amelanchier sp.	—	—	3	0.0 ± 0.0	—	—	—	—
Betula alleghaniensis	63	8.1 ± 5.6	70	11.2 ± 13.0	60	4.9 ± 3.7	83	8.4 ± 1.7
B. papyrifera	—	—	—	—	—	—	3	0.1 ± 0.2
Cornus alternifolia	3	0.0 ± 0.0	—	—	—	—	—	—
Corylus cornuta	10	0.2 ± 0.3	—	—	—	—	—	—
Dirca palustris	30	0.4 ± 0.4	—	—	—	—	—	—
Fraxinus americana	10	0.6 ± 1.0	—	—	17	0.4 ± 0.4	3	0.0 ± 0.0
F. nigra	3	0.2 ± 0.3	10	0.5 ± 0.4	3	0.2 ± 0.3	7	0.1 ± 0.2
Ostrya virginiana	63	2.9 ± 2.9	47	1.8 ± 1.5	70	3.8 ± 3.7	47	1.7 ± 2.2
Picea glauca	3	0.0 ± 0.1	7	0.2 ± 0.3	3	0.1 ± 0.1	—	—
Populus grandidentata	—	—	17	1.1 ± 0.8	—	—	—	—
P. tremuloides	—	—	17	1.2 ± 2.0	—	—	—	—
Prunus serotina	—	—	17	0.5 ± 0.8	—	—	10	0.3 ± 0.3
Quercus rubra	—	—	10	0.2 ± 0.4	—	—	—	—
Thuja occidentalis	7	0.2 ± 0.2	7	0.2 ± 0.2	—	—	17	0.7 ± 0.8
Tilia Americana	43	2.8 ± 2.9	57	7.6 ± 9.7	53	2.8 ± 0.7	30	6.7 ± 11.3
Tsuga canadensis	63	12.9 ± 6.6	27	1.7 ± 1.9	60	6.8 ± 1.8	30	2.4 ± 2.2
Ulmus Americana	—	—	—	—	17	0.2 ± 0.1	10	0.3 ± 0.4
U. rubra	7	0.0 ± 0.1	—	—	3	0.0 ± 0.0	—	—

	Unmanaged		Managed	
	Old growth	Second growth	Uneven-aged	Even-aged
Richness (no. of species)	16	16	11	13
Density (stems/ha)	1,124.9 ± 165.6	969.1 ± 195.6	911.2 ± 175.8	706.8 ± 74.1
Basal area (m^2/ha)	34.0 ± 3.6	31.0 ± 3.0	23.4 ± 1.2	24.3 ± 0.6
Mean dbh (cm)	11.7 ± 1.3	16.7 ± 1.0	12.4 ± 1.8	17.5 ± 1.5
Mean height (m)	9.5 ± 1.0	13.9 ± 0.9	11.5 ± 1.2	14.7 ± 1.0
* Mean stand biomass (metric tonnes/ha)	236.2 ± 48.8	201.7 ± 19.2	176.0 ± 21.9	159.4 ± 11.1

* Biomass estimated from $Y = 46.699 + 0.246$ (BH) from Crow (1978); B = stand basal area (m^2/ha) and H = mean stand height (m) where mean height is based on dominant and codominant trees.

The similarity in composition of understory vegetation (herbaceous species and woody plants <1 m in height) among the treatments and baselines can be compared using the DCA ordinations of individual sample plots (Figure 5). Based on presence and absence of understory plants recorded in the fall of 1998, the plots in the unmanaged forests (Figure 5a) were generally less variable in composition than plots in the managed forests (Figure 5b). Those plots from the unmanaged second-growth forests occupied the least volume as defined by the three axes, suggesting the least amount of plot-to-plot variation (Figure 5a), while those in the old-growth still occupy a central position in the cluster of points, but were more variable in composition (Figure 5a) compared to the unmanaged second growth.

The variation in understory composition measured in managed forests was in part associated with logging roads and skid trails. In Figure 5b, outlier plots 41, 55, 72, 84, and 95 were located either on or near logging roads or skid trails.

Table 3. Species richness (summed for three replications per treatment) and mean stem density (# ha^{-1}, N = 3) for shrubs and small trees (≥1 m in height and <1.5 cm dbh).

	Unmanaged				Managed			
	Old growth		Second growth		Uneven-aged		Even-aged	
Species	Mean density (stems/ha)	STD	Mean density (stems/ha)	STD	Mean density (stems/ha)	STD	Mean density (stems/ha)	STD
Abies balsamifera	—	—	252.7	229.9	—	—	229.3	164.6
Acer rubrum	4	6.9	0.7	1.2	—	—	—	—
A. saccharum	1,900.7	1,918.3	89.3	85.6	176.7	116.3	200.7	256.2
A. spicatum	5.3	9.2	—	—	—	—	—	—
Alnus rugosa	—	—	0.7	1.2	—	—	0.7	1.2
Betula alleghaniensis	4	6.9	—	—	—	—	—	—
Cornus alternifolia	2	3.5	—	—	—	—	—	—
Corylus cornuta	73.3	121.8	23.3	35.3	7.3	6.4	31.3	26.1
Dirca palustris	45.3	37.4	12.7	15.1	15.3	11.4	15.3	17.9
Fraxinus americana	8	13.8	—	—	12	20.8	3.3	5.8
F. nigra	3.3	5.8	2.7	4.6	—	—	—	—
Lonicera canadensis	—	—	6	6	0.7	1.2	2	3.5
Ostrya virginiana	30	48.5	94.7	113.5	59.3	92.5	104.7	93.2
Picea glauca	—	—	2.7	4.6	—	—	1.3	2.3
Populus grandidentata	—	—	—	—	—	—	1.3	2.3
Prunus serotina	—	—	9.3	12.8	0.67	1.2	60.7	86.7
Quercus rubra	—	—	—	—	—	—	0.7	1.2
Ribes sp.	—	—	2	2	1.3	1.2	—	—
Sambucus pubens	—	—	1.3	2.3	210	353.3	—	—
Tilia americana	—	—	0.7	1.2	—	—	—	—
Tsuga canadensis	—	—	—	—	—	—	0.7	1.2
Ulmus americana	—	—	—	—	0.7	1.2	0.7	1.2

	Unmanaged		Managed	
	Old growth	Second growth	Uneven-aged	Even-aged
Richness (no. of species)	10	14	10	14
Density (stems/ha)	2,076	498.7	484	652.7
% of total stem density				
Acer saccharum	92	18	36	31
Tsuga canadensis	0	0	0	1

