Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A.

C.M. Hale, J. Pastor, and K.A. Rusterholz

Abstract: Extended rotation of managed temperate hardwood forests is sometimes presumed to provide the important compositional and structural features of old-growth hardwood forests. However, the features of temperate hardwood old-growth and managed stands of extended rotation age have not been fully quantified and compared. This study compared quantitative parameters (density and volume of logs and snags, coarse woody debris volume (volume of logs + volume of snags), the proportion of hollow logs, basal area and tree, sapling, large seedling and small seedling densities), distributional patterns (diameter class and rot class of live trees, decay class of logs), and vascular plant species composition and diversity in old-growth and mature, managed sugar maple (*Acer saccharum* L.) – basswood (*Tilia americana* L.) and northern red oak (*Quercus rubra* L.) stands. Old-growth forests had higher coarse woody debris volumes and higher proportions of hollow logs, of live trees in large diameter classes, of logs in decay classes 1 and 2, and of live trees in rot classes 3–5 than the mature, managed forests. Old-growth and mature, managed forests did not differ significantly in plant species composition. These results indicate that, while older extended-rotation, managed stands can be very similar compositionally to old-growth forests, they differ quantitatively in structural features.

Résumé : On présume parfois qu'une révolution prolongée des forêts tempérées feuillues aménagées leur procure les principales caractéristiques floristiques et structurales des forêts feuillues primitives. Toutefois, les caractéristiques des peuplements tempérés feuillus primitifs et aménagés avec une révolution prolongée n'ont pas encore été pleinement quantifiées et comparées. Cette étude compare les paramètres quantitatifs (densité et volume des billes au sol et des chicots, volume des gros débris ligneux (volume des billes au sol + volume des chicots), proportion des billes creuses au sol, surface terrière et densité des arbres, des gaules, des grand semis et des petits semis), patrons de distribution (classe de diamètre et classe de pourriture des arbres vivants, classe de décomposition des billes au sol), ainsi que la composition spécifique et la diversité des plantes vasculaires, dans des peuplements primitifs et aménagés mûrs d'érable à sucre (*Acer saccharum* L.) – tilleul (*Tilia americana* L.) et de chêne rouge (*Quercus rubra* L.). Les forêts primitives avaient des volumes de gros débris ligneux plus élevés et de plus grandes proportions de billes creuses au sol, d'arbres vivants dans les classes de gros diamètres, de billes au sol dans les classes de décomposition 1 et 2 et d'arbres vivants dans les classes de pourriture 3–5 que les forêts mûres aménagées. Par contre, les forêts primitives et les forêts mûres aménagées ne différaient pas de manière significative quant à leur composition en espèces végétales. Ces résultats indiquent que les peuplements aménagés plus âgés à révolution prolongée diffèrent quantitativement des forêts primitives par leurs caractéristiques structurales, même s'ils peuvent avoir une composition très similaire.

[Traduit par la Rédaction]

Introduction

Concern over the loss of biodiversity and the protection of remaining intact ecosystems has grown significantly in the last two decades (Thomas et al. 1988; Crow et al. 1994). This concern is magnified as the landscape that we live in, and upon which we rely for physical, economic and spiritual sustenance, has become more widely and significantly altered by human activities. The preservation of old-growth forests is important to the preservation of overall biodiversity. Old-growth forests are valuable as examples of ecosystems relatively unaltered by widespread anthropogenic changes (Harmon and Hua 1991; Harmon et al. 1990; Nyberg et al. 1987; Ottawa National Forest 1991; Barnes 1989; Greene 1988; Juday 1988; Whitney 1987).

In the Lake Superior region, few old-growth hardwood stands remain outside of the Boundary Waters Canoe Area Wilderness (Heinselman 1973), the Porcupine Mountains Wilderness (Frelich and Lorimer 1991), and the Sylvania Wilderness Area (Pastor and Broschart 1990; Frelich et al. 1993). Other than these large wilderness areas, the remaining stands are generally small and isolated from the larger forest matrix. To maintain the special features of old-growth across the landscape we must consider managing the forested landscape to include not only reserves but also areas designed to enhance or restore old-growth features in managed forests through silvicultural practices (Curtis 1997).

Extending rotation of hardwood forests from 60–80 years to 80–120+ years is one strategy proposed to enhance or

Received September 30, 1997. Accepted March 27, 1999.

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restore old-growth features in managed forests (Minnesota Department of Natural Resources 1995). It is hoped that important old-growth features (species diversity, coarse woody debris characteristics, live tree characteristics) will be maintained in managed stands with such long rotation ages. However, the compositional and structural characteristics of managed hardwood forests of extended rotation age-classes in Minnesota have not been quantified nor has their similarity to old-growth stands been demonstrated (Tyrrell et al. 1998).

