RESEARCH ARTICLE

Stand Dynamics in an Old-Growth Hardwood Forest in Southern Illinois, USA

James J. Zaczek[1]
John W. Groninger
Department of Forestry
Southern Illinois University
Carbondale, IL 62901-4411 USA

J. W. Van Sambeek
North Central Research Station
202 Natural Resources Building
University of Missouri-Columbia
Columbia, MO 65211-7260 USA

[1] Corresponding author e-mail: zaczek@siu.edu

Natural Areas Journal 22:211–219

ABSTRACT: Kaskaskia Woods, a 7.4-ha old-growth hardwood forest in southern Illinois, USA, has been managed as a natural area and protected from disturbance since 1933. In 1935, eight 0.1-ha plots were installed and all trees 4 cm dbh or larger were tagged and inventoried. Trees were remeasured for survival, ingrowth (new trees >4 cm), and diameter (dbh) in 1940, 1958, 1965, 1973, 1978, 1983, and 1997. Stand basal area steadily increased from 22.7 m^2 ha^{-1} in 1935 to 34.3 m^2 ha^{-1} in 1997. Less than 25% of the trees alive in 1935 were still alive in 1997. For oaks and hickories, density drastically declined from 338 trees ha^{-1} to 81 trees ha^{-1}, while relative basal area was reduced somewhat (from 56.2% to 50.2%) during the same period. Recruitment of oak (*Quercus* L. spp.) and hickory (*Carya* Nutt. spp.) has failed because no ingrowth survives. In contrast, sugar maple (*Acer saccharum* Marsh.) became the most numerous species (increasing from 156 to 346 trees ha^{-1}) and second greatest in basal area (6.9 m^2 ha^{-1}) by 1997. However, low survival of the most recent sugar maple ingrowth cohort suggests that additional recruitment of this species may be limited. From 1935 to 1997, diversity, as measured by the Shannon index, declined and richness dropped from 26 to 20 tree species. In the coming decades, without disturbance, it appears likely that sugar maple will become more dominant in the natural area and that oak, hickory, or other associated species will continue to decline or perhaps totally disappear from this protected forest.

Dinámica de Árboles en un Bosque Maduro de Madera Dura en el Sur de Illinois, USA

RESUMEN: Kaskaskia Woods, un bosque maduro de madera dura de 7,4 ha en el sur de Illinois, USA, ha sido manejado como un área natural y protegido de disturbios desde 1933. En 1935, ocho plots de 0,1 ha se instalaron y todos los árboles de cuatro cm dap o mayores fueron marcados e inventariados. Los árboles fueron remedidos en supervivencia, renovales (nuevos árboles de más de cuatro cm dap), y diámetro (dap) en 1940, 1958, 1965, 1973, 1978, 1983 y 1997. El área basal de los árboles aumentó sostenidamente de 22,7 m^2 ha^{-1} en 1935 a 34,3 m^2 ha^{-1} en 1997. Menos del 25% de los árboles con vida en 1935, estuvieron vivos en 1997. La densidad de los robles y los nogales disminuyó drásticamente de 338 árboles ha^{-1} a 81 árboles ha^{-1}, mientras el área basal relativa disminuyó solo un 6% (de 56,2% a 50,2%) durante el mismo período. El reclutamiento de robles (*Quercus* L. spp.) y nogales (*Carya* Nutt. spp.) falló porque no sobrevivieron los renovales. Contrariamente, el arce dulce (*Acer saccharum* Marsh.) se transformó en la especie más numerosa (aumentando de 156 a 346 árboles ha^{-1}) y con la segunda área basal (6,9 m^2 ha^{-1}) en 1997. No obstante, la baja supervivencia de la cohorte de los renovales más recientes del arce dulce sugieren que el reclutamiento adicional de esta especie puede estar limitado. Desde 1935 a 1997, la diversidad, medida como el índice de Shannon, disminuyó y la riqueza cayó de 26 a 20 especies de árboles. En las próximas décadas, sin disturbios, pareciera que el arce dulce se hará más dominante con una continua disminución o tal vez la total desaparición del roble, nogal u otra especie asociada en este bosque protegido.

