

STRUCTURAL AND COMPOSITIONAL DIFFERENCES BETWEEN OLD-GROWTH AND MATURE SECOND-GROWTH FORESTS IN THE MISSOURI OZARKS

Stephen R. Shifley¹, Lynn M. Roovers², and Brian L. Brookshire³

Abstract: There are currently only about 7,900 acres (3,200 ha) of remnant old-growth forest in Missouri, but public land management plans call for old-growth acreage to increase to more than 200,000 acres (81,000 ha). To develop a better quantitative understanding of the transitions that are likely as current forests mature to an old-growth state, we compared a number of characteristics measured for two old-growth sites with values for two mature second-growth sites. The stocking and the basal area of both live and dead trees were similar for the old-growth and second-growth forests. The diameter distribution (number of trees by dbh class) for all species combined had a negative exponential (reverse-J) shape that varied little from old-growth to second-growth. However, the old-growth sites consistently had more trees ≥ 17 inches (43 cm) dbh than did the second-growth sites. The absolute number of these larger trees was small; 14 per acre (35 per ha) for the old-growth sites compared to 7 per acre (17 per ha) for the mature second-growth sites. The white and red oak species groups dominated the overstories at all sites. Mean volume of down woody debris ≥ 4 inches in diameter was $476 \text{ ft}^3 \cdot \text{ac}^{-1}$ ($33.3 \text{ m}^3 \cdot \text{ha}^{-1}$) on the old-growth sites vs. $240 \text{ ft}^3 \cdot \text{ac}^{-1}$ ($16.8 \text{ m}^3 \cdot \text{ha}^{-1}$) on the second-growth comparison site.

INTRODUCTION

Old-growth forests currently occupy approximately 7,900 acres (3200 ha) in Missouri, roughly 0.05 percent of the existing forest land in the state (Shifley 1994). Most of these tracts are less than 100 acres (40 ha) and held in some form of protective status. Public land management plans in Missouri call for at least 10 percent of the publicly-owned forested acreage to be managed as old-growth. This will eventually increase the amount of old-growth forest in the state to over 200,000 acres (81,000 ha). These acreages are necessarily rough estimates because there is no precise definition of what conditions constitute an old-growth forest.

Table 1 summarizes characteristics that are typically associated with old-growth forests. While this list is comprehensive, it lacks the quantitative detail to provide a rigorous definition of the old-growth condition. Hence, the acreage of what is called old-growth forest can change when definitions are modified or when different individuals interpret the existing definitions.

Virtually every old-growth tract in Missouri has been subjected to some degree of past anthropogenic disturbance. Fire (pre- and post-European settlement) and limited livestock grazing have affected every old forest in the state. Most Missouri old-growth remnants also have had a few trees selectively harvested during the past century. Despite these disturbances, existing remnant old-growth forests provide the best available information about the likely future development of forests managed for old-growth characteristics.

¹Research Forester, USDA Forest Service, North Central Forest Experiment Station, 1-26 Agriculture Building, University of Missouri, Columbia, MO 65211.

²Geographer, USDA Forest Service, North Central Forest Experiment Station, 1-26 Agriculture Building, University of Missouri, Columbia, MO 65211.

³Silviculturist, Missouri Department of Conservation, P.O. Box 180, Jefferson City, MO 65102-0180.

Table 1. Characteristics reported in literature to be associated with Midwestern old-growth forests^a.

Defining characteristics from Meyer (1986)	Defining characteristics from Parker (1989)	Defining characteristics from Martin (1991)
Diverse species distribution for dominant trees. Relatively high percentage of shade tolerant trees.	Tree species richness 20 to 40. Herbaceous species richness 17 to 53. Breeding bird species richness 18 to 33.	High species richness/diversity. Species richness ≥ 20 canopy trees.
Multi-layered canopy. Wide range in tree height and age.		Uneven-aged with canopy species in several size classes.
Live trees ≥ 14 inches dbh are $\geq 25\%$ of stocking.		Several large canopy trees.
		Large, high-quality commercially important trees. (indicative of no past harvest)
Dominant trees ≥ 100 years.	Mean age of overstory 135 to 210 years. Maximum age of overstory 190 to 375 years.	Oldest trees ≥ 200 years.
	Overstory density approximately 65 to 173 trees \cdot ac ⁻¹ (≥ 4 in dbh).	Overstory density approximately 100 trees \cdot ac ⁻¹ (≥ 4 in dbh).
	Overstory basal area in the range of 110 - 150 ft ² \cdot ac ⁻¹ .	Overstory basal area ≥ 90 ft ² \cdot ac ⁻¹ .
Evidence of large tree decadence: broken and dead tops, rot, cavities. Large dead snags and large down logs. Large logs in streams and drainages.	From 8 to 18 snags \cdot ac ⁻¹ (≥ 4 in dbh). Down wood 7 to 11 tons \cdot ac ⁻¹ .	Logs and snags present in various sizes and stages of decay.
Variable understory density --from open to dense. Variable degree of herbaceous ground cover.	Gaps are 7-8% of forest, randomly distributed, range 0.012 - 0.09 ac in size.	Treefall gaps formed by windthrow.
	Annual mortality 0.6-0.9 %.	
		Plant and animals that prefer old- growth.
		Undisturbed soils and soil macropores.
		Little or no evidence of human disturbance.
	Volume 16,000 to 25,000 bd.ft. \cdot ac ⁻¹ .	

^a cm = 2.54(inches), trees \cdot ha⁻¹ = 2.471(trees \cdot ac⁻¹), basal area m² \cdot ha⁻¹ = 0.2296(basal area ft² \cdot ac⁻¹),
Mg \cdot ha⁻¹ = 2.241(tons \cdot ac⁻¹)

In this paper we compare and contrast a range of structural and compositional characteristics measured in two remnant old-growth forests with the same characteristics measured in two mature second-growth forests. This work provides new information about similarities between second-growth and old-growth forests. It also identifies some characteristics that differ sufficiently to be useful in judging where a given forest lies along the gradient from second-growth to old-growth.

STUDY SITES

The two old-growth and two second-growth sites evaluated in this study are shown in Figure 1 and described below.