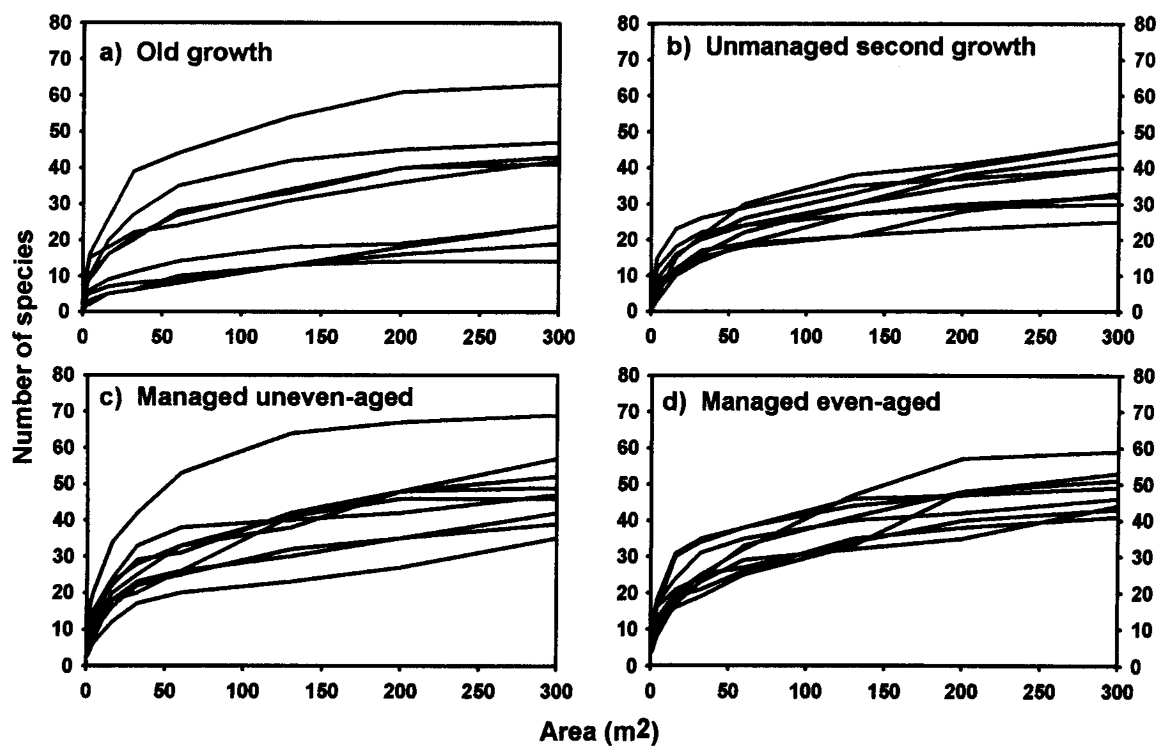
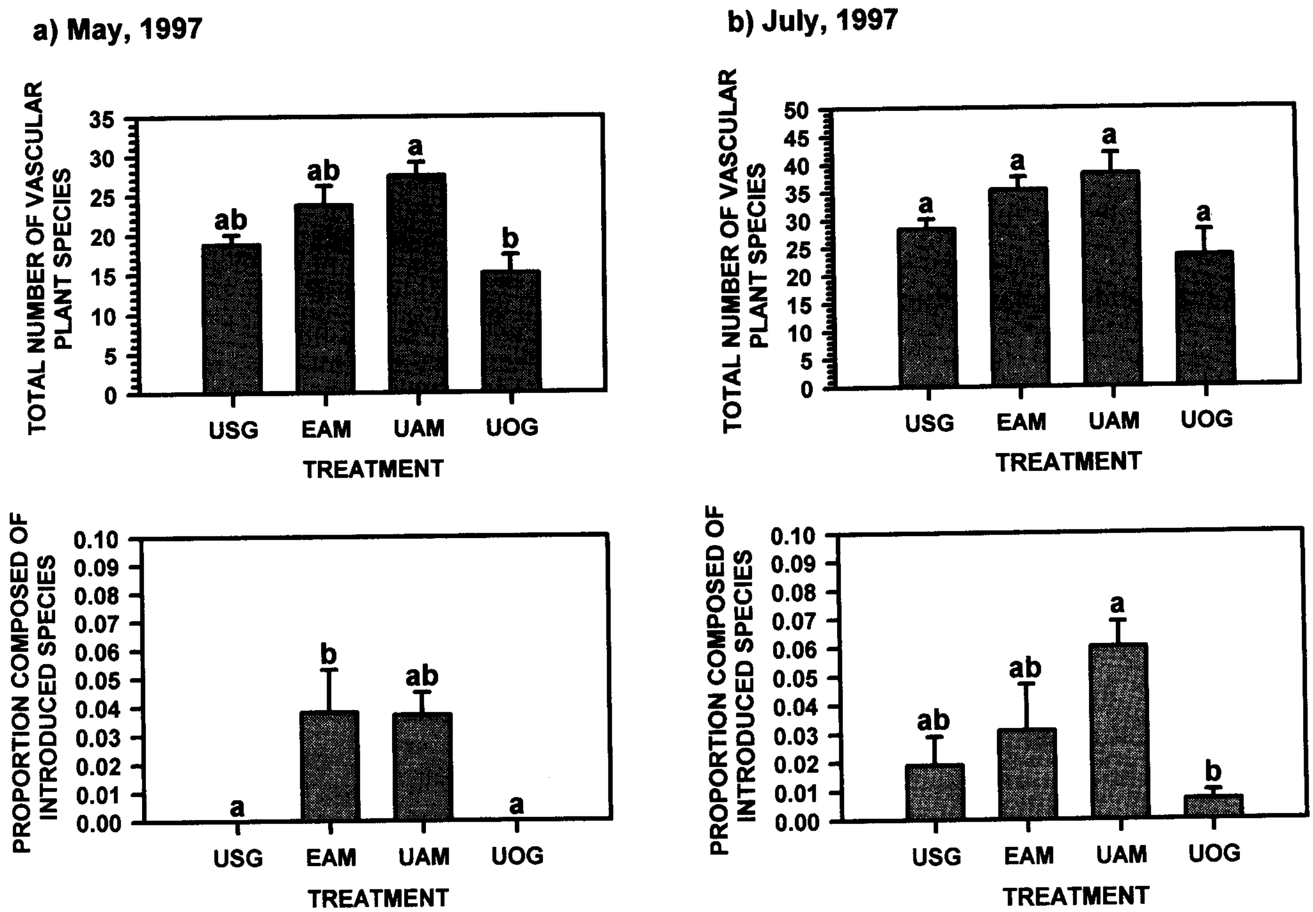


Figure 3. Species area curves for herbaceous species and woody plants <1 m tall in the (a) old growth, (b) unmanaged second-growth, (c) managed uneven-aged, and (d) managed even-aged forests. Each line represents a series of nested plots.