The defining characteristics of old growth will depend on the particular forest type. In Minnesota hardwood forests, old growth is provisionally defined as stands with dominant trees of 120+ years and lacking significant human or natural disturbance. In contrast to forests dominated by long-lived species such as those in the Pacific Northwest, in hardwood forests of the Great Lakes Region, after 120 years and with minimal disturbance, the successional dynamics have largely been played out, and there is little subsequent change in the composition and relative abundance of dominant tree species. In addition, timber harvesting did not begin in much of the Upper Great Lakes region until after 1870. Therefore, as a first approximation this definition of old growth, based solely on age, seems reasonable. However, age alone is clearly not the feature of primary interest and in uneven-aged stands it may not even be definable. To move beyond age as a criterion for old-growth condition and towards a more biologically meaningful definition we must begin to quantify and describe the characteristics unique to old growth in each forest type. Such features, would include amounts and size distribution of coarse woody debris, climax species live tree composition, canopy structure, and understory species composition (Barnes 1989; Boerner and Cho 1987; Casson et al. 1994; Downs and Abrams 1991; Fralish et al. 1991; Hammit and Barnes 1989; Tyrrell and Crow 1994*a*, 1994*b*). Then comparisons with extended rotation forests can be made to determine what features they already share with old growth and which are lacking.

Accordingly, the objective of this study was to quantify and compare overstory and understory plant species composition, diversity and structure, coarse woody debris characteristics and the size-class distributions and levels of heart rot of live trees in mature managed (80–120+ years old) and undisturbed old-growth sugar maple (*Acer saccharum* L.) – basswood (*Tilia americana* L.) and northern red oak (*Quercus rubra* L.) stands.

Methods

Site selection and study area

Stands were selected from the Minnesota Department of Natural Resources (DNR) Natural Heritage Information System, Minnesota County Biological Survey reports, old-growth candidate stand evaluations, and from state and federal forest inventory databases (Table 1). Eleven old-growth maple–basswood and 10 old-growth oak stands were identified throughout the range of each cover type in Minnesota (Fig. 1). All old-growth stands were uneven aged, contained average canopy trees of at least 120 years old (often older), and lacked any evidence of natural or human disturbance, such as cut stumps.

A combination of historic records, landowner interviews, and coring of average canopy trees was used to confirm the old-growth status of each stand. Precise age determinations of old-growth stands were impossible, in part, because most of the large canopy trees (60+ cm diameter at breast height (DBH)) were hollow. Therefore, we cored five average-sized canopy trees (30–50 cm DBH) in each stand (Applequist 1958; Wenger 1984). We presumed that, if the average-sized canopy trees were at least 120 years old, then the larger trees (60+ cm DBH), present in all old-growth stands, were much older yet. In addition, old-growth stands contained natural stumps and logs of large trees indicating that stand development had progressed beyond the life expectancy of at least some canopy trees. Since timber harvesting in Minnesota before the 1870s was minimal, it is reasonable to assume that remnant stands of forests from this period that have experienced no management in the last 120 years, have never been significantly altered through anthropogenic means, and represent old-growth condition.

Within 20 miles (1 mile = 1.609 km) (often less) of each old-growth stand, we located a mature, uneven aged, managed stand (approximately 80–120+ years since stand origin) that matched the geomorphology, soil type, slope, and aspect of the old-growth stand (Table 1). The mature, managed stands (hereafter referred to as mature stands) had experienced varying levels and types of past human disturbance such as selective logging, cattle grazing, and (or) firewood removal (Table 1).

Maple–basswood stands were distributed from the northwest to the southeast corner of the state (Fig. 1). Oak stands were distributed in the southeast corner of the state with one pair located in the northwest (Fig. 1). Stand sizes ranged from 3 to 73 ha (Table 1). Slope and aspect were closely matched within old-growth and mature pairs (Table 1). However, there was considerable variability in topographic setting from pair to pair with slopes ranging from 0 to 34° in both cover types. Generally, the steepest slopes faced north to northeast. Soil types in the maple–basswood and oak sites were generally loamy and well drained but also rocky where the slopes were steep (Table 1).

Understory vascular plant species composition and structure

We sampled species composition and relative abundance of understory vascular plants and tree seedlings and saplings in a single 20 × 50 m plot in each stand. The plot was placed in the interior of the stand to minimize effects due to roads, trails, edges and wet depressions in or around the stand. Sampling was completed between June 4 – August 24, 1993 and 1994.

Saplings (<10 cm and ≥3 cm DBH) were tallied by species in the entire 20 × 50 m plot. Large seedlings (<3 cm DBH and >0.5 m tall) were tallied by species in three 10 × 10 m subplots, randomly located within the 20 × 50 m plot. Small seedlings (≤0.5 m tall) were tallied by species in twenty-five 1 m diameter circular subplots; one subplot was placed randomly within each 4 m section around the perimeter of the 20 × 50 m plot.

The structure and composition of ground cover, shrub, subcanopy, and canopy vegetational layers were sampled as a releve (Mueller-Dombois and Ellenberg 1974; Almendinger 1991) in a randomly placed 20 × 20 m subplot within the 20 × 50 m plot. Vegetation in the 20 × 20 m plot was divided by visual inspection into height-interval (0–0.5, 0.5–2, 2–5, 5–10, 10–20, and 20+ m) and life-form layers (broad-leaved deciduous, needle-leaved evergreen, shrub, herbaceous, graminoid, etc.). Each height-interval/life-form layer identified was assigned an overall percent cover (total percent cover of all layers >100). Within each height-interval or life-form layer, all species were identified and their percent cover recorded (total percent cover within a layer ≤100).

Live trees and coarse woody debris

We sampled coarse woody debris (snags and logs) and trees (≥10 cm DBH) using four randomly placed, nonintersecting

Table 1. Study site locations and descriptions.