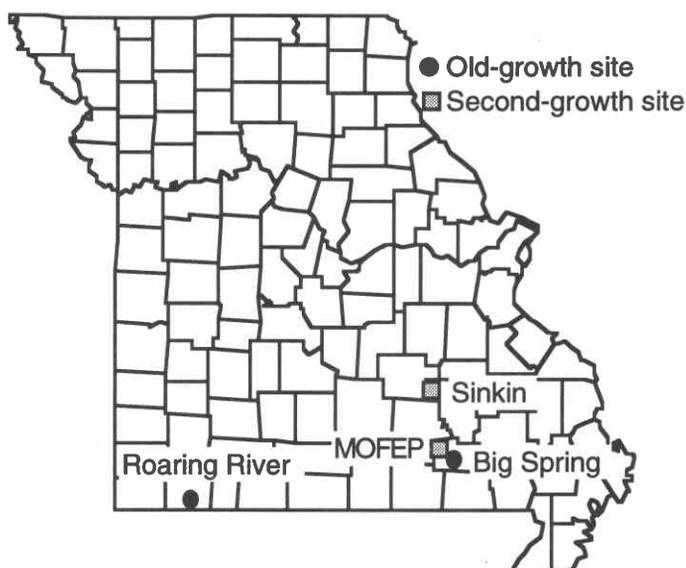


Figure 1. Location of old-growth and second-growth study sites in Missouri.

Big Spring (old-growth)

The Big Spring site is a 330-acre tract in the Ozark National Scenic Riverway in Carter County. Prior documentation for the site classified the tract as a mixture of old-growth and old second-growth oak and oak-shortleaf pine forest (Nigh and others 1992). Forest associations are xero-mesic to xeric oak-hickory and oak-pine. Our increment cores from 13 dominant and codominant trees showed ages ranging 63 to 141 years. Some trees on the tract exceeded 200 years (Nigh and others 1992). There is evidence of past selective logging at a few sites along the ridges and in the bottoms. Elevation at the site ranges from 480 to 820 feet (150 to 250 m) with most slopes ranging from 20 to 40 percent. Soils are very cherty loams and silt loams that are well- to excessively-drained.

Roaring River (old-growth)

The Roaring River site is a 120-acre old-growth tract in Roaring River State Park in Barry County. A prior dendrochronological study at the site reported white oaks in the 200 to 250 year age class (Stahle and others 1985). Forest associations are principally xeric oak-hickory. With the exception of some past selective logging along the tops of the ridges that border the site, anthropogenic disturbance appears to have been limited to periodic fires that were historically common throughout the Ozarks (Ladd 1991). Elevation ranges from 1260 to 1440 feet (380 to 440 m) with slopes typically ranging from 20 to 70 percent. Most soils are cherty and moderately- to excessively-drained. Some ridgetop soils have a fragipan at approximately 14 inches (35 cm). Available water capacity and fertility are low, and rock outcrops occur at several locations on the site.

Sinkin Experimental Forest (second-growth)

The 4,100 acre (1660 ha) Sinkin Experimental Forest, located in Dent and Reynolds Counties, was used as a second-growth comparison site. Prior to establishment as an experimental forest in 1950, the tract was treated much like other forests in the area. It was extensively logged for shortleaf pine⁴ between 1900 and 1920; grazing and burning were common in the following years. Since 1950 grazing and wildfire have been excluded from the Sinkin. Numerous silvicultural studies have been established on the experimental forest, but the majority of the acreage is well-stocked, second-growth, oak-hickory and oak-pine forest in the 70- to 90-year age class. Elevation ranges from 1000 to 1350 feet (300 to 410 m) with slopes typically from 10 to 35 percent. Soils are cherty loams and cherty silt-loams. For this study, we excluded areas that had been harvested since 1950.

MOFEP (second-growth)

MOFEP, the Missouri Forest Ecosystem Project is a large-scale study of the impacts of silvicultural treatments on an array of ecosystem attributes (Brookshire and Hauser 1993). The MOFEP study includes 9 large, contiguous experimental tracts or compartments. We used the 3 compartments in the Peck Ranch Wildlife Area (MOFEP compartments 7, 8, and 9 in Carter County) as second-growth comparison sites. These three compartments range in size from 825 to 1240 acres (334 to 502 ha), lie in a single township, are the closest ones to the Big Spring old-growth site, and generally have been excluded from harvest for longer than the other MOFEP sites (approximately 40 years). All utilized data were collected prior to implementation of experimental treatments planned for the sites. With the exception of the exclusion of harvesting, these mature second-growth oak-hickory forests are fairly typical of Ozark forest sites. More than ninety percent of the MOFEP comparison plots were on ecological land types (ELTs) that support dry to xeric chert or limestone forest similar to the old-growth sites. Soils on the MOFEP sites are generally well- to excessively-drained and cherty. Site conditions for MOFEP compartments 7, 8, 9 are described in great detail by Brookshire and Hauser (1993).

METHODS

In 1992, thirty 0.25 ac (0.1 ha) circular inventory plots per tract were systematically established at the Big Spring and Roaring River sites. On each main plot all trees ≥ 4 inches (10 cm) dbh were inventoried. Trees ≥ 1 inch (2.5 cm) and < 4 inches (10 cm) dbh were inventoried on a concentric 0.025 ac (0.01 ha) circular subplot. Species and dbh were recorded for each tree. The number of cavities with smallest dimension ≥ 0.8 inch (2 cm) was also recorded for each tree at the Big Spring site and for trees on every second plot at the Roaring River site. The length and mid-point diameter of each piece of down wood with minimum diameter ≥ 4 inches (10 cm) was measured on the 0.25 ac (0.1 ha) main plot. Each piece of down wood was classified by decay stage using a system described by Maser and others (1979) for western conifers (Table 2). Volume of each down log was computed as the volume of a cylinder of known length and midpoint diameter. The ground area covered by each down log was computed as the product of its length and diameter.

In 1992-93, nearly identical protocols were used to sample 96 plots systematically distributed across the Sinkin Experimental Forest. The only deviation was that cavities were not measured. Of the 96 plots on the Sinkin, 73 were utilized in this comparison. The remaining 23 were excluded because they fell in areas that had been subjected to harvest or other disturbance since the experimental forest was established in 1950.

⁴Scientific names for all species are given in Table 4.

Table 2. Decomposition classes used to classify down logs. From Maser and others (1979).