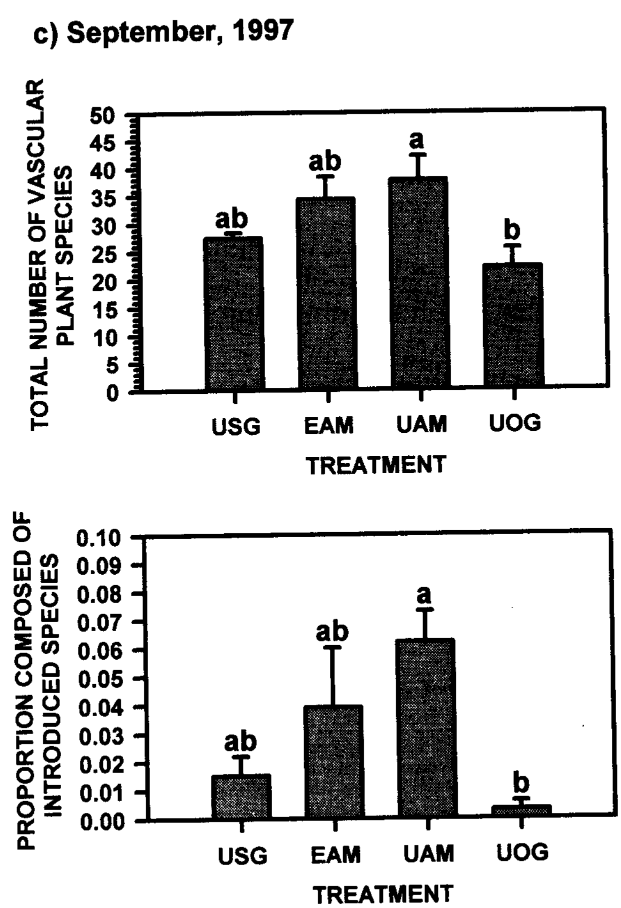


Figure 4. Comparing total number of vascular plants (herbaceous species and woody plant < 1 m high) sampled in (a) May, (b) July, and (c) September by treatments: USG = unmanaged second-growth, EAM = managed even-aged, UAM = managed uneven-aged, UOG = old-growth. Each bar represents the average from ten 10 × 10 m plots in each of three replications. The proportion of total flora consisting of exotic species is also shown by treatment. Means with the same letter are not significantly different ($P < 0.05$).

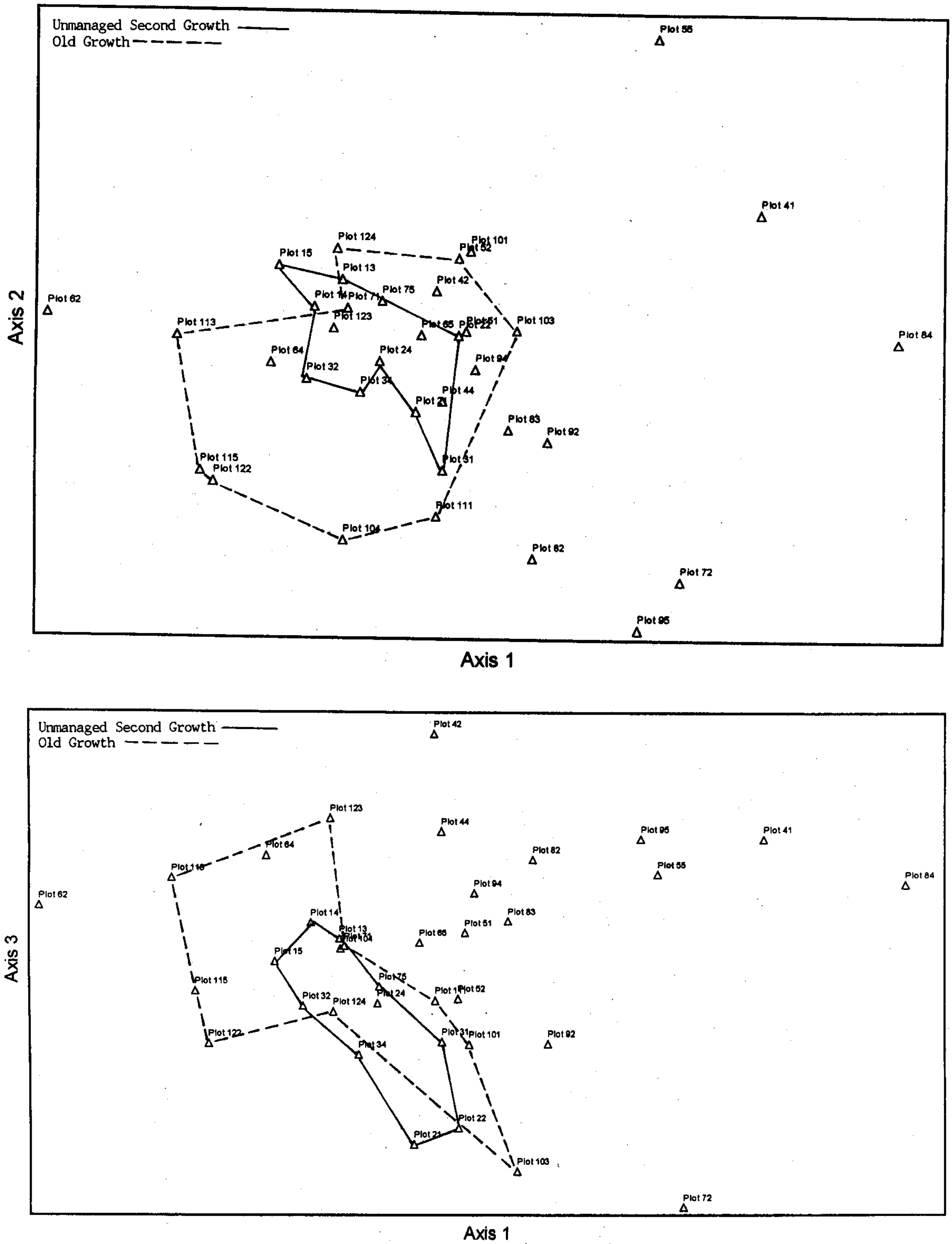


Figure 5a. Application of Detrended Correspondence Analysis (DCA) where relative position along the three axes reflects similarity in plant composition (wood species <1 m in height and herbaceous species) for 36 10 × 10 m plots sampled in September 1998. Lines connect plots from the same treatment or baseline (top) axes 1 and 2, unmanaged second-growth and old-growth; (bottom) axes 1 and 3, unmanaged second-growth and old-growth (continued on next page).