Site name[a]	Slope and aspect	Soil and landform[b,c]	Size (ha)	Mean canopy tree age[d]	Stand history[e]
Maple–basswood					
Townsend Woods[f]	16, W	LLW, 5A	12	138	X
Ahlman[g]	11, W	LLW, 35A	16	144	A, C
Lowry Woods[f]	4, E	LLW, 33	8	172	X
Baker[g]	1, W	LLW, 33	12	126	A
Bello Lake[f]	1, N	LLW, 22A	8	124	X
Pelton Lake[g]	0, LV	LLW, 22A	10	104	A
Big Island[f]	4, NW	SSW, 13	16	134	X
Johnson Lake[g]	0, LV	SSW, 13	8	92	A
Dinosaur Island[f]	4, NE	LLP, 10C	36	136	X
Isle 27[g]	1, NW	LLP, 10C	6	77	A
Taylor Woods[f]	0, LV	LLW, 35B	41	164	X
Doerr[g]	0, LV	LLW, 33	16	101	A, C
Wray[f]	26, N	SSR, 40	8	161	X
Hauser[g]	24, NW	SSR, 40	12	123	A, B
Richardson[f]	33, N	SSR, 40	10	152	X
Prokasky[g]	34, N	SSR, 40	16	118	A
Wolsfeld old growth[f]	9, W	LLW, 35B	3	142	X
Wolsfeld mature[g]	8, S	LLW, 35B	5	154	A
St. Charles[f]	4, W	SSR, 40	73	128	X
St. Charles, Dog[g]	8, W	SSR, 40	11	128	A
Sugarbush RNA[f]	2, W	XLW, 11	57	157	X
Oak					
Arrowpoint[f]	3, SE	LLW, 11	10	105[h]	X
Bebensee[g]	4, SE	LLW, 11	16	72[i]	A
Caledonia old growth[f]	22, NW	SSR, 40	8	135	X
Caledonia mature[g]	28, N	SSR, 40	8	119	A
Denmark[f]	3, NE	LLW, 38	44	135	B
Ceridian[g]	2, N	SLW, 29	8	81	A, B
Leon[f]	2, NE	RLW, 39	4	139	X
Conrad[g]	2, N	LLW, 39	26	68[i]	A
Evers Woods[f]	4, SE	SSR, 40	32	130	X
Hoffman[g]	6, SE	SSR, 40	12	88	A
White Water[f]	10, NE	SSR, 40	10	86[i]	X
Signal Point[g]	9, NE	SSR, 40	10	92	A
Heintz 25[f]	2, NW	SSR, 40	6	98[h]	X
Heintz 36[g]	4, N	SSR, 40	8	111	A
Sheldon 27[f]	22, E	SSR, 40	18	128	X
Sheldon 28[g]	23, SE	SSR, 40	16	102	A
Zimmerman[f]	28, NE	SSR, 40	8	129	X
Vernon[g]	22, N	SSR, 40	32	104	A
Melcher Ridge[f]	26, NE	SSR, 40	36	164	X
Kronebush[g]	24, N	SSR, 40	53	105	A

[a] Matched old-growth and mature or managed stands are listed consecutively.

[b] LLW, silty loam, well drained; RLW, silty loam over rock, well drained; SLW, sandy loam, well drained; XLW, loam over sand and loam, well drained; SSR, steep, stony–rocky.

[c] 10C, Brainerd-Pierz Drumlin; 11, Itasca Moraine; 13, Crow Wing Outwash Plain; 22A, Marcell Moraine; 29, Mississippi Valley Outwash; 33, Lonsdale-Lerdal Till; 35A, Prior Lake Moraine; 35B, Emmons-Faribault Moraine; 38, Kenyon-Taopi Plain; 39, Harmony-Plainview Uplands; 40, Red Wing-La Crescent Uplands.

[d] Values are the mean of five canopy trees cored.

[e] A, selective logging (<50% basal area); B, cattle grazing; C, firewood removal; X, no significant disturbance.

[f] Old growth.

[g] Mature, managed.

[h] Young ages are due to high incidence of hollow canopy trees.

[i] Young ages are due to recent harvesting of canopy trees.

Fig. 1. Locations of maple–basswood and oak study sites in Minnesota. Each symbol represents two study sites, the old-growth and mature paired sites (see Table 1).