Index terms: mixed hardwood forest, old-growth forest, stand dynamics, succession

INTRODUCTION

Remnant old-growth forest stands have been protected from natural and human-caused disturbances with the goal of studying and preserving their unique characteristics, such as tree species and structural composition, floral species diversity, and wildlife habitat. Determining patterns of vegetation change within forests that have been protected from disturbances such as fire and cutting can help guide management activities and improve understanding of forest ecosystem processes. However, despite protection from anthropogenic disturbances, or perhaps because of protection, especially from fire, successional processes ultimately alter tree species composition and stand structure. This process has been occurring for oak-dominated stands of the eastern deciduous forest biome, especially on mesic sites, where oaks (*Quercus* L. spp.) and some other associated species generally fail to regenerate and are replaced by shade-tolerant mesophytic species (Weaver and Ashby 1971, Lorimer 1984, Parker et al. 1985, Crow 1988, Abrams and Downs 1990, Fralish et al. 1991, Fralish 1997, Tyrell et al. 1998, Hicks and Holt 1999).

Consistent with these findings, previous reports from Kaskaskia Woods, a protected area in southern Illinois, USA, have noted the increasing importance of mesophytic sugar maple (*Acer saccharum* Marsh.) at the expense of oak and hickory (*Carya* Nutt.) species (Schlesinger 1976, 1989; Fralish 1997). Increased importance of shade-tolerant sugar maple has been widely associated with decreased tree seedling regeneration, probably through complete utilization of light reaching the midstory. Additional changes in stand structure may occur because tree species differ in their requirements for resources, thereby impacting carrying capacity. Also, deadwood dynamics are highly variable among old-growth stands of differing species composition (McGee et al. 1999). These species-related changes in resource availability and stand structure could have important implications for long-term development and function of old-growth forest ecosystems.

We documented the incremental changes in stand structure and composition at Kaskaskia Woods that have accompanied the increased importance of sugar maple since the onset of forest protection and data collection in 1935.

METHODS

Study Site

Kaskaskia Woods in Hardin County, Illinois, was acquired by the U.S. Forest Service in 1933. It has been managed as a natural area within Shawnee National Forest's Kaskaskia Experimental Forest. Kaskaskia Woods is located within the Shawnee Hills Section of the Interior Lowland Plateau (Keys et al. 1995) in nonglaciated southern Illinois (Lat. 37.5° N, Long. 88.3° W). The stand is contained in the hill section of Braun's (1950) western mesophytic region and near the center of the region known as the Central Hardwood Forest (Clark 1976). The soils are well-drained silt loams composed of mixed loess with weathered limestone and sandstone bedrock primarily of the Alford (fine-silty, mixed, mesic Typic Hapludalf) and Baxter (clayey, mixed, mesic Typic Paleudult) soil series in which productivity depends largely on moisture availability. Annual precipitation averages 112 cm with approximately 60% falling between April and September (Schlesinger 1989). Aspect is generally northeast.

The area has not been subjected to fire, grazing, logging, or any other silvicultural treatments nor are there reports of significant blowdowns, wildfires, or pathogen outbreaks since its purchase in 1933. Apparently, Kaskaskia Woods was never cleared. However, increment coring in 1965 indicated that a majority of the trees were either more than 160 years old or 80 to 100 years old. The area was apparently selectively cut for railroad ties in the 1880s, which left most of the yellow-poplar (*Liriodendron tulipifera* L.), hickory, and oaks less than 30 cm dbh. An abrupt change in diameter growth rates suggests that an additional selective cut took place in the 1910s, when some white oak (*Quercus alba* L.) and hickory trees were probably cut for stave wood and handle stock (Schlesinger 1976). With this disturbance history and other characteristics, the stand possesses attributes common to old-growth eastern deciduous forests (Parker 1989, Martin 1992, Tyrell et al. 1998). Furthermore, the stand meets the definition of mesic old-growth deciduous forests in the Central Hardwood Region in that overstory canopy trees exceed 150 years old and are 80–160 cm dbh, little anthropogenic disturbance has occurred in the last 80 to 100 years, and there is an all-aged multilayered structure with an understory of shade-tolerant trees (Campbell 1987, Spetich et al. 1997).