These plots had some of the highest species counts. For all plots sampled, the count averaged 29 species per plot. Plot 55, located on a logging road in an managed even-aged forest, had an abundance of disturbance and edge species—e.g., *Chrysanthemum leucanthemum, Circeum alpina, Epilobium ciliatum, Hieracium aurantiacum, Plantago major, Rumex acetosella, Taraxacum officinalis*—for a total of 57 species. Plot 84, located on a skid trail in an managed uneven-aged forest, was dominated by graminoids including 11 species of *Carex* as well as disturbance species, e.g., *Rumex obtusifolius* and *Cirsium vulgare*. The inclusion of *Scirpus* and *Juncus* among the graminoids and *Onoclea sensibilis* and *Osmunda claytoniana* among the ferns suggests that plot 84 was located on a wet site. Plot 95, located in the managed uneven-aged

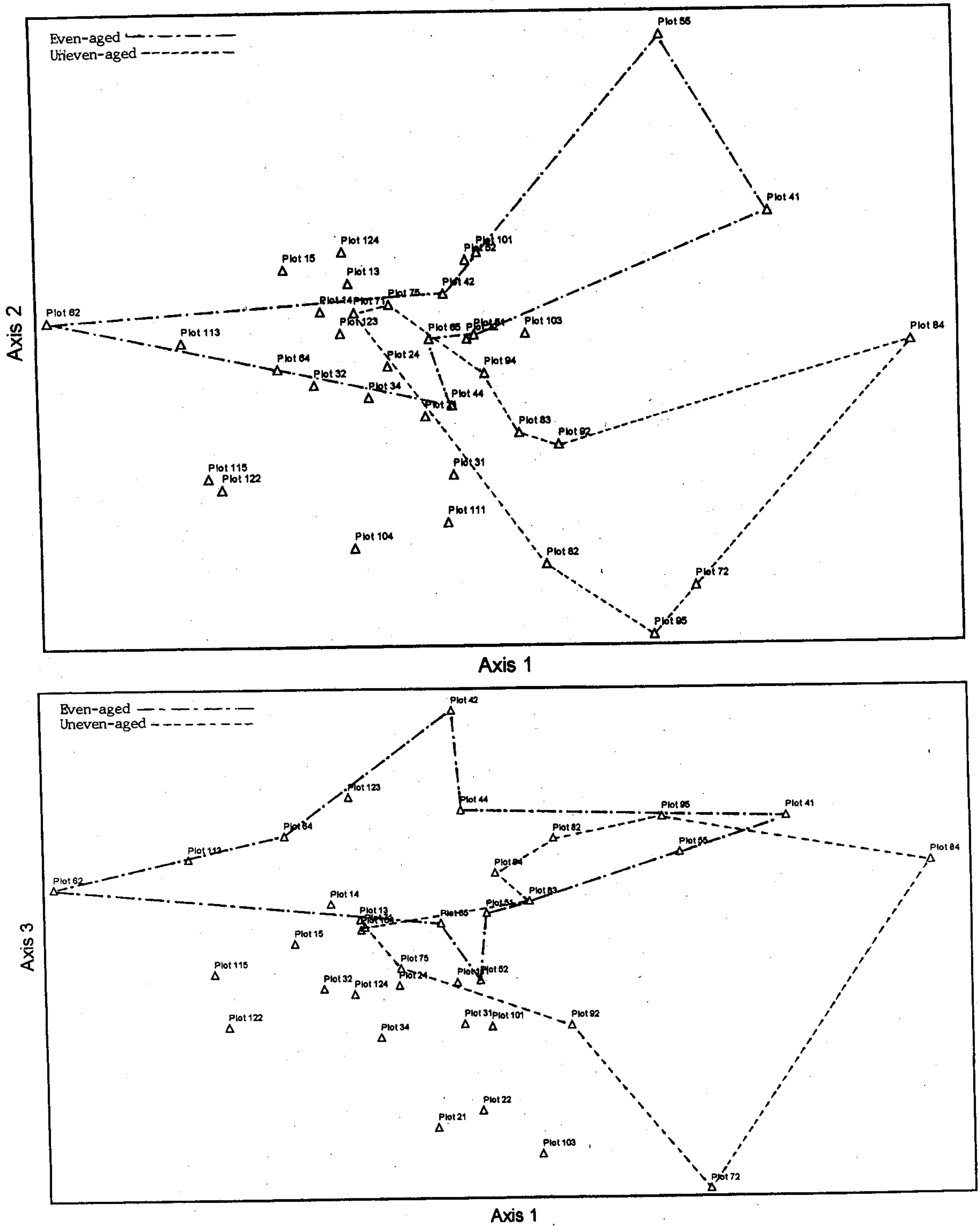


Figure 5b. Application of Detrended Correspondence Analysis (DCA) where relative position along the three axes reflects similarity in plant composition (wood species <1 m in height and herbaceous species) for 36 10 × 10 m plots sampled in September 1998. Lines connect plots from the same treatment or baseline (top) axes 1 and 2, even-aged and uneven-aged; (bottom) axes 1 and 3, even-aged and uneven-aged.

forest, had the greatest richness recorded for understory species—60 species. Plot 95 had relatively few graminoids (five *Carex* species, no *Scirpus* or *Juncus*), but did have a rich assortment of both woodland and disturbance species. At the opposite end of axis 1 (Figure 5b), Plot 62 had a hemlock overstory with an understory that included *Coptis tribolia, Cornus canadensis, Oxalis acetosella* var. *monta,* and four species of *Lycopodium.*

The relationships expressed in the DCA ordination represent differences in the composition of the understory vegetation. The total number of woody species <1 m in height and herbaceous species recorded for managed forests were nearly double the number sampled in the unmanaged forests (Table 4). Increases occurred in all major vegetative groups—summer green herbs, graminoids, ferns and allies, woody species—and so the

Table 4. Number of species and relative proportions of understory plants (woody species <1 m in height and herbaceous species) by species group and treatment/baseline area. Sampling was conducted in 36 10 × 10 m plots (3 per replication) in September 1998.

	Old-growth		Unmanaged second- growth		Managed uneven-aged		Managed even-aged	
Species groups	No. species	% of total	No. species	% of total	No. species	% of total	No. species	% of total
Summer green herbs	24	43.6	28	41.8	49	44.5	41	36.9
Graminoids	12	21.8	10	14.9	28	25.5	25	22.5
Ferns and allies	9	16.4	10	14.9	11	10.0	15	13.5
Woody	10	18.2	19	28.4	22	20.0	30	27.0
Total no. species	55		67		110		111	

relative proportions of understory species by major group remained relatively constant across managed and unmanaged conditions (Table 4).