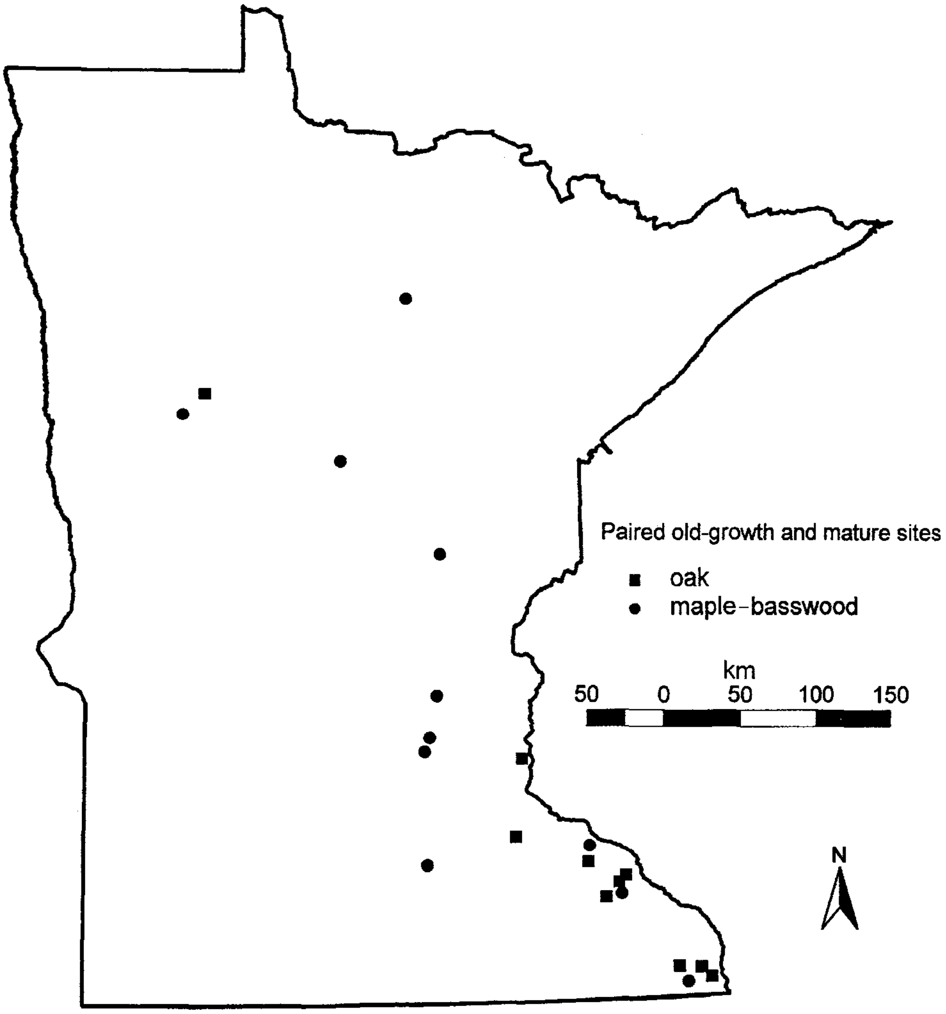


Table 2. Visual indicators of rot classes for live trees.

Rot class	Visual indicators of rot (Carpenter et al. 1989)
(1) Localized–minor	Any combination of small to medium limb knots or stem galls, small healed overgrowths, stem lesions with exposed rot, small holes, or adventitious budding
(2) Localized–moderate	Any combination of large limb knots or stem galls, small open splits or holes, small to medium healed splits, or small to medium stem lesions with exposed rot
(3) Extensive–spreading	Any combination of large limb knots or stem galls, medium open splits or holes with obvious rot, large healed splits, or medium to large stem lesions with exposed rot
(4) Partially hollow	Large open splits and (or) limb holes with obvious active rot or <50% of the length of the main bole visibly hollow
(5) Hollow	≥50% of the length of the main bole visibly hollow

2 × 100 m belt transects (hereafter referred to as "transects") in each stand (Greig-Smith 1964). The species, DBH, and canopy position (canopy or subcanopy) of all live trees (≥10 cm DBH) rooted within the transects were recorded. Five rot classes were developed for live trees (Table 2) based on visual indicators of rot (Carpenter et al. 1989). Rot classes ranged from 1, very minor or no evidence of rot, to 5, an obviously hollow bole (Table 2). Each tree was assigned to a rot class based on visual indicators of rot.

The species, dimensions (length and small, middle and large diameters), decay class (Harmon et al. 1986), and estimate of percent hollow (nearest 10%) were recorded for each log or portion of a log ≥15 cm diameter within each transect. The Harmon et al.

Table 3. Diversity indices.

Index*	References	Emphasis
Richness	n/a	Number of species
Shannon's $H' = [-\Sigma p_i \ln (p_i)] - [(s-1)/2N]$	Shannon and Weaver 1964; Poole 1974	Integrates the number of species and relative abundance; derived from information theory; measure of entropy for the sample; full formula is an expanding series; the first two terms are shown here
Relative $H' = H'/\ln (s)$	Magurran 1988	Represents the evenness of the relative abundance of the species present; the percentage of relative entropy for a system
Simpson's $D = \Sigma p_i^2$	Magurran 1988	A measure of dominance by one or a few species; the probability that two individuals selected from the population at random will be of the same species
Margalef: $(s-1)/(\ln N)$	Magurran 1988	Derived by fitting data; no theoretical explanation beyond how author believes species numbers and relative abundance may be related
Menhinick: $s/(N)^{0.5}$	Magurran 1988	Derived by fitting data; no theoretical explanation beyond how author believes species numbers and relative abundance may be related
Hurlbert's: $[N/(N-1)]/(1-\Sigma p_i^2)$	Washington 1984	Related to H' and D above; the probability of interspecific encounters

*p_i, proportion of N made up by the ith species; s, number of species recorded; N, total number of individuals.

(1986) decay class system includes five decay classes ranging from freshly fallen logs (decay class 1) to well-decayed logs that are incorporated into the forest floor (decay class 5). For all snags (≥10 cm DBH) within each transect, the species, dimensions (height, DBH, and estimated top diameter), decay class (Harmon et al. 1986), fragmentation class (Tyrrell 1991), and percent hollow were recorded. Three fragmentation classes, ranging from a newly formed snag with an intact crown (fragmentation class 1) to a bole with few large branches (fragmentation class 3), were used (Tyrrell 1991).