Sampling Methods

In 1935, eight 0.1-ha plots were installed in a 7.4-ha upland area that lies within a local transition zone between xeric oak-hickory and mesic mixed hardwoods communities. All live trees 4 cm dbh (1.3 m above ground) or larger were permanently identified with numbered tags and inventoried for species, dbh, and total height. Subsequently, living tagged trees in the plots were remeasured for dbh in 1940, 1958, 1965, 1973, 1978, 1983, and 1997. Ingrowth—living trees not recorded in a previous sample that had grown to be 4 cm dbh or larger—were also tagged and subsequently measured. In the late 1990s the plot corner boundary stakes were replaced and all live trees were retagged.

Statistical Analyses

Net basal area growth was calculated by summing the basal area of all live trees in all plots at a measurement date and subtracting the amount of basal area present at the previous date. At each sample date, basal area lost to mortality was estimated by summing basal area from the most recent measurement of those trees found dead or those missing. This slightly underestimated the true amount of basal area lost to mortality, because the amount of growth added after the most recent measurement but before death could not be determined. Gross basal area growth was determined by adding mortality to net growth. Because of unequal intervals of time between measurement periods, growth was standardized to an annual basis at each sample date by dividing the basal area growth by the number of years since the previous inventory. Species diversity was characterized by calculating the Shannon-Weiner index (H′) using $\log_{10}$ based on density (H′-Den) and basal area (H′-BA) for living trees >4 cm dbh for each plot at each measurement date and averaged across all plots (Magurran 1988).

RESULTS

Since 1935, basal area for all species combined gradually and relatively consistently increased, except for the 1983 measurement, from an initial 22.7 m^2 ha^{-1} to 34.3 m^2 ha^{-1} in 1997 (Figure 1). At the same time, the density of trees declined (Figure 1). This decline in density resulted from mortality of existing trees and fewer trees replacing them as ingrowth. For example, by 1965, 479 of the 892 trees ha^{-1} present in 1935 had died and ingrowth only accounted for 448 additional trees ha^{-1}. By 1997, 675 trees ha^{-1} had died, leaving less than 25% of the original trees still alive. Tree density declined somewhat to 788 trees ha^{-1} over the first 43 years and dropped more rapidly to 588 trees ha^{-1} during the last 20 years. The remaining trees tend to be large overstory trees, and there is a reduced number of saplings and poles in the understory.

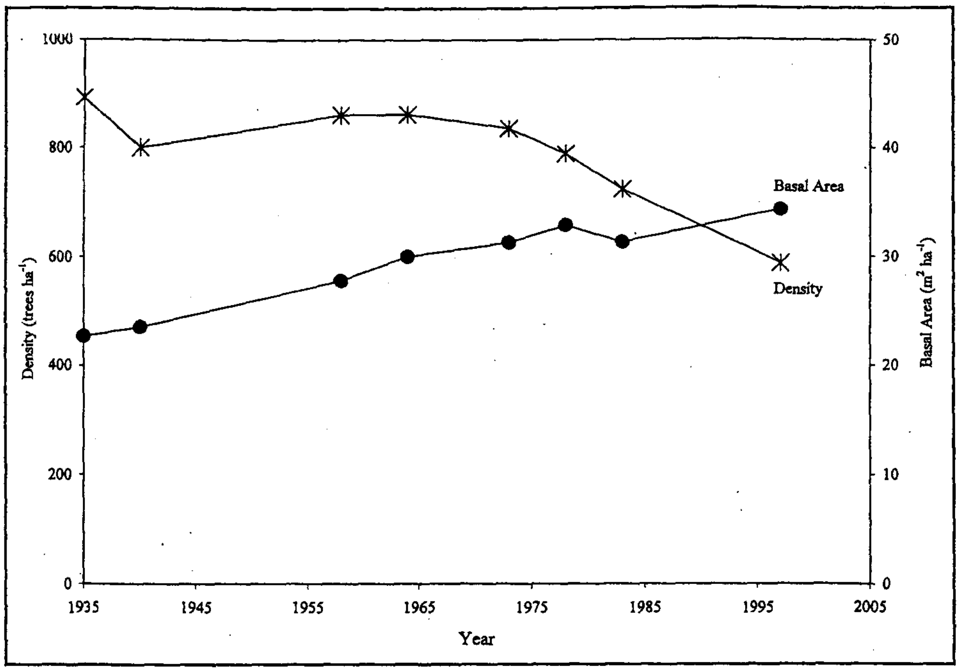

Figure 1. Density (trees ha^{-1}) and basal area (m^2 ha^{-1}) of live trees > 4 cm dbh since 1935 within Kaskaskia Woods, Hardin County, Illinois.