Decomposition Class	Defining characteristics
Class 1	Round log, bark intact, small twigs present, log elevated on support points
Class 2	Round log, bark intact, twigs absent, log elevated on support points
Class 3	Round log, traces of bark, twigs absent, log sagging near ground
Class 4	Round to oval log, bark absent, twigs absent, log entirely on ground
Class 5	Oval log, bark absent, twigs absent, log entirely on ground

The MOFEP sites were sampled with a total of 210 plots during 1990-91. Plot location was random subject to the constraint that at least one plot had to fall in each identified forest stand. The 0.5 ac (0.2 ha) circular main plots were used to sample trees ≥ 4.5 inches (11.4 cm) dbh. Trees ≥ 1.5 inches (3.8 cm) and < 4.5 inches (11.4 cm) dbh were sampled on four circular 0.05 ac (0.02 ha) subplots. The MOFEP samples included species and dbh for each tree. Percent of the ground covered by down wood ≥ 2 inches (5 cm) in diameter on the MOFEP sites was sampled along four 56.5-foot (17.3 m) transects originating at plot center and oriented along the cardinal directions. Percent cover was computed as the percent of the transect length actually covered by down logs larger than the 2-inch (5 cm) size threshold.

Per acre values for each characteristic were computed by plot and summarized to obtain means and variances for each tract. Stocking percent was computed from the tree area ratio equations of Gingrich (1967), Rogers (1983), and Stout and others (1987). Importance values for each tract (all plots combined) were computed as $[0.5(\text{relative number of trees} + \text{relative basal area})]$. Two types of statistical comparisons were made among characteristics observed at the study sites. The first test was a one-way analysis of variance by site for the 4 sites with all plots per site used in the comparison ($n = 343$). The null hypothesis is that the characteristic of interest (e.g. basal area, number of trees, etc.) is equal on all sites. Although this is an appropriate test for differences among the specific sites, the procedure introduces the problem of pseudoreplication (Hurlbert 1984) if multiple observations per tract are used to make inferences concerning the more general comparison of old-growth vs. second-growth sites. A more appropriate and more conservative comparison of old-growth and second-growth forest characteristics can be made by using a t-test to evaluate the null hypothesis that the means observed for the two old-growth sites were equal to those for the two second-growth sites ($n=4$). Whenever possible, this second statistical test was also performed and reported.

RESULTS

Structural Characteristics

The most notable trend that emerges from a comparison of composite stand characteristics for the old-growth and mature second-growth forests is the similarity across all sites. (Table 3). Although the MOFEP site had substantially fewer trees per acre than the other sites, the MOFEP sampling scheme excluded live trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh. Observations on the Sinkin indicate that live trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh would add approximately $150 \text{ trees} \cdot \text{ac}^{-1}$ ($350 \text{ trees} \cdot \text{ha}^{-1}$) and $1.3 \text{ ft}^2 \cdot \text{ac}^{-1}$ ($0.3 \text{ m}^2 \cdot \text{ha}^{-1}$) of basal area to the MOFEP means. This addition would bring the mean number of trees $\cdot \text{ac}^{-1}$ on the MOFEP sites in line with the observed values for the other sites, although the mean basal area would still be somewhat lower.

Table 3. Comparison of composite stand characteristics for old-growth (Big Spring and Roaring River) and second-growth (Sinkin and MOFEP) study areas. Values in parentheses are standard deviations for values by plot at that site. Values are for trees ≥ 1 inch (2.5 cm) dbh except as noted^a.

Site	Sample size	Live trees number \cdot ac ⁻¹	Live basal area ft ² \cdot ac ⁻¹	Stocking percent	Dead trees number \cdot ac ⁻¹	Dead basal area ft ² \cdot ac ⁻¹
Big Spring	30	582 (209)	104 (12)	88 (12)	68 (44)	8.3 (6.3)
Roaring River	30	623 (191)	108 (23)	96 (18)	77 (57)	12.5 (8.4)
Sinkin	73	675 (297)	102 (21)	91 (17)	90 (86)	9.1 (6.9)
MOFEP ^b	210	439 (161)	90 (13)	82 (9)	15 (11)	7.4 (5.8)

^a Trees \cdot ha⁻¹ = 2.471(trees \cdot ac⁻¹); basal area m² \cdot ha⁻¹ = 0.2296(basal area ft² \cdot ac⁻¹).

^b MOFEP data includes only live trees ≥ 1.5 inches dbh and only standing dead trees ≥ 4.5 inches dbh.

One-way ANOVA using all plots to test for differences among the 4 sites showed significant differences in the mean number ($p < 0.001$, 339 d.f.), basal area ($p < 0.001$, 339 d.f.), and stocking percent ($p < 0.001$, 339 d.f.) for live trees per acre. However, the differences did not follow patterns that could be used to readily distinguish the old-growth sites from the second growth sites. MOFEP means were uniformly smaller than the other three sites which were statistically indistinguishable from one another (Tukey-Kramer HSD, $\alpha = 0.05$) for all three dependent variables. Adjusting for trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh that were excluded from the MOFEP sampling, eliminates the significant difference among sites in the number of live trees per acre.

The number of standing dead trees per acre was also significantly different among sites (one-way ANOVA by site, $p < 0.001$, 339 d.f.) with the MOFEP mean smaller than the other three sites (Tukey-Kramer HSD, $\alpha = 0.05$). Again this was at least partially due to sampling procedural differences at the MOFEP site. Basal area of standing dead trees followed a somewhat different pattern. Means were significantly different among sites (one-way ANOVA by site, $p < 0.001$, 339 d.f.), but in this case the Big Spring and MOFEP means were significantly larger than the Roaring River and Sinkin sites (Tukey-Kramer HSD, $\alpha = 0.05$).

A comparison of the means of the two old-growth sites with that of the two second-growth sites showed no significant differences in the number, basal area, or stocking of live trees, nor for the number or basal area of standing dead trees (2 d.f. with p -values of 0.74, 0.25, 0.46, 0.65, and 0.44, respectively). Nor were the mean differences of sufficient magnitude to generally be considered of practical importance, statistical tests notwithstanding.

At first glance, a comparison of the number of live trees by diameter class also shows little difference among the old-growth and second-growth sites (Figure 2A). At all sites the diameter distribution (based on all tree species) had a negative exponential shape commonly associated with uneven-aged forests. The greatest absolute difference in the diameter distributions occurred for trees in the 2-inch (5 cm) dbh class. The MOFEP site had fewer trees of this size than the other three sites, due primarily to the fact that trees < 1.5 inches (3.8 cm) were not included in the MOFEP sample. The greatest *relative* difference in the number of trees per acre, however, occurred for trees larger than 8 inches (20 cm) dbh. That portion of the diameter distribution is redrawn at higher resolution to highlight those differences (Figure 2B).