Analyses

Overstory and understory plant species composition were analyzed using cluster analysis and diversity indices. TWINSPAN was used to determine possible differences in species composition between old-growth and mature forests in each cover type (Ludwig and Reynolds 1988). The results reported here use the complete data set of all species in all releve height-interval or life-form layers and cover classes. Shannon H', relative H', richness, and four other diversity indices (Table 3) were calculated for species diversity (herbaceous, shrub, and tree species), familial diversity (herbaceous and woody families), and structural diversity (height-interval or life-form layers). Each index places emphasis on specific interactions or relationships related to species diversity (Table 3). Early spring ephemeral species, which may have been detectable only at the sites sampled earliest in the season, were excluded from all analysis.

Structural variables, including basal area, tree density, sapling density, large seedling density, small seedling density, snag volume, snag density, volume of logs, density of logs, coarse woody debris volume (the sum of log and snag volumes), and the proportion of hollow versus solid logs, were compared in old-growth versus mature stands using pairwise comparisons. In cases where the data being compared were normally distributed, a standard paired-sample t test, assuming unequal variance was used. In cases where at least one of the data sets being compared was not normally distributed a nonparametric Mann–Whitney rank sum test was used (Glantz 1992).

The diameter-class and rot-class distributions of live trees and the decay-class distributions of coarse woody debris in old-growth and mature stands were compared using the nonparametric Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981; Steel and Torrie 1980). This method tests for the differences in range, dispersion, and skewness of distributions.

Determining indicators of old growth

Stepwise logistic regression (SAS Institute Inc. 1995) was used to determine which structural variables were the most valuable in distinguishing old-growth stands from mature stands (Trexler and Travis 1993). Seven independent variables were used in the analysis: basal area, sapling density, large seedling density, small seedling density, volume of logs, volume of snags, and coarse woody debris volume (the sum of log and snag volumes). The independent variables were standardized to a Z distribution, with the mean = 0 and standard deviation = 1.

The stepwise logistic regression model predicts the probability of a stand being classified as old growth. A classification table was produced, showing the proportion of false negatives (old growth misclassified as mature) and the proportion of false positives (mature misclassified as old growth) at various probability levels, to evaluate the predictive abilities of the models produced by logistic regression.

Results

Live trees

Live tree basal area was statistically higher in old-growth stands compared with mature stands in maple–basswood ($p = 0.05$) but not in oak ($p = 0.12$) forests (Table 4). Tree density was the same in old-growth and mature stands for both maple–basswood ($p = 0.87$) and oak ($p = 0.26$) forests

Table 4. Comparison of structural variables in old-growth and mature maple–basswood and oak forests.

		Maple–basswood forests		Oak forests	
		Old growth	Mature	Old growth	Mature
Basal area (m^2/ha)	Range	14–51	14–32	19–47	17–43
	Mean	31[b]	25[b]	32	28
Density (stems/ha)					
Trees	Range	175–388	213–388	238–488	300–563
	Mean	338	357	380	410
Saplings	Range	8–617	11–1643	45–766	13–723
	Mean	255	419	315	310
Large seedlings	Range	190–5200	100–3620	450–2100	170–1230
	Mean	1536	1322	874	649
Small seedlings	Range	19–520	10–362	21–210	17–123
	Mean	154	132	87	65
Snag volume (m^3/ha)	Range	0–65	0–22	0–75	0–29
	Mean	27[b]	8[b]	27	13
Snag density (no./ha)	Range	0–75	0–88	0–88	0–63
	Mean	34	24	33	28
Volume of logs (m^3/ha)	Range	12–121	12–89	21–68	9–74
	Mean	55[b]	40[b]	48	34
Density of logs (no./ha)	Range	100–613	100–562	263–513	100–788
	Mean	420[b]	306[b]	388	431
CWD volume (m^3/ha)[a]	Range	26–146	12–89	34–143	9–98
	Mean	88[b]	49[b]	75[b]	46[b]

[a] Coarse woody debris (CWD) volume is the sum of measured volume of logs and snags.

[b] The difference of means of old-growth versus mature stands is significant at $p \leq 0.05$. For maple–basswood, N = 11 old-growth and mature stands. For oak, N = 10 old-growth and mature stands.

(Table 4). There were no differences in the density of saplings (p = 0.60, p = 0.48), large seedlings (p = 1.0, p = 0.22), or small seedlings (p = 1.0, p = 0.14) for maple–basswood or oak forests, respectively, in old-growth compared with mature stands (Table 4).

The diameter-class distribution patterns of live trees were similar in both cover types (all species combined). The proportion of live trees declined exponentially from the smallest to the largest size classes (Fig. 2). However, for both cover types the old-growth stands had a higher proportion of trees in the two largest diameter classes compared with mature stands (Fig. 2).

The proportion of live trees in each rot class (Table 2) decreased exponentially from rot class 1 (least rotted) to rot class 5 (hollow bole) (Fig. 2). Old-growth oak stands had a higher proportion of trees in rot classes 2–4 compared with mature stands. Old-growth maple–basswood stands had a higher proportion of trees in rot class 4 (partially hollow) compared with mature stands (Fig. 2).