Not only did basal area and density change within the stand; there were relatively dramatic changes in species composition as well (Table 1). Among overstory trees, the once relatively numerous oak (black, *Quercus velutina* Lam.; northern red, *Q. rubra* L.; scarlet, *Q. coccinea* Muenchh.; and white) and hickory (shagbark, *Carya ovata* [Mill.] K. Koch; mockernut, *C. tomentosa* [Poir] Nutt.; and pignut, *C. glabra* [Mill.] Sweet) species declined from a total of 338 trees ha^{-1} in 1935 to 81 trees ha^{-1} in 1997. Based on relative density comparisons, most species or species groups declined while a few exhibited little change in 62 years (Figure 2). The notable exception to this was sugar maple, which increased from a relative density of 17% at the onset of the experiment to a dominant 59% in 1997.

Although density declined for oak and hickory, relative basal area dropped only slightly from 56.2% to 50.2% during the same period (Figure 3). The relative basal area of yellow-poplar increased from 16.1% to 23.9% concurrent with a reduction in the number of trees (from 23.5 to 19.8 trees ha^{-1}), reflecting the declining numbers of massive trees in the overstory. Combining data for the shade-tolerant flowering dogwood (*Cornus florida* L.) and shade-intolerant sassafras (*Sassafras albidum* [Nutt.] Nees.), there were 247 trees ha^{-1} in 1935 (Table 1). By 1997, sassafras was extirpated and only 7 trees ha^{-1} of flowering dogwood remained. Although present in 1935, black walnut (*Juglans nigra* L.), eastern redcedar (*Juniperus virginiana* L.), and persimmon (*Diospyros virginiana* L.) were no longer found in the plots in 1997. Black cherry (*Prunus serotina* Ehrh.) and serviceberry (*Amelanchier arborea* [Michx. f.] Fern.) occurred as ingrowth after 1935, but also were not present in 1997. In contrast, sugar maple (*Acer saccharum* Marsh.) increased from 156 trees ha^{-1} and 1.1 m^2 ha^{-1} of basal area in 1935 to 346 trees ha^{-1} and 6.9 m^2 ha^{-1} in 1997.

Among tree species that have the potential to become overstory trees, ingrowth has been primarily from shade-tolerant species. Of these ingrowth stems, 61% were sugar maple and 22% were white ash (*Fraxinus americana* L.). Prior to the 1983 cohort, survival of sugar maple ingrowth was relatively high (65%). However, the 1983 cohort showed a large drop in survival (Table 2). In contrast to sugar maple and white ash, in 1997 there was not a single surviving ingrowth tree of oak or hickory that developed over the period of the study. In other words, the only oak and hickory trees alive in 1997 were those that were