Management also affected the composition of rare species. A total of 157 understory species (woody species <1 m and herbaceous plants) were recorded in the 36 10 × 10 m plots; 66 species or 42.0% of the total were sampled in only one treatment or baseline. The number of species and the proportion of the total flora unique to one treatment or baseline were greater in managed forests compared to unmanaged forests (Table 5). Only four understory species—*Corallorhiza maculata, Impatiens capensis, Equisetum sylvaticum, and Fraxinus nigra*—were unique to the old-growth forest.

Structure

Managed stands, both even- and uneven-aged, differed in their structural complexity compared to unmanaged forests. Differences in forest structure are obvious in the vertical profiles (Figure 6). A few, large overstory trees with large canopies dominated the old-growth (Figure 6a). In addition to the emergent overstory extending to 25–30 m in height, a subcanopy existed at 10–15 m, and a regenerating forest was common at 2–3 m within the old-growth forest. Variations in tree sizes and canopy gaps created a complex canopy structure. In contrast, the unmanaged second-growth forest had few gaps, a uniform canopy forming a single stratum with little understory development (Figure 6b).

Harvesting decreases tree density and the stand basal area (Table 2), and, as a result, creates gaps in the canopy that allow understory development (Figures 6c and 6d). Comparisons of canopy projections provided in Figure 6 suggest differences in crown size (and perhaps shape) that are related to management. Thinning the maturing forest further reduced the range in crown sizes by eliminating the largest trees from the stand. Based on observation, the larger crowns tended to be more complex in their shapes. While the managed forests are structurally more complex than unmanaged second-growth, they are less complex compared to old-growth.

Table 5. The number of woody species <1 m in height and herbaceous species unique to a single treatment or baseline. Sampling was conducted in September 1998.

Treatment/baseline	No. species unique to area	Total no. species	% total
Old-growth	4	55	7.3
Unmanaged second-growth	5	67	7.5
Managed uneven-aged	31	110	28.2
Managed even-aged	26	111	23.4

Distribution of tree diameters provides another means for comparing forest structure (Figure 7). The old-growth control has the classic reversed-J (negative exponential) distribution in which the number of trees declines rapidly with increasing size classes. Old-growth also has stocking in the largest diameter classes, averaging 32 trees/ha >50 cm dbh (Figure 7a). Managed uneven-aged forests (Figure 7c) also have negative exponential diameter distributions, but with fewer saplings in the 1.5–5.0 cm size class and with many fewer trees >50 cm dbh when compared to old-growth. Unmanaged second-growth has a unimodal distribution with the 10–15 cm dbh class as the modal class (Figure 7b). Even-aged management produces a more even distribution of trees among the dbh classes (Figure 7d). The dominance of sugar maple in all size classes and in all treatments is evident in Figure 7.

Differences in structural complexity are also apparent in the horizontal distribution of basal area. Larger plot-to-plot variation in the basal area of both live and dead trees was found in old forests compared to maturing forests (Figures 8a and 8b). Differences in mean basal area (or biomass) between young and old forests were not large (Table 2), but they did vary greatly in the organization or distribution of their biomass (Figure 6).

Management further reduced the plot-to-plot variation in the basal area of live trees. Less variation was found in managed forests (Figures 8c and 8d) compared to either of the two unmanaged baselines (Figures 8a and 8b). The amount and variation of standing deadwood was greatly reduced in managed forests compared to unmanaged old-growth but comparable to that measured in the unmanaged second-growth.

Discussion

The results of our study reflect both direct and indirect effects of forest management on the composition and structure of the forest. Direct effects include the effects of harvesting activities (including road building) on residual trees and on understory species, as well as the disturbance to the forest floor and mineral soil. In our study, harvesting did not include the complete removal of the overstory, but the selective removal of trees from the forest in one, or in the case of two replicates (Table 1), two thinnings. Because of the relatively short time between treatment and our measurements (≈ 5–7 yr) and the lag in response time for woody vegetation, direct effects are likely to predominate when measuring the response of woody species ≥1.5 cm in dbh. Indirect effects