The second growth sites had 1.5 to 2 times as many trees between 9 and 17 inches (23 and 43 cm) as the old-growth sites, but this relationship shifts for larger diameter classes. On average the old-growth sites had 14 trees per acre (35 trees per ha) larger than 17 inches (43 cm) dbh compared to 7 trees per acre (17 trees per ha) for the second-growth sites. This difference may appear rather minor, but in terms of basal area (rather than the number of trees) these large trees have much greater impact (Figure 2C). A graphic based on tree volume or biomass would further accentuate the influence of the largest diameter trees.

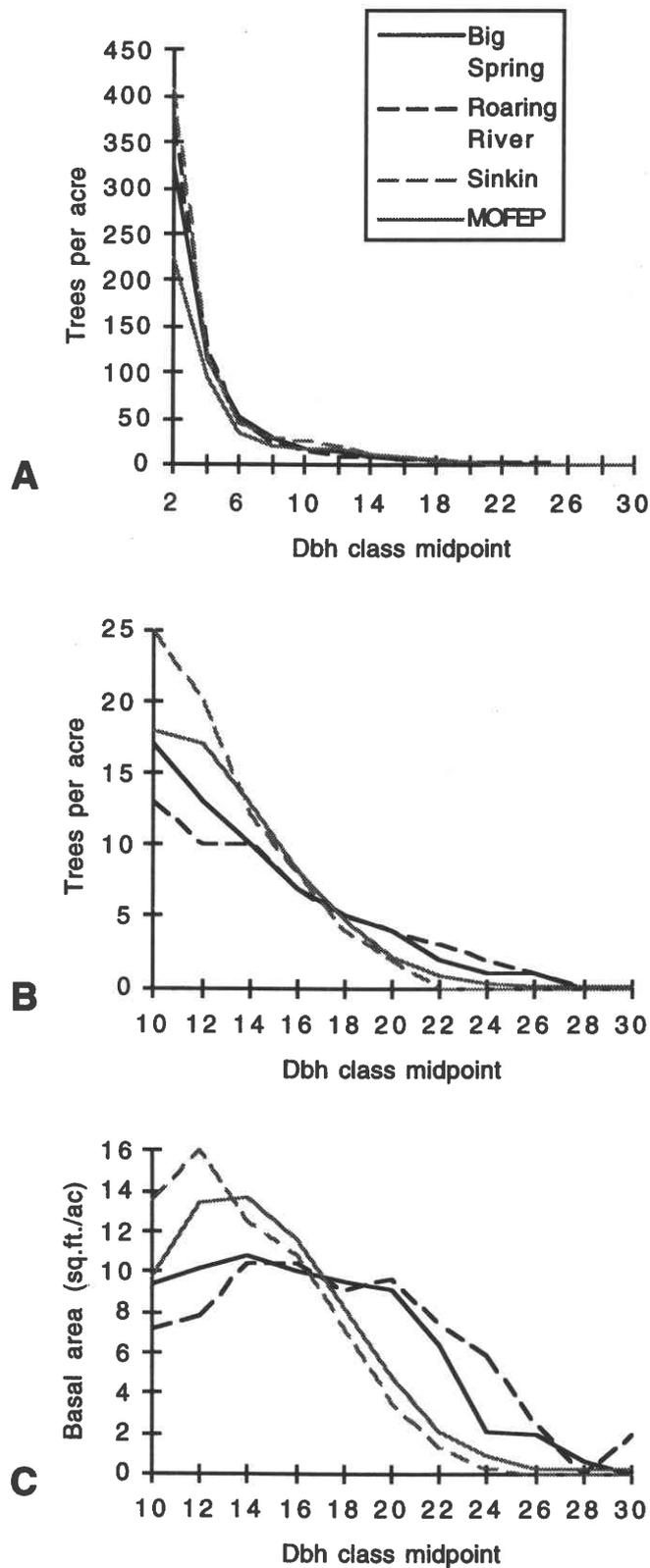


Figure 2. Three views of the diameter distribution (all species) for old-growth and second growth sites showing (A) number of trees ≥ 1 inch dbh (≥ 1.5 inches for MOFEP), (B) number of trees ≥ 9 inches dbh, and (C) basal area of trees ≥ 9 inches dbh.

The functional importance of these relatively few large trees must not be overlooked. One feature that inevitably stands out when walking through an old forest is the large trees, which people tend to notice and recall disproportionate to their low frequency. If humans tend to ascribe high relative importance to large individual trees, other organisms may also do so, either individually or collectively. The largest trees provide the highest and strongest perches. They provide the greatest surface area and volume and the largest cavities. Larger trees are also more likely to have cavities that can be used as nesting sites by wildlife. Observations of cavities by tree size on the Big Spring and Roaring River tracts showed a 15 percent probability of a 10-inch (25 cm) dbh tree having a cavity; that probability increased linearly to over 60 percent for a 25-inch (64-cm) dbh tree.

For all sites the diameter distribution of standing dead trees followed the same general shape as the diameter distribution of live trees, at approximately 10 percent the frequency of live trees. This result was consistent across all sites and might serve as a rule of thumb for the amount and size distribution of dead-standing wood in the maturing oak forests.

Species Composition

The total number of tree species (tree species richness) was greatest on the Sinkin and MOFEP sites. The number of tree species observed by site was 43, 40, 36, and 33 for Sinkin, MOFEP, Big Spring and Roaring River, respectively. This difference of seven in the tree species richness between the two old-growth and two second-growth sites was near the margin of statistical significance (t-test, $p = 0.08$, 2 d.f.) However, the higher species richness values on the second-growth sites were consistent with expectations given the larger sample sizes on those sites. All other factors being equal, the greatest number of species would be expected on these two tracts with the most samples. Because each site had only a single observation for species richness, statistical differences in species richness among all four sites could not be analyzed using one-way ANOVA.

It is informative to compare importance values for species by site. In Table 4, importance values and their ranks are given for all woody species that attained a diameter of at least one inch (2.5 cm) dbh (1.5 inches or 3.8 cm dbh for the MOFEP site). White oak, black oak, scarlet oak and dogwood have high importance values at all sites. Shortleaf pine has a high value at sites other than Roaring River where it did not occur. The high importance value for dogwood is strictly a function of the large number of dogwood stems that are common in the lower canopy strata at these sites. Species importance rank order at a given site does not change if some species or groups of species (e.g. species generally relegated to the understory) are dropped from consideration. Also, the values in Table 4 can be used to compute the importance values for subsets of species.