Coarse woody debris

There was a significantly greater volume of logs (p = 0.05) and snags (p = 0.04) in maple–basswood old-growth stands compared with mature stands, although these parameters were not statistically significant ($p \geq 0.07$) in oak forests (Table 4). However, the overall coarse woody debris volume of logs and snags combined was significantly higher in old-growth stands compared with mature stands for both maple–basswood and oak cover types ($p \leq 0.05$) (Table 4). In contrast, the density of snags was the same in old-growth compared with mature stands for both cover types ($p \geq 0.18$), and the density of logs was significantly higher in old-growth compared with mature stands for maple–basswood (p = 0.04) but not oak (p = 0.97) forests (Table 4).

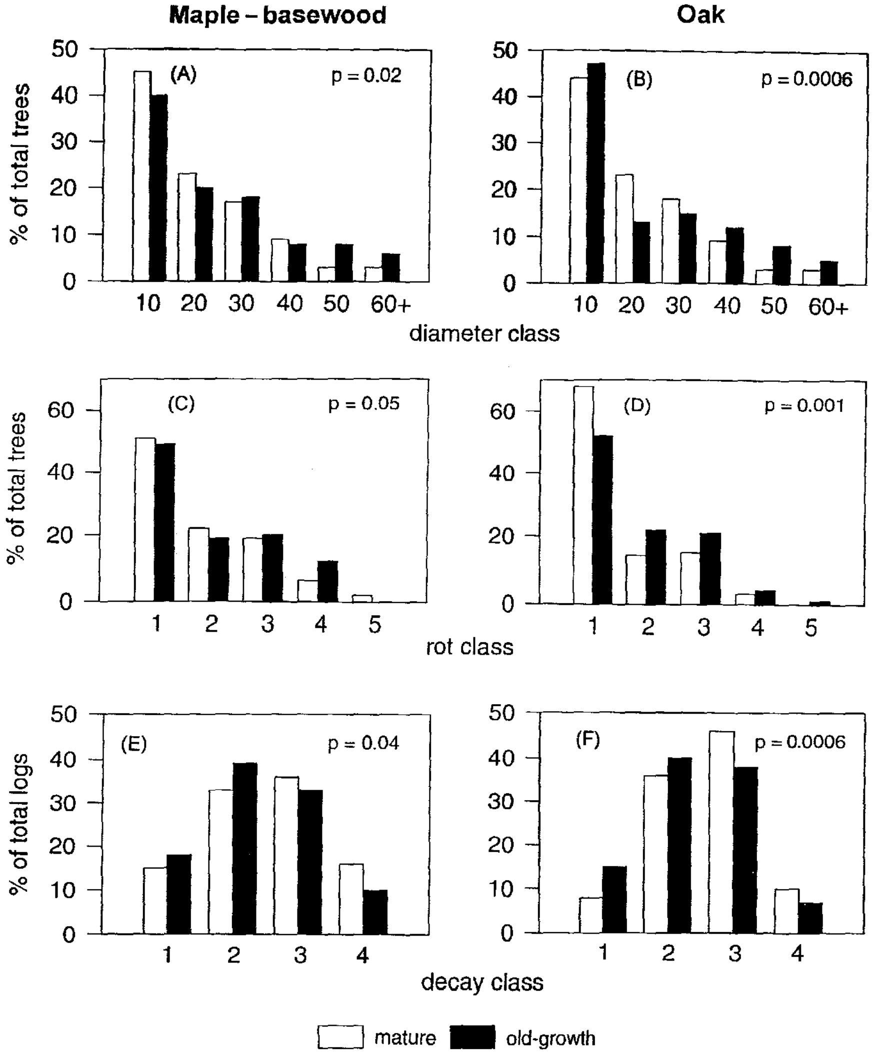
Decay-class distributions for logs did not differ significantly (p = 0.08) in maple–basswood compared with oak forests. Both cover types had a majority of the down logs in decay classes 2 and 3, which represent moderately to well-colonized states of decay (Fig. 2). For both cover types, the old-growth stands had a higher proportion of logs in decay classes 1 and 2 compared with the mature stands (Fig. 2). Old-growth maple–basswood stands had a higher proportion of hollow logs compared with mature maple–basswood (23 vs. 15%, p = 0.09); comparable values for oak stands were (15 vs. 6%, p = 0.003).

Overstory and understory species composition, diversity, and structure

Many of the paired old-growth and mature stands remained together in the finest TWINSPAN divisions when overstory or understory compositional differences were evaluated. The TWINSPAN divisions reflected plant compositional differences based on the geographic distribution of pairs from north to south rather than differences between old-growth and mature.

Herbaceous, shrub, and tree species diversity were similar in old-growth and mature stands for each cover type ($p \geq 0.06$) except that the relative H' for herbaceous family diversity was higher in old-growth maple–basswood stands compared with mature stands (0.87 and 0.79, respectively). There were no significant differences in plant family diversity between old-growth and mature oak stands. There were

Fig. 2. Diameter class (A and B), rot class of live trees (C and D), and decay-class distributions of down logs (E and F) for old-growth and mature, managed maple–basswood and oak stands. The *P* values indicate the level of significance of the distributional difference (Kolmogorov–Smirnov test; Sokal and Rohlf 1981) for old-growth versus mature stands.



no significant differences in structural layer diversity between old-growth and mature maple–basswood and oak stands.