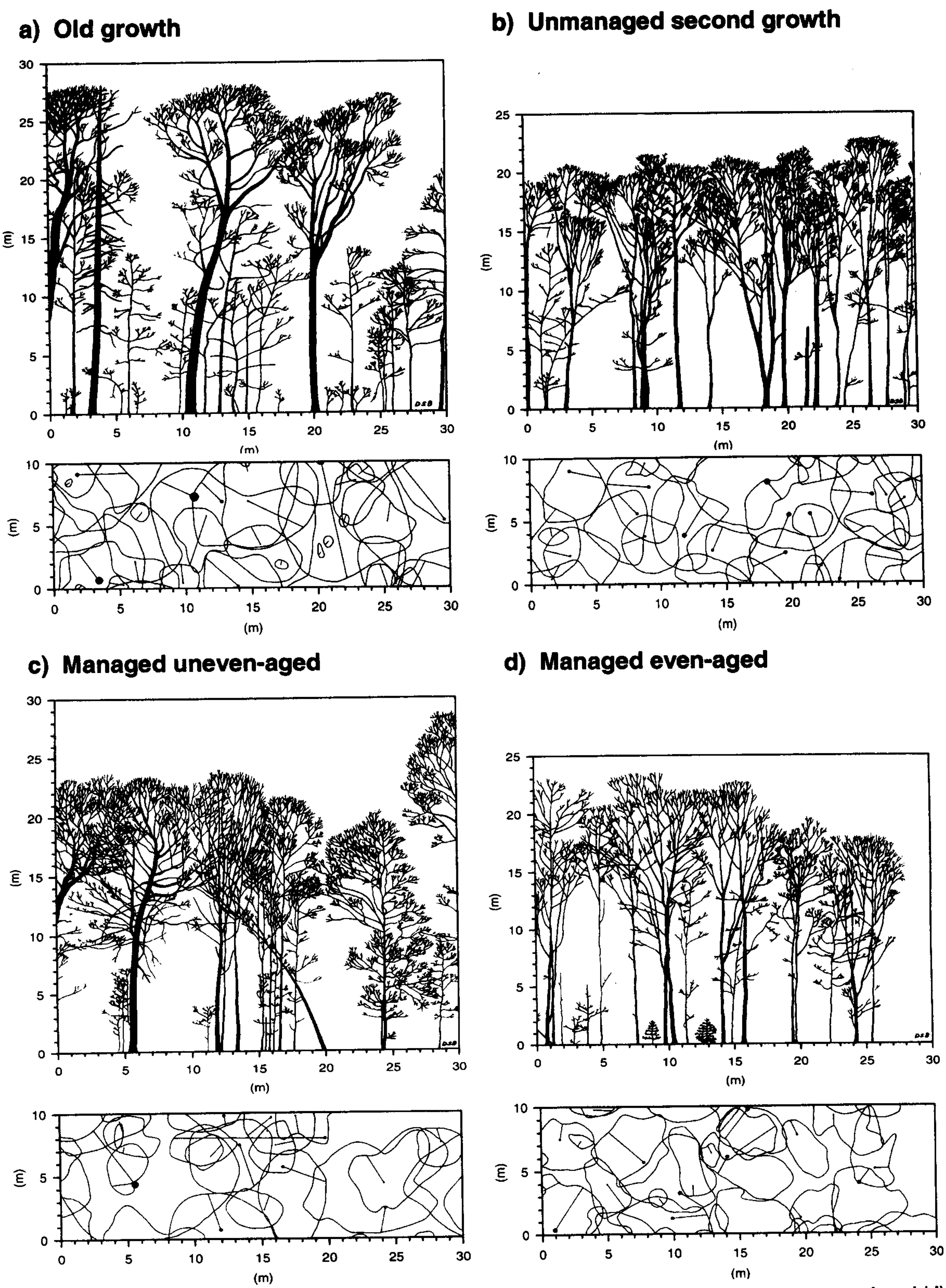


Figure 6. Vertical profiles of (a) old-growth, (b) unmanaged second-growth, (c) managed uneven-aged, and (d) managed even-aged northern hardwood forests along a 30 m transect. Horizontal crown projects are provided under each vertical profile.

include changes in the understory microclimate related to reductions in canopy density following thinning and changes in competitive interactions among residual trees, shrubs, and other plants following the thinning of overstory trees. Understory vegetation, including herbaceous species and small woody plants, should be sensitive to both direct and indirect effects given the timeframe of our study. Separating the direct from the indirect effects as measured by differences in the composition and structure of understory vegetation, however, proved difficult.

Although unmanaged and managed forests were not significantly different in their diversity as measured by richness

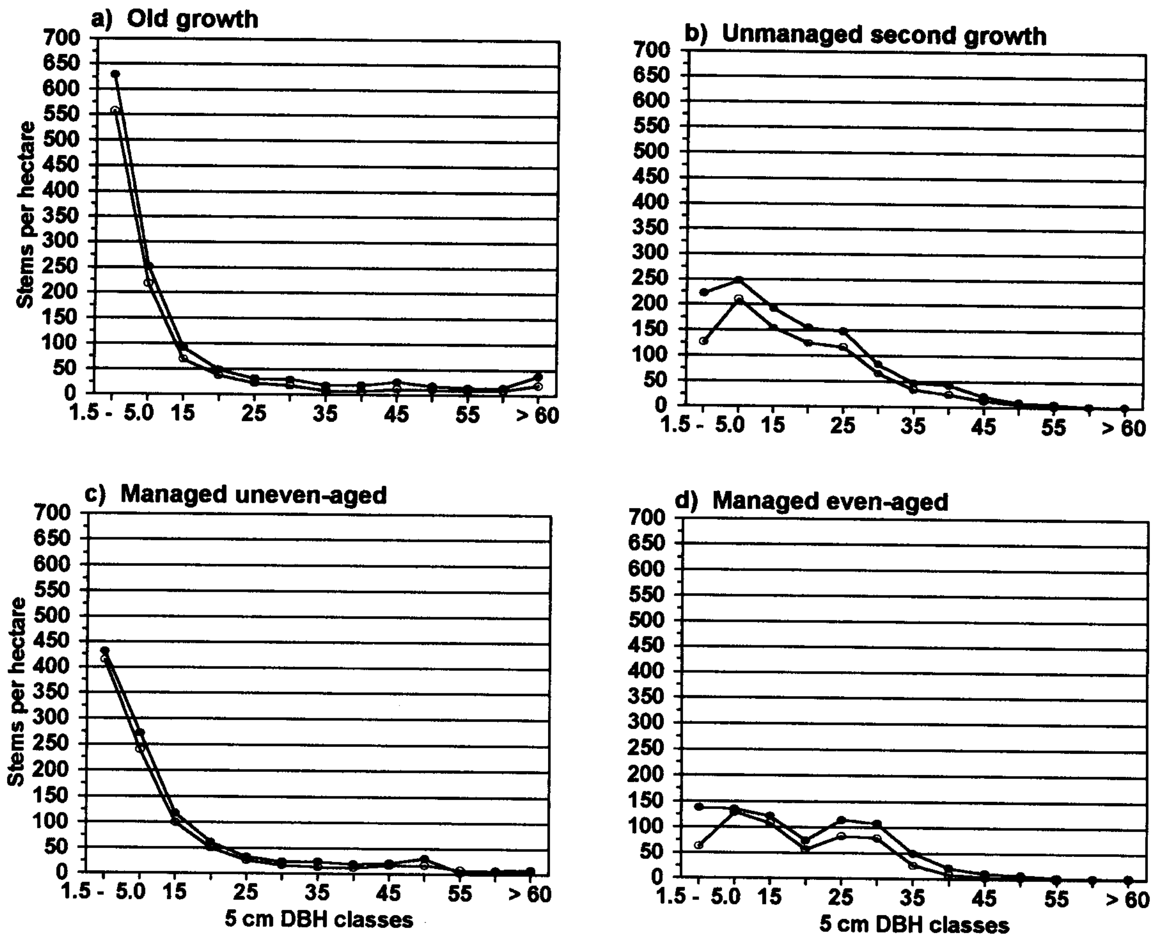


Figure 7. Distribution of tree sizes as represented by the number of stems ha^{-1} by 5 cm dbh classes for (a) old growth, (b) unmanaged second-growth, (c) managed uneven-aged, and (d) managed even-aged northern hardwood forests. Closed circles (•) and open circles (o) denote the distributions for all tree species and sugar maple, respectively.

of woody species ≥1.5 cm in dbh, we did find differences in composition of overstory trees as well as subcanopy trees and shrubs that were related to management practices. Uneven-aged management increased the importance of the already strongly dominant sugar maple. When managing northern hardwoods, it is common to favor sugar maple when marking trees for harvesting. That is, other species are harvested to improve the growing space for sugar maple. It is also a common practice in mixed stands of late and early successional species to selectively harvest early successional species because of the high likelihood of mortality before the next harvest entry. This practice reduces the richness of tree species and removes trees that are potential den (wildlife) trees as well as sources of coarse woody debris. Furthermore, the selection of individual trees for harvesting, which is the basis for uneven-aged management, favors the shade-tolerant sugar maple over midtolerant and intolerant species. Foresters have long recognized the tendency for increased abundance of shade-tolerant species such as sugar maple under uneven-aged management (e.g., Trimble 1965, Crow and Metzger 1987).