It is interesting to note that both maple and pawpaw were minor components in these relatively dry old-growth forests. This is in sharp contrast to values reported for more mesic old-growth sites (e.g. Kucera and McDermott 1955, Shotola and others 1992, Wuenscher 1967) where sugar maple is typically more than 20 percent of the total basal area and pawpaw may constitute more than 5 percent of the woody stems in the understory.

Some patterns in forest composition are more easily discerned by examining species groupings by size class. Figure 3 illustrates how the relative importance of various species groups changes with increasing diameter class. Although relatively rare in the smaller diameter classes, the white and red oak groups dominate the overstories at all sites. On the two old-growth sites, the white oaks have greater relative importance in the largest diameter classes than do the red oaks.

Although the composite diameter distribution for all species combined has a negative-exponential shape (as shown in Figure 1), individual species do not necessarily follow that form. For white oak, red oak, and shortleaf pine groups which dominate the overstory at these sites, the composite number of trees by diameter class has a unimodal distribution on all sites (Figure 4). However, on the old-growth sites the peak of the diameter distribution is shifted to the right and the number of trees in the smaller size classes is substantially fewer than observed for the second-growth

Table 4. Importance values and their ranks for woody plants on old-growth (Big Spring and Roaring River) and second-growth (Sinkin and MOFEP) sites. Importance values are computed as $\{(relative\ number\ of\ trees + relative\ basal\ area)/2\}$ for all live trees sampled. Species are arranged in decreasing rank order for the Big Spring site. Nomenclature follows Little (1953).

Common name	Scientific name	Big Spring		Roaring River		Sinkin		MOFEP	
		IV	Rank	IV	Rank	IV	Rank	IV	Rank
Flowering dogwood	<i>Cornus florida</i>	24.0	1	17.6	2	16.7	2	8.8	4
White oak	<i>Quercus alba</i>	22.5	2	20.8	1	22.7	1	17.9	3
Black oak	<i>Quercus velutina</i>	6.9	3	15.3	3	15.0	3	18.3	2
Scarlet oak	<i>Quercus coccinea</i>	6.5	4	0.4	24	3.9	6	18.8	1
Shortleaf pine	<i>Pinus echinata</i>	5.5	5	<0.1	--	12.9	4	5.9	6
Mockernut hickory	<i>Carya tomentosa</i>	5.3	6	10.8	4	2.3	8	4.5	8
Black hickory	<i>Carya texana</i>	4.4	7	2.2	9	1.5	12	5.1	7
Post oak	<i>Quercus stellata</i>	4.2	8	1.5	11	1.4	14	8.4	5
Blackgum	<i>Nyssa sylvatica</i>	3.8	9	2.3	8	6.4	5	3.0	9
S. red oak	<i>Quercus falcata</i>	2.9	10	<0.1	--	<0.1	--	<0.1	--
N. red oak	<i>Quercus rubra</i>	1.6	11	5.9	6	1.7	10	<0.1	--
Red maple	<i>Acer rubrum</i>	1.6	12	3.0	7	2.1	9	0.8	13
Chinkapin oak	<i>Quercus muehlenbergii</i>	1.2	13	1.1	14	0.8	16	0.4	14
Winged elm	<i>Ulmus alata</i>	0.9	14	0.7	20	0.1	30	0.2	21
Grape	<i>Vitis</i> spp.	0.8	15	1.9	10	<0.1	--	0.2	18
Slippery elm	<i>Ulmus rubra</i>	0.8	16	0.4	23	3.5	7	0.2	19
Serviceberry	<i>Amelanchier</i> spp.	0.7	17	7.4	5	0.1	32	0.1	23
Bitternut hickory	<i>Carya cordiformis</i>	0.7	18	<0.1	35	0.7	17	0.1	26
Pignut hickory	<i>Carya glabra</i>	0.7	19	0.3	26	1.5	11	2.0	11
Sassafras	<i>Sassafras albidum</i>	0.6	20	1.0	15	1.2	15	2.5	10
Buckthorn	<i>Rhamnus</i> spp.	0.6	21	0.7	19	0.1	29	0.3	15
Ironwood	<i>Ostrya virginiana</i>	0.4	22	0.7	18	1.4	13	<0.1	36
Green ash	<i>Fraxinus pennsylvanica</i>	0.4	23	<0.1	--	0.2	24	<0.1	31
Black walnut	<i>Juglans nigra</i>	0.4	24	0.1	34	0.6	20	0.2	22
Blackjack oak	<i>Quercus marilandica</i>	0.4	25	0.1	28	<0.1	34	1.3	12
White ash	<i>Fraxinus americana</i>	0.4	26	1.3	13	0.2	27	0.1	24
Eastern redbud	<i>Cercis canadensis</i>	0.3	27	0.7	17	0.4	22	0.2	17
Blueberry	<i>Vaccinium</i> spp.	0.3	28	<0.1	--	<0.1	--	<0.1	37
Persimmon	<i>Diospyros virginiana</i>	0.3	29	<0.1	--	<0.1	41	0.2	16
Bluebeech	<i>Carpinus caroliniana</i>	0.3	30	<0.1	--	0.7	18	<0.1	--
Paw paw	<i>Asimina triloba</i>	0.2	31	<0.1	--	<0.1	--	<0.1	40
N. pin oak	<i>Quercus palustris</i>	0.1	32	<0.1	--	<0.1	--	<0.1	--
Basswood	<i>Tilia americana</i>	0.1	33	0.2	27	<0.1	37	<0.1	--
Viburnum	<i>Viburnum</i> spp.	0.1	34	<0.1	--	<0.1	--	<0.1	35
Gumbemelia	<i>Bumelia lanuginosa</i>	0.1	35	<0.1	--	<0.1	39	<0.1	32
Black cherry	<i>Prunus serotina</i>	<0.1	36	<0.1	36	0.2	28	0.1	27
Wild plum	<i>Prunus americana</i>	<0.1	37	0.9	16	<0.1	--	0.1	28
American elm	<i>Ulmus americana</i>	<0.1	38	0.1	33	<0.1	--	0.1	30
Sugar maple	<i>Acer saccharum</i>	<0.1	--	1.3	12	<0.1	38	<0.1	42
Spicebush	<i>Lindera benzoin</i>	<0.1	--	0.5	21	<0.1	--	<0.1	--
Shagbark hickory	<i>Carya ovata</i>	<0.1	--	0.5	22	<0.1	--	<0.1	43