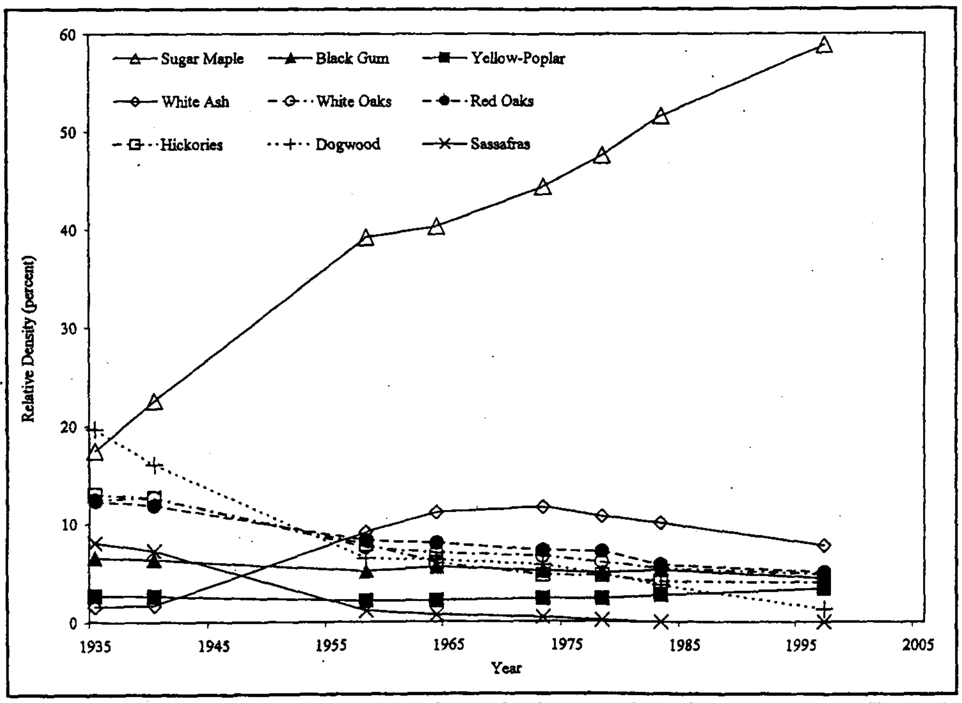

Figure 2. Relative density (percent) over time for predominant species and species groups in Kaskaskia Woods, Hardin County, Illinois.

Table 1. Density (trees ha^{-1}) and basal area (m^2 ha^{-1}) of tree species present over time at Kaskaskia Woods, Hardin County, Illinois.

Species Code[a]	Density (trees ha^{-1}) 1935	1940	1958	1965	1973	1978	1983	1997	Basal Area (m^2 ha^{-1}) 1935	1940	1958	1965	1973	1978	1983	1997
ACSA	156	180	337	347	371	376	373	346	1.020	1.240	2.547	2.916	3.765	4.189	4.816	6.874
FRAM	14	14	79	96	98	85	73	46	0.078	0.077	0.232	0.305	0.387	0.394	0.424	0.427
QUAL	111	101	65	61	56	48	40	28	3.422	3.716	4.393	4.708	5.170	5.374	5.539	5.512
NYSY	58	51	44	48	43	40	38	26	2.045	2.062	1.726	1.808	1.866	1.890	1.668	1.496
LITU	23	21	19	19	20	19	20	20	3.642	3.773	4.596	4.969	5.500	5.838	6.455	8.199
BETU[b]	14	11	55	61	62	60	58	19	0.088	0.054	0.139	0.164	0.206	0.229	0.228	0.120
QUVE	53	42	32	32	30	27	23	17	2.885	3.182	4.406	4.958	5.217	5.365	5.042	4.777
FAGR	5	6	12	15	12	12	12	17	0.103	0.114	0.187	0.217	0.244	0.262	0.303	0.385
CAGL	56	48	32	25	20	20	14	10	1.306	1.337	1.483	1.503	1.442	1.479	1.303	1.385
CATO	31	28	21	17	12	11	10	10	1.354	1.416	1.580	1.589	0.865	0.886	0.895	1.061
ULRU	0	0	1	2	2	2	2	10	0.000	0.000	0.006	0.010	0.014	0.018	0.021	0.052
COFL	175	128	56	54	48	38	27	7	1.491	0.974	0.259	0.274	0.247	0.199	0.158	0.036
QUCO	40	36	27	26	21	21	12	7	2.601	2.965	4.087	4.513	4.267	4.645	2.873	2.238
ASTR	0	0	0	0	0	0	0	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
QURU	17	17	12	11	10	9	6	5	0.652	0.808	1.061	1.155	1.307	1.334	0.977	1.193
CAOV	30	25	15	10	7	6	6	4	0.517	0.534	0.570	0.559	0.582	0.572	0.592	0.519
ULAM	5	7	26	16	9	7	5	4	0.060	0.066	0.057	0.046	0.022	0.023	0.016	0.022
MORU	21	11	0	0	0	0	0	2	0.278	0.240	0.000	0.000	0.000	0.000	0.000	0.004
CECA	0	0	2	5	6	2	1	2	0.000	0.000	0.005	0.011	0.015	0.004	0.003	0.005
SAAL	72	58	10	6	4	1	0	0	0.958	0.800	0.214	0.101	0.044	0.027	0.000	0.000
JUNI	6	6	4	2	2	1	0	0	0.126	0.141	0.084	0.070	0.073	0.069	0.000	0.000
DIVI	1	1	0	0	0	0	0	0	0.026	0.027	0.000	0.000	0.000	0.000	0.000	0.000
JUVI	1	1	0	0	0	0	0	0	0.002	0.003	0.000	0.000	0.000	0.000	0.000	0.000
PRSE	0	0	2	4	1	0	0	0	0.000	0.000	0.004	0.006	0.003	0.000	0.000	0.000
AMAR	0	1	2	1	1	1	1	0	0.000	0.002	0.005	0.002	0.003	0.003	0.002	0.000
unspec.	4	4	4	1	0	0	0	0	0.015	0.016	0.014	0.003	0.000	0.000	0.000	0.000