Some trees and shrubs ≥1.5 cm dbh but located in the lower to mid-canopy—including large individuals of leatherwood, beaked hazel, as well as other shade-tolerant subcanopy species—were missing from managed forests. These compositional and structural features of old-growth develop slowly, and their presence reflects frequent small-scale disturbances (gap dynamics) and the absence of large-scale stand-replacing disturbances. This structural and compositional element of old-growth could develop with time following reductions in canopy density, although repeated entries to harvest might eliminate the rarer components (e.g., *Acer spicatum, Cornus alternifolia*) of structural complexity in the lower to mid-canopy of the managed forest.

There were no statistically significant differences in species richness for woody plants in the understory between managed and unmanaged forests; however, there were differences in species abundance and dominance. Specifically, sugar maple was less dominant (as measured by stem density) in the unmanaged second-growth, the managed uneven-aged, and the managed even-aged compared to the old-growth (Table 3). Established sugar maple reproduction and the abundance of sugar maple seed produced almost every year in the overstory are sufficient, however, to ensure the continued dominance by this species in all the study sites.

Retaining tree species other than sugar maple is both a biodiversity and an economic issue when managing northern hardwoods in the Great Lakes region (Stearns 1986, Niese and Strong 1992, Crow et al. 1994). Stands containing midtolerant species frequently are more valuable than those strongly dominated by shade-tolerant species (Erdmann 1986). On productive sites, faster growing species such as basswood, white ash, and northern red oak are typically larger in dbh, taller in height, have longer clear boles, and are less subject to forking and branch-caused defects than maple (Erdmann 1986). Intensive treatments to reduce the competition from established sugar maple regeneration will be necessary to favor species other than sugar maple in these forests.

Without question, logging has caused significant changes in the composition and structure of hemlock-hardwood forests in the Great Lakes region. Following logging, mixed forests of hemlock and hardwoods regenerated to hardwoods (Davis et al. 1996). In our study, the scarcity of eastern hemlock in managed forests and in unmanaged second-growth forests was not surprising because seed sources were often rare or absent. Eastern hemlock was also absent, however, in the understory where seed sources were present. The absence of regenerating hemlock can be attributed to multiple factors, including the interactions between the life history of the species, and the physical environment, natural disturbance, and browsing (Mladenoff and Stearns 1993). For example, each year the forest floor in maple-dominated forests is covered with an abundance of leaf litter that could easily bury the small hemlock seedlings that do germinate (Koroleff 1954). Further, the brief abundance of light in the understory during the spring in deciduous forests is likely to provide a competitive advantage to seedling of sugar maple compared to hemlock (Davis et al. 1996). Hemlock seedlings have an advantage over sugar maple seedlings only when hemlock dominates the overstory (Frelich et al. 1993, Davis et al. 1996).

Herbaceous cover and other measures of understory development are clearly affected by overstory characteristics (Alaback and Herman 1988, Whitney and Foster 1988, Nemati and Goetz 1995). Harvesting reduces canopy density, for example, increasing light in the understory and thus promoting vegetative development (Reader and Bricker 1992, Heilman et al. 1996, Thomas et al. 1999). The increase in species richness under managed conditions in our study was also a result of disturbance to the forest floor and mineral soil because of harvesting. The highest richness values obtained for understory plants in managed forests were associated with logging roads and permanent openings created in the forest canopy. Many of these new arrivals in the understory were ruderal or *r*-selected species that have life history characteristics (e.g., rapid development, early reproduction, small size, single reproduction period in lifespan) that make them competitive in disturbed environments (Grime 1979). Although these plant species added to local richness, they are often common in the landscape and region, and thus they do not enhance richness at these larger spatial scales.

Our results do not speak to the possibility of species losses under managed conditions over time (i.e., a lag in response to disturbance). Reader and Bricker (1992), however, recorded how many species either disappeared or occurred less frequently 2 yr after an individual-tree selection harvest in a deciduous forest. They found a similar percentage of herbaceous species disappeared from plots in the uncut forest (9–13 %) as within the harvested forest (3–12 %). Further, the percentage of herbaceous species in the Reader and Bricker (1992) study that occurred less frequently 2 yr after cutting was significantly smaller in the harvested forest than in the uncut forest. These results, however, are still short-term.

Although species richness is probably the least ambiguous metric of diversity available, it does not indicate the species present. The issue of biological diversity has more to do with which species are present or not present than it does with the number of species. We presented community attributes that do not measure the response of individual understory species to forest manipulation. Nor was our sampling specifically designed to detect rare species or predict the future of rare plant populations (Green and Young 1993). These limitations are important to keep in mind when interpreting our results.

Some of the differences in occurrence and importance values for tree species can be attributed to differences in stand development. Old-growth forests were more diverse in their structure (more canopy gaps, larger variation in size and shape of canopy gaps, multistored canopies, greater structural heterogeneity in the understory), had greater variation in the richness of understory species (some high, some low), and had vastly different distributions of stem densities and biomass than unmanaged second-growth forests. These results are consistent with those for other studies in which distinct differences were found in the structure of the living and dead vegetation when comparing second growth with old growth (e.g., Hale et al. 1999, McGee et al. 1999).

A characteristic of old-growth northern hardwoods is the variation in understory conditions related to the complex canopy structure, as well as to forest floor features such as pit and mound microtopography and the occurrence of large woody debris (Gore and Patterson 1986, Tyrrell and Crow 1994a and b, Hale et al. 1999). In our study, the variation found in the composition and spatial distribution of understory vegetation in the old growth is likely associated with structural complexity in the overstory. Multiple canopy strata and canopy gaps of various sizes create a more heterogeneous microclimate in the understory in old growth compared to the more uniform second-growth forest (Nauertz, unpublished data). Large woody debris and tip-up mounds common to old growth create diversity niches for germination and establishment of plants in the understory of old growth; these structural components are largely missing or greatly reduced in second-growth forests (Tyrrell et al. 1998, McGee et al. 1999). This structural complexity produces the large range of responses obtained in species–area relationships (Figure 3), and it produces a patchy mosaic of understory vegetation. Differences in complexity and variation between managed and unmanaged forests are also evident in the vertical canopy profiles (Figure 6) and the plot-to-plot variation in basal area (Figure 8). These elements of structural complexity are often reduced through management. Although managed stands are more heterogeneous than unmanaged second-growth forests, managed stands did not obtain the structural complexity found in old growth.