Indicators of old growth

Logistic regression produced similar models for distinguishing old-growth from mature stands in both covertypes (Table 5). Of the seven independent variables included in the analysis, total coarse woody debris volume was the only variable that was a significant indicator of old-growth condition. The model parameters indicate that, as coarse woody debris volume increases, so does the probability that a stand would be assigned to an old-growth designation. In comparison with assigning old-growth or mature designations randomly (50% probability of being old growth), only two old-growth and three mature oak stands were classified incorrectly, and only two old-growth and four mature maple–basswood stands were classified incorrectly (Fig. 3) (predictive abilities of 82 and 80% for oak and maple–basswood forests, respectively).

Discussion

Our results indicate that, in Minnesota, maple–basswood and oak old-growth forests are characterized by higher volumes of coarse woody debris (Tables 4 and 5, Figs. 3), a higher proportion of hollow logs, a higher proportion of live trees in large diameter classes (Fig. 2), a higher proportion of logs in decay classes 1 and 2 (Fig. 2), and a higher proportion of live trees in rot classes 3–5 (Fig. 2) compared with mature stands.

Other studies quantifying coarse woody debris patterns in hardwood forests of this region also have reported an increase in coarse woody debris volumes with increasing forest age (Tyrrell and Crow 1994*a*; Mller and Liu 1991; Gore and Patterson 1986). While higher volumes of coarse woody debris characterize old-growth hardwood forests, we were not able to determine specific cut-off values correlated with old-growth condition because of the high spatial variability of down logs in both the old-growth and mature stands (Table 4) resulting from natural disturbance patterns and differences in anthropogenic disturbance histories in the

Fig. 3. Relationship between probability of a stand being classified as old growth (determined by the logistic regression models in Table 5) and the volume of coarse woody debris in each stand. When a probability level of ≥ 0.50 is used as a cutoff for predicting old-growth status, two old-growth and four mature maple–basswood stands would be misclassified, and two old-growth and three mature oak stands would be misclassified. For maple–basswood, $N = 11$ old-growth and mature stands. For oak, $N = 10$ old-growth and mature stands. Overlapping points gives the appearance of smaller total N for each cover type.

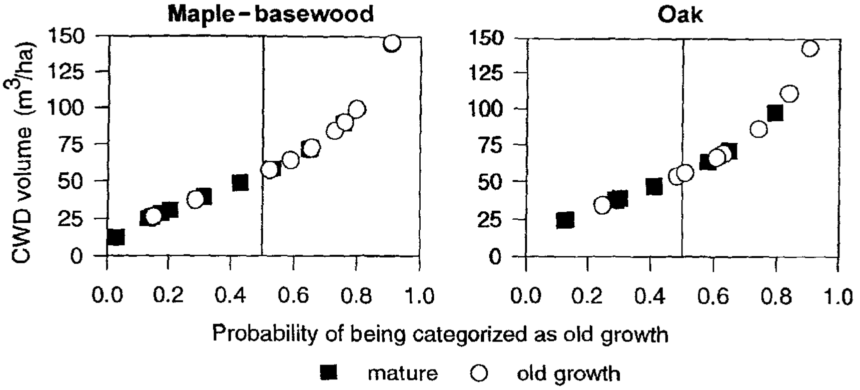


Table 5. Logistic regression models indicating that, of the seven forest parameters measured, coarse woody debris volume was the most important for predicting old growth versus mature classification.

Cover type	Model	P	Adjusted R^2
Oak	logit = –8.7030 + 2.1571[ln (CWD volume)]	0.015	34
Maple–basswood	logit = –10.7423 + 2.6927[ln (CWD volume)]	0.009	36

Note: Coarse woody debris (CWD) volume is the sum of log and snag volumes (m^2/ha). Back transformation of the logit yields the probability of being classified as old growth (SAS Institute Inc. 1995); logit = log $[P/(1 - P)]$, where P is the probability of being classified as old growth.

managed stands (Table 1). Because coarse woody debris was the only significant parameter in the logistic model, this high variability was primarily responsible for the few misclassifications of old-growth and mature stands by the logistic regression model (Fig. 3).

The density of logs and (or) snags alone is insufficient as an indicator of old-growth condition (Table 4). These parameters are highly variable because of different disturbance patterns. For example, four of the mature oak stands had been selectively logged within the past 10 years. Two stands appeared to have been logged using whole-tree removals and two using bole-only removals with large amounts of residual left on the sites. These differences contributed to high variability of snag, log, and coarse woody debris parameters in mature stands. Additionally, selective harvesting can cause an increase in the number of snags due to mechanical or soil compaction injury to trees not harvested, which later results in tree death.

Snag volume was a relatively small portion of the total coarse woody debris volume but contributed significantly to the selection of coarse woody debris volume as the primary indicator of old-growth condition in the logistic regression (Table 5). Although snag density did not differ significantly between old-growth and mature in either maple–basswood or oak forests, snags were of larger diameters in the old-growth stands. Therefore, the difference in snag volume between old-growth and mature sites was significant (Table 4).

The proportion of live trees in rot classes with extensive levels of rot (rot class 3–5; Table 2) was higher in old-growth stands than mature stands. Berry and Beaton (1972) documented a 50–75% incidence of rot in old-growth oak forests of Indiana. In oak forests, it is common for a tree to lose several large limbs over its lifetime, often because of the presence of rot. In maple–basswood forests surveyed in this study, most large trees had some substantial rot and all basswood trees over 50 cm DBH that we attempted to core were hollow or had soft centers.