[a] Species codes as follows: ACSA - *Acer saccharum*, AMAR - *Amelanchier arborea*, ASTR - *Asimina triloba*, CAGL *Carya glabra*, CAOV - *C. ovata*, CATO - *C. tomentosa*, CECA - *Cercis canadensis*, COFL - *Cornus florida*, DIVI - *Diospyros virginiana*, FAGR - *Fagus grandifolia*, FRAM - *Fraxinus americana*, JUNI - *Juglans nigra*, JUVI - *Juniperus virginiana*, LITU - *Liriodendron tulipifera*, MORU - *Morus rubra*, NYSY - *Nyssa sylvatica*, PRSE - *Prunus serotina*, QUAL - *Quercus alba*, QUCO - *Q. coccinea*, QURU - *Q. rubra*, QUVE - *Q. velutina*, SAAL - *Sassafras albidum*, ULAM - *Ulmus americana*, ULRU - *U. rubra*

[b] = BETU is combined *Carpinus caroliniana* and *Ostrya virginiana*

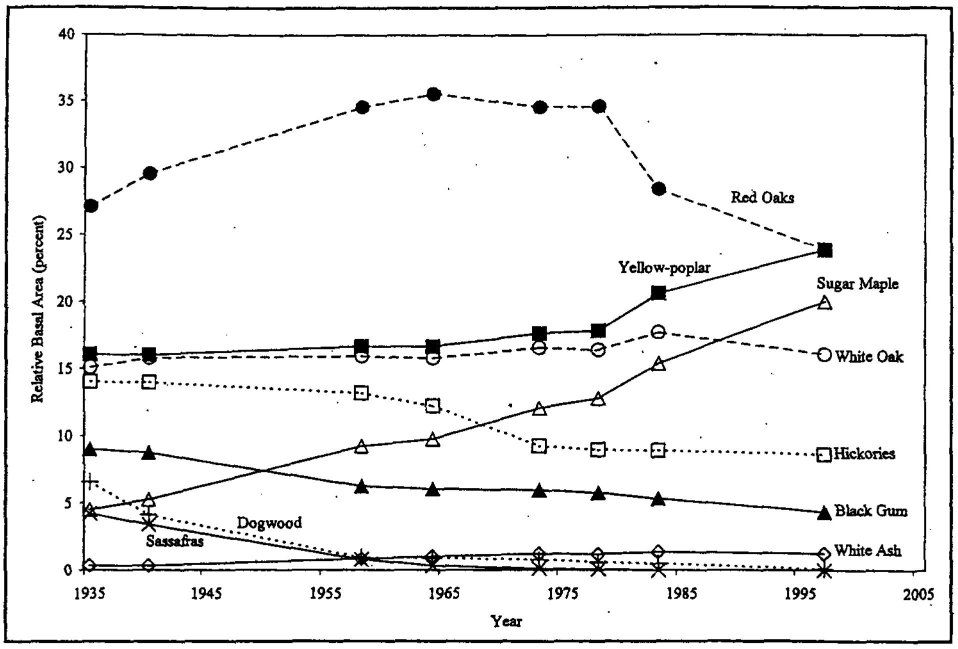

Figure 3. Relative basal area (percent) over time for predominant species and species groups in Kaskaskia Woods, Hardin County, Illinois.