The treatments in our study included a limited range of management conditions—i.e., treatments consisted of thin-

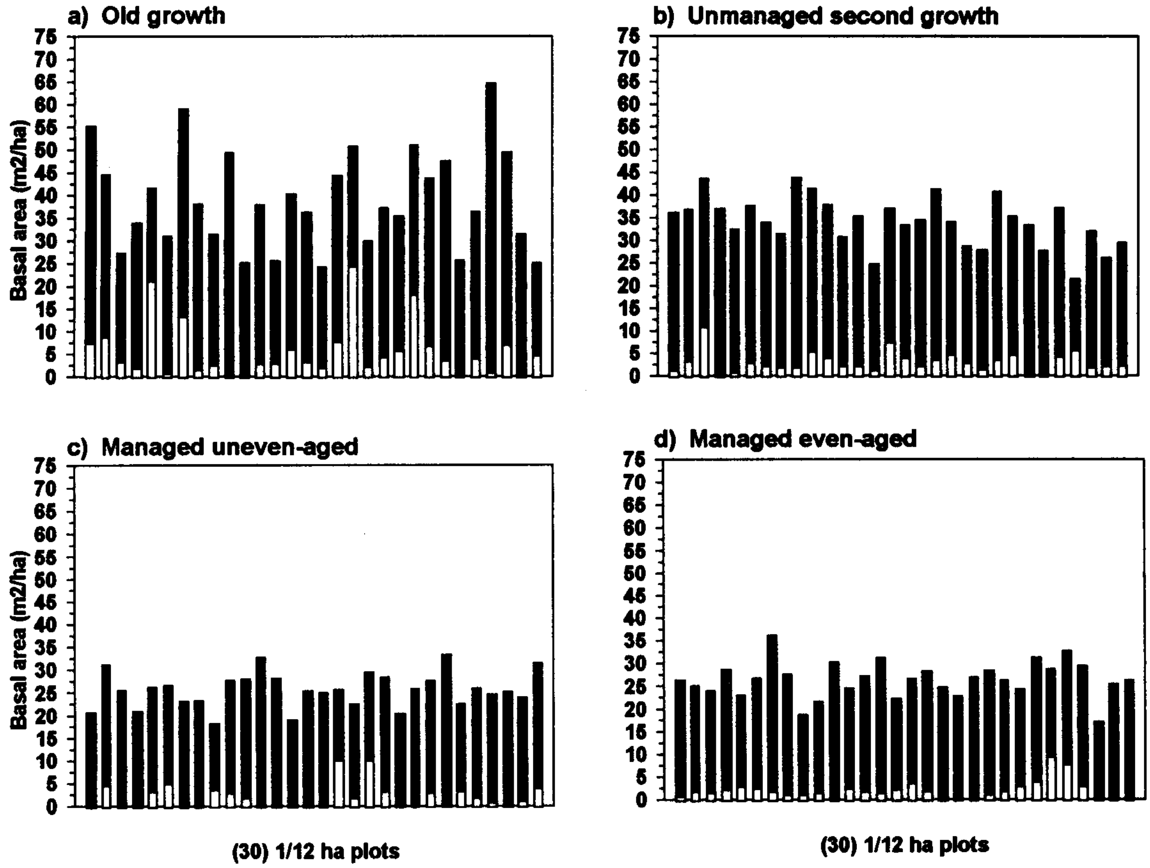


Figure 8. Plot to plot variation in live and dead components of total basal area (m^2 ha^{-2}) for (a) old growth, (b) unmanaged second-growth, (c) managed uneven-aged, and (d) unmanaged second-growth northern hardwood forests. Closed bars and open bars represent the basal area of living and standing dead trees, respectively. Patterns for biomass follow similar trends.

ning individual trees or small groups of trees within the same ecosystem. Furthermore, uneven-aged management tended to be applied to older forests and even-aged management to younger forests (see Figure 2). Differences in composition and structure between even-aged and uneven-aged management could be also related to stand age and related differences in stand development as well as differences in management.

Conclusion

Although species richness for woody vegetation ≥1.5 cm dbh was similar between managed and unmanaged conditions, species composition and abundance differed between the two conditions. Disturbance associated with forest harvesting creates opportunities for *r*-selected species to colonize the site. The greater plant species richness in managed forests was due in part to the presence of both native and nonnative species adapted to disturbance. Although lower richness was found in old-growth compared to managed forests, results from species-area curves and variances associated with plot means suggest high variability in richness of herbaceous and small woody plants. This may be related to the structural (horizontal and vertical) heterogeneity present in old forests, that in turn produces a diversity of habitats and physical environments.

Management alters forest development processes, resulting in younger forests that are more uniform (i.e., less spatial heterogeneity) in their structure and composition compared to old-growth. Existing hardwood management guides are designed to maximize production of commercial products, improve tree quality, and promote economic efficiency. Such objectives are appropriate and desirable in many places, but managing to retain old-growth characteristics and managing to maximize structural complexity to promote plant and animal diversity are equally important management goals for other places. New management guides are needed for increasing the structural complexity in managed forests by (1) increasing the range of tree sizes, (2) promoting the development of multistoried canopies, (3) increasing the abundance and range of sizes for canopy gaps, and (4) retaining and increasing standing and downed coarse woody debris to the forest canopy and understory. Many of these attributes can be obtained by retaining the cohort of older trees that currently exist in most second-growth northern hardwood forests in the Great Lakes region. Most of these trees are considered culls by foresters because of their poor commercial quality. They do, however, contribute much to the structural complexity of these forests.

In the sugar maple dominated forests that we studied, there is also a critical need to develop management strategies that promote recruitment of tree species other than sugar maple into the forest canopy. Selection against sugar maple in the overstory, retention of ash, oak, basswood, birch, hemlock, white pine in the overstory, underplanting species other than sugar maple, and the removal of advanced reproduction of sugar maple (at least in small patches in the understory) are strategies that might increase the richness of northern hardwood forests in our study area. Intensive management will be needed to increase the richness of tree species in these forests.

In addition to the stand level attributes, landscape considerations need to be incorporated into management guides. A well-developed mosaic of forest patches that includes three distinct types—hemlock, sugar maple, and a mix of the two species—is characteristic of old growth hemlock-hardwood in the Lake States region (Frelich et al. 1993, Frelich and Reich 1996, Davis et al. 1996). A landscape perspective is needed to appreciate the spatial heterogeneity of forest ecosystems. If management guidelines for northern hardwoods are modified to include the compositional and structural features mentioned above at both a stand and landscape scale, then both even-aged and uneven-aged management strategies have a greater potential for supporting human uses of the resource as well as the diversity of native plant species.

Because a large share of the global diversity resides in managed landscapes (Pimentel et al. 1992), managed forests such as those we studied are vital to conserving biological diversity as well as for producing sustainable goods and services. Managed ecosystems deserve much more of our attention when considering the conservation of ecological diversity (Lugo et al. 2001). In addition, more attention should be given to the appropriate standards for comparing managed and unmanaged ecosystems. Too often, old growth is assumed to be the only appropriate baseline for managed forests. Both unmanaged old-growth and unmanaged second-growth are needed for comparisons with managed northern hardwood forests. Both are rare, however, in the landscape.

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