Previous research (Harmon et al. 1986; Tyrrell and Crow 1994*a*) suggested that old-growth stands would have a large proportion of down logs in advanced stages of decay (decay classes 3 and 4) and relatively fewer in the earlier decay classes (1 and 2). In contrast, old-growth maple–basswood and oak forests in this study had a larger proportion of logs in decay classes 1 and 2 compared with mature stands. Several factors may contribute to these differences in decay-class distributions. First, the forest system studied by Tyrrell and Crow (1994*a*) (Sylvania Wilderness Area) is estimated to be between 2000 and 4000 years old (Frelich and Lorimer 1991), which is much older than the old-growth stands in this study. Compared with live trees in our study, those in the Tyrrell and Crow (1994*b*) study had a larger maximum diameter and were likely to produce larger logs. Larger logs would decompose more slowly (Harmon et al. 1986) and persist longer in advanced states of decay. In the Tyrrell and Crow (1994*a*) study, the coarse woody debris was dominated by conifer logs, which are more decay resistant than hardwood logs and persist on the forest floor even in advanced states of decay.

The proportion of hollow logs in old-growth maple–basswood and oak stands was significantly higher compared with mature stands. In a subsequent study on hollow versus solid log decay rates and decompositional pathways, Hale and Pastor (1998) demonstrated that hollow logs decay faster and move more rapidly through decay classes 3 and 4 than do solid logs. This partially may explain the higher proportion of logs in decay classes 1 and 2 in old-growth forests in this study. As the proportion of hollow logs increases, a shift in log decay-class distribution towards decay classes 1 and 2 would occur as a result of losses in decay classes 3 and 4.

Old-growth stands had a higher proportion of live trees in large diameter classes as compared with mature stands (Fig. 2). Old-growth stands in both cover types also had higher basal area of live trees than mature stands (Table 4), as might be predicted by the distributional shift towards larger diameter classes. However, because of lower tree density in old-growth stands and high site to site variability the difference in basal area between old-growth and mature stands was only statistically significant in maple–basswood stands (Table 4).

TWINSPAN divisions were based largely on geography and only secondarily on old-growth versus mature status. The nature of the areas in which remnant old-growth stands were located resulted in site features, such as slope and aspect, being highly correlated with the geographical location of the stands. The steepest slopes were in the southeastern parts of the state with slopes decreasing further north. Similarly, species composition appeared to be dominated by the results of climatic change from the southern to northern regions of the state.

Implications for management and preservation

There are two caveats we would like to make regarding possible management implications of the results of this study. The first is that many of the mature stands in this study were significantly older than conventional rotation age in Minnesota. In fact, most of the mature stands in this study were identified as "overmature" and in a "state of degradation;" only a few were of average rotational age (80 years). Second, while a 20 × 20 m releve has been shown to accurately document the species composition of common species (Minnesota Department of Natural Resources, County Biological Survey Program),[2] it undersamples rare species. If the compositional differences between old-growth and mature forests are, in fact, largely the presence of rarer, long-lived, poorly colonizing, perennial species, then a single releve would likely miss many of these species. Sampling schemes specifically designed to address the relationship of old-growth forests to rare plant species is needed. If old-growth provides important refugia for rare plants, then managers need to assess the degree to which different types and intensities of management affect the long-term viability of these species (Casson et al. 1994; Coffin and Pfannmuller 1988; Meier et al. 1995; Rogers 1982; Spies 1990; Whitney and Foster 1988). If the seed bank or rootstock of these rare species are destroyed by management practices, then species recovery may not be possible, even if longer rotations and improved methods are employed in managed forests.

While old-growth and mature, managed stands differed significantly in coarse woody debris volumes, log decay-class distributions, proportions of hollow logs, and live tree diameter-class and rot-class distributions (Table 4, Figs. 2 and 3), the species composition and diversity of mature forests were very similar to that of the old-growth forests. In contrast to plant species composition and diversity, basal area, volume of logs and snags, and the incidence of advanced rot were lower in mature stands compared with old-growth stands. The maintenance or enhancement of these structural characteristics is more easily accomplished by silvicultural treatments (such as leaving or creating snags, leaving green "legacy" trees, and dropping cull trees to provide coarse woody debris (Franklin et al. 1989)) than the maintenance of species diversity. Our study indicates that, if planned carefully, a silviculturally managed forest can maintain some structural characteristics similar to old growth, such as snags and large logs in advanced stages of decay, that may enhance the functional diversity of managed forests. These changes may allow harvesting of trees while also protecting biological diversity and long-term site productivity (Franklin et al. 1989; Mladenoff et al. 1994; Mladenoff and Pastor 1993; Keddy and Drummond 1996; Roskoski 1980; McCune and Menges 1986; Gore and Patterson 1986).

Acknowledgments

Funding for this study was provided by the Minnesota Legislature, ML 1993, Chapter 172, Section 14, Subdivision 6(c), as recommended by the Legislative Commission on Minnesota Resources from the Minnesota Future Resources Fund. The authors thank Dr. Lucy Tyrrell and an anonymous reviewer for their valuable commentary in the preparation of this paper.

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