Table 4 (continued)

Eastern redcedar	<i>Juniperus virginiana</i>	<0.1	--	0.3	25	0.1	31	0.2	20
Red mulberry	<i>Morus rubra</i>	<0.1	--	0.1	29	0.2	26	0.1	29
Ozark chinkapin	<i>Castanea ozarkensis</i>	<0.1	--	0.1	30	<0.1	--	<0.1	--
Greenbrier	<i>Smilax</i> spp.	<0.1	--	0.1	32	<0.1	--	<0.1	--
Sycamore	<i>Platanus occidentalis</i>	<0.1	--	<0.1	--	0.7	19	<0.1	41
Hackberry	<i>Celtis occidentalis</i>	<0.1	--	<0.1	--	0.4	21	<0.1	33
Butternut	<i>Juglans cinerea</i>	<0.1	--	<0.1	--	0.3	23	<0.1	--
Hawthorn	<i>Crataegus</i> spp.	<0.1	--	<0.1	--	0.2	25	0.1	25
Shellbark hickory	<i>Carya laciniosa</i>	<0.1	--	<0.1	--	0.1	33	<0.1	--
Honeylocust	<i>Gleditsia triacanthos</i>	<0.1	--	<0.1	--	<0.1	35	<0.1	38
Chokecherry	<i>Prunus virginiana</i>	<0.1	--	<0.1	--	<0.1	36	<0.1	--
Blue ash	<i>Fraxinus quadrangulata</i>	<0.1	--	<0.1	--	<0.1	42	<0.1	--
Swamp chest. oak	<i>Quercus michauxii</i>	<0.1	--	<0.1	--	<0.1	43	<0.1	--
Shumard oak	<i>Quercus shumardii</i>	<0.1	--	<0.1	--	<0.1	--	<0.1	34
Sumac	<i>Rhus</i> spp.	<0.1	--	<0.1	--	<0.1	--	<0.1	39
Poison ivy	<i>Rhus radicans</i>	<0.1	--	<0.1	--	<0.1	--	<0.1	44

tracts. The mean diameters of the combined white oak, red oak, and shortleaf pine species groups was 7.7 and 8.8 inches (19.6 and 22.4 cm) for the Big Spring and Roaring River sites, respectively, while those for the Sinkin and MOFEP sites were 6.3 and 6.0 inches (16.0 and 15.2 cm), respectively. The unimodal shape of the diameter distributions in Figure 3 are largely due to the white oak group. When considered separately, the diameter distribution for the red oak group has a unimodal shape on the Big Spring and MOFEP sites. The diameter distribution of shortleaf pine by itself did not have a distinctly unimodal shape at any of the four sites.

Down Woody Debris

Mean volume of down woody debris at least 4 inches (10 cm) in diameter on the Big Spring and Roaring River sites was about twice the volume observed at Sinkin (Table 5). There were no distinguishable patterns within decomposition classes, but the classes had been developed for western conifers (Maser and others 1979). Using these class definitions, the majority of the volume consistently fell into classes 3 and 4.

Within each tract the variability in the volume of down wood among plots was high. The coefficient of variation for the total volume of down wood by plot was in the range of 70 to 75 percent. Nevertheless, analysis of variance for the mean volume of down wood per acre for the Big Spring, Roaring River, and Sinkin sites (one-way ANOVA based on all plots per site) showed significant differences among sites ($p < 0.001$, 130 d.f.). Pairwise comparison of means for these three sites (Tukey-Kramer HSD, $\alpha = 0.05$) showed no significant difference between Big Spring and Roaring River, but values for those two sites were significantly larger than for the Sinkin. Because of procedural differences in sampling, compatible estimates of down wood volume were not available for the MOFEP site. The mean volume of down wood at least 2 inches (5 cm) in diameter on the MOFEP site is in the approximate range of 200 to 300 $\text{ft}^3 \cdot \text{ac}^{-1}$ (14 to 21 $\text{m}^3 \cdot \text{ha}^{-1}$), depending on the set of assumptions used to estimate the volume of down logs. But even at the high end, these estimates are markedly lower than observed at Big Spring and Roaring River. Because a comparable estimate of down wood volume was not available for the MOFEP sites, it was not possible to use a t-test to evaluate differences in down wood volume between the two old-growth and the two second-growth sites.

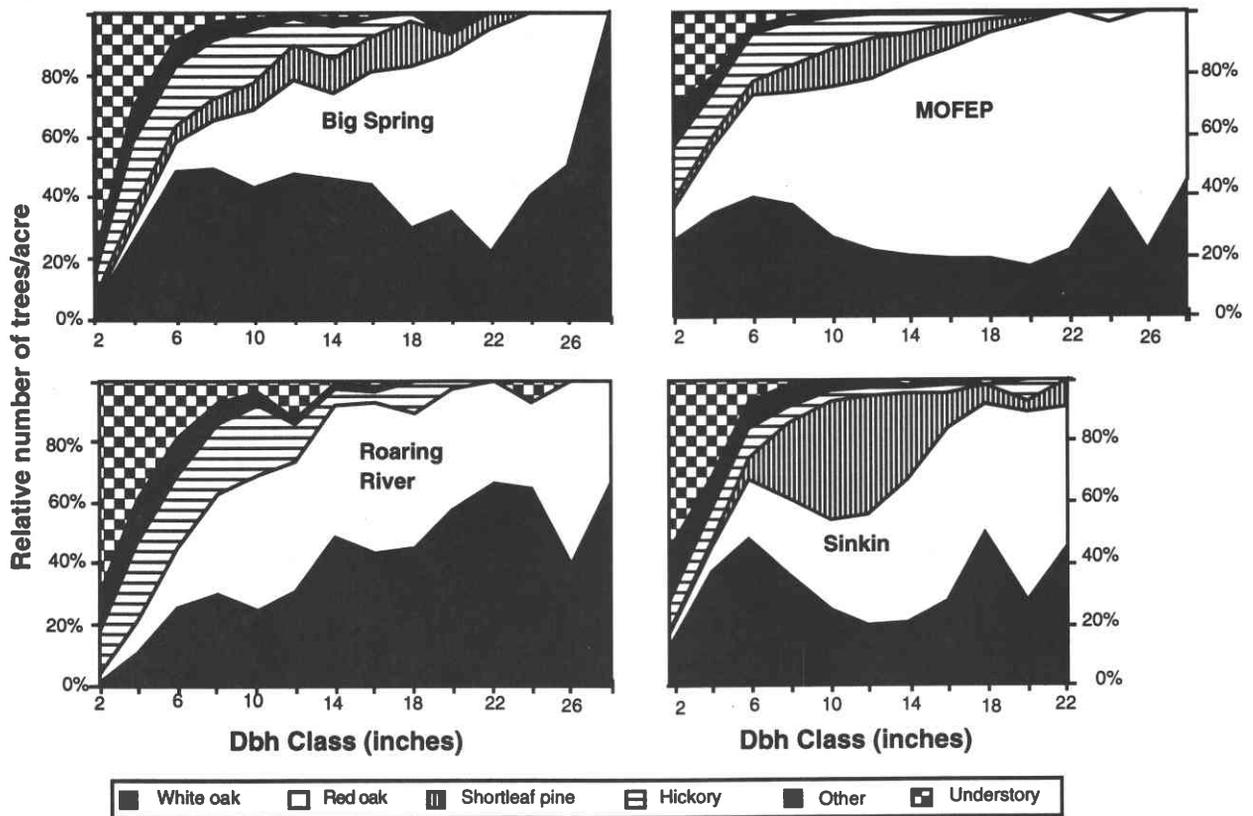


Figure 3. Relative number of trees per acre by 2-inch dbh class midpoint and major species groups. The white oak group includes white, post, chestnut, and chinkapin oak. The red oak group includes northern red, southern red, scarlet, black, and blackjack oaks. Hickory includes all *Carya* spp. Understory species include dogwood, blackgum, ironwood, bluebeech, serviceberry, pawpaw, buckthorn, redbud, vines, and shrubs.

The mean percent cover for the two old-growth and two second-growth sites (Table 5) was 1.56 and 1.29 percent, respectively. This difference was not statistically significant ($p = 0.33$ for t-test with 2 d.f.).

Table 5. Mean volume of down woody debris and percent of ground covered by down wood^a. Values include pieces ≥ 4 inches (10 cm) diameter for Big Spring, Roaring River and Sinkin; ≥ 2 inches (5 cm) diameter for MOFEP. Class definitions are from Maser and others (1979) and summarized in Table 2.

Site	(newly fallen)			(decomposed)		Total all classes ft ³ •ac ⁻¹	Percent of ground covered by down wood
	Class 1 ft ³ •ac ⁻¹	Class 2 ft ³ •ac ⁻¹	Class 3 ft ³ •ac ⁻¹	Class 4 ft ³ •ac ⁻¹	Class 5 ft ³ •ac ⁻¹		
Big Spring	15.6	28.1	192.6	180.1	40.7	457.1	1.50
Roaring River	3.1	74.9	265.1	104.1	47.6	494.8	1.61
Sinkin	16.0	45.5	104.9	57.1	16.7	240.2	1.09
MOFEP	--	--	--	--	--	--	1.49

^aVolume m³•ha⁻¹ = 0.06997(volume ft³•ac⁻¹)

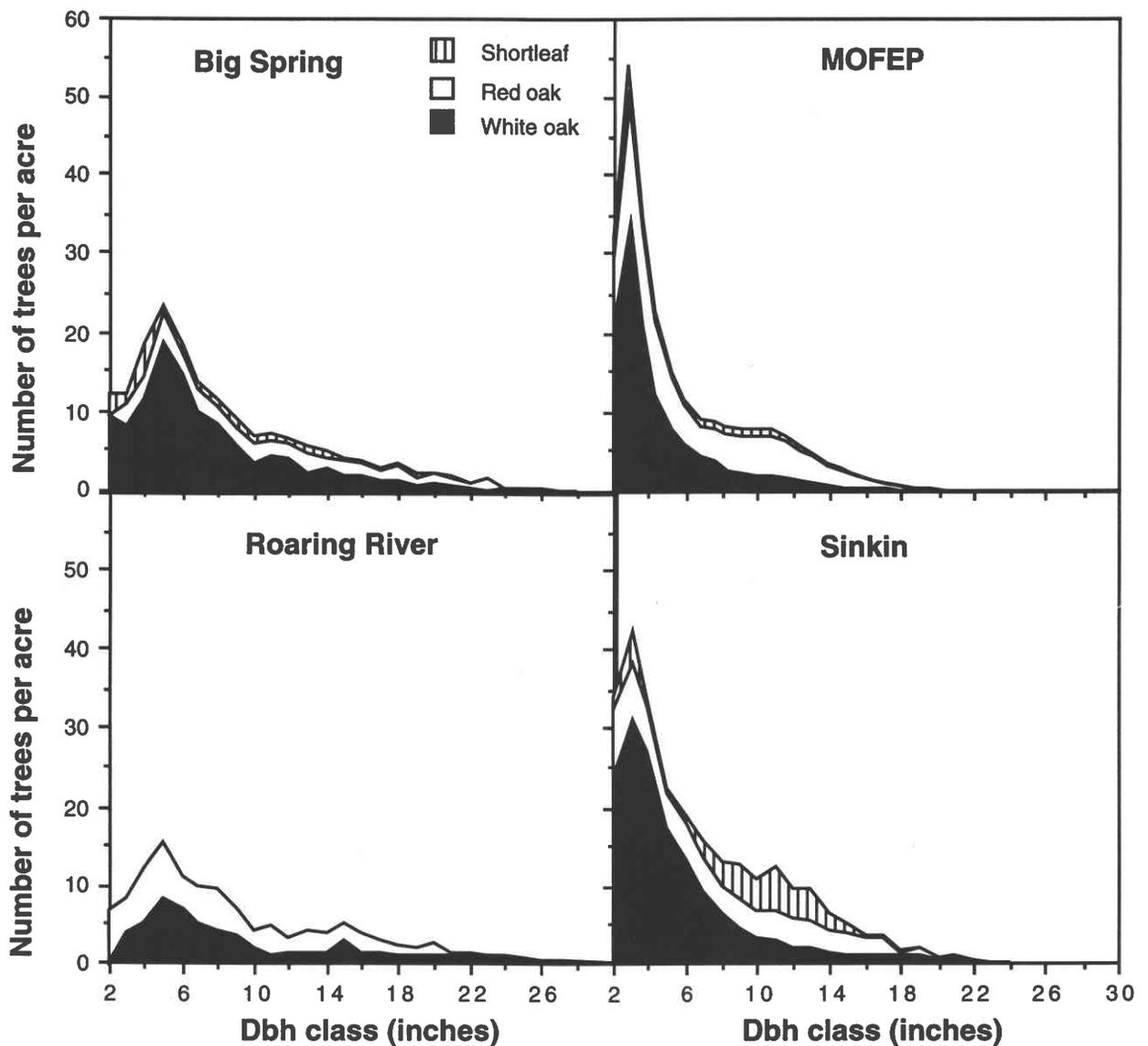


Figure 4. Number of trees per acre by major species groups. The white oak group includes white, post, chestnut, and chinkapin oaks. The red oak group includes northern red, southern red, scarlet, black, blackjack, and pin oaks.

CONCLUSIONS

Composite stand characteristics such as basal area and stocking were remarkably similar for the old-growth and second-growth stands compared. Likewise, the diameter distributions for all species combined had a negative exponential shape that was similar for the old-growth and second-growth tracts.

However, the old-growth tracts consistently had more trees per acre ≥ 17 inches (43 cm) dbh than did the second-growth sites. The absolute number of these large trees was small at all sites--an average of 14 per acre (35 per ha) for old-growth sites and 7 per acre (17 per ha) for second-growth sites. The overstories at all four sites were dominated by the red and white oak groups, and shortleaf pine was a substantial overstory component for all sites except Roaring

River. Dogwood was the dominant understory species at all sites. When considered jointly, the white oaks, red oaks, and shortleaf pine had unimodal diameter distributions at all sites, although the old-growth sites had fewer and larger trees of these species. Down wood on the old-growth sites was between 450 and 500 ft³•ac⁻¹ (31 and 35 m³•ha⁻¹), about double that observed for the Sinkin Experimental Forest.

The data we examined indicate that the composite density of second-growth Ozark oak forests may change relatively little as they mature to an old-growth state. Some of the most readily observed changes should be shifts in the number and basal area of trees larger than 17 inches (43 cm) dbh, corresponding changes in the diameter distribution of the dominant overstory species, and large increases in the volume of down wood.

ACKNOWLEDGMENTS

The authors thank Tim Bray, Ken Davidson, Tucker Fredrickson, John Jurgensmeyer, Keith Hayes, Mike Jenkins, Randy Jensen, David Larsen, Lorren Leatherman, Nancy Mikkelson, Mike Mueller, Rudy Peiters, Hoyt Richards, David Roberts, Brian Schweiss, and Steve Westin for their efforts to collect and/or manage the inventory data upon which this study is based. They also thank Henry F. Barbour, Christopher A. Nowak, and an anonymous reviewer for their helpful comments on an earlier version of this manuscript.

LITERATURE CITED

- Brookshire, B. and C. Hauser. 1993. The Missouri Forest Ecosystem Project. pp289-307 *In* A. R. Gillespie, G. R. Parker, P. E. Pope, and G. Rink. Proceedings, 9th Central Hardwood Forest Conference. March 8-10, 1993, W. Lafayette, IN. U.S. Dept. of Agric. For. Serv. Gen. Tech. Rept. NC-161, N. Cent. For. Exp. Station, St. Paul, MN. 515p.
- Gingrich, S. F. 1967. Measuring and evaluating stand density in upland hardwood forests in the Central States. *For.Sci.* 13:38-53.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 52(2):187-211.
- Kucera, C. L. and R. E. McDermott. 1955. Sugar maple-basswood studies in the forest-prairie transition of central Missouri. *Am. Mid. Nat.* 54(2): 495-503.
- Ladd, D. 1991. Reexamination of the role of fire in Missouri oak woodlands. pp67-80 *In* G.V. Burger, J. E. Ebinger, and G. S. Wilhelm (eds.). Proceedings of the Oak Woods Management Workshop, Eastern Illinois Univ., Charleston, IL.
- Little, E. L., Jr. 1953. Checklist of native and naturalized trees of the U.S. (including Alaska). U.S. Dept. of Agric. For. Serv. Agric. Hand. 41. 471p.
- Martin, W. H. 1991. Defining old-growth deciduous forests: seeing the forest and the trees. pp139-145 *In* D. Henderson and L. D. Hedrick. Restoration of old growth forests in the interior highlands of Arkansas and Oklahoma. Proceedings of a Conference September 19-20, 1990. Winrock International, Morrilton, AR. 190p.
- Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. pp78-95 *In* J. W. Thomas (ed.). Wildlife habitats in managed Forests: the Blue Mountains of Oregon and Washington. U.S. Dept. of Agric. For. Serv. Agric. Hand. 553. 512p.
- Meyer, J. 1986. Management of old growth forests in Missouri. Habitat Management Series No. 3. Missouri Department of Conservation, Jefferson City, MO. 16p.
- Nigh, T., C. Putnam, and D. Moore. 1992. Draft Missouri Natural Area Nomination: Big Spring Pines. Missouri Department of Conservation, Jefferson City, MO. 12p.

- Parker, G. R. 1989. Old-growth forests of the Central Hardwood region. *Nat. Areas J.* 9(1):5-11.
- Rogers, R. 1982. Guides for thinning shortleaf pine. pp217-255 *In* Proceedings, Second Biennial Southern Silvicultural Research Conference, Nov. 4-5, 1982, Atlanta, GA. . U.S. Dept. of Agric. For. Serv. Gen. Tech. Rept. SE-24, S. For. Exp. Station, Asheville, NC.
- Shifley, S. R. 1994. Old growth forests in the central states: observations on a unique resource. pp 527-528 *In* Foresters Together: meeting tomorrow's challenges. Society of American Foresters National Convention Proceedings, November 7-10, 1993, Indianapolis, IN 580p.
- Shotola, S. J., G. T. Weaver, P. A. Robertson, and W. C. Ashby. 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. *Am. Mid. Nat.* 127: 125-138.
- Stahle, D. W., J. G. Hehr, G. G. Hawks, Jr., M. K. Cleaveland, and J. R. Baldwin. 1985. Tree-ring chronologies of the southcentral United States. Tree-Ring Laboratory and the Office of the State Climatologist. Dept. of Geography, Univ. of Arkansas, Fayetteville, AR. 135p.
- Stout, S. L., D. A. Marquis, and R. L. Ernst. 1987. A relative density measure for mixed-species stands. *J. For.* 85 (7):45-47.
- Wuenschel, J. E. 1967. A vegetational analysis of a virgin hardwood stand in east-central Missouri. M.S. Thesis, University of Missouri, Columbia, MO. 79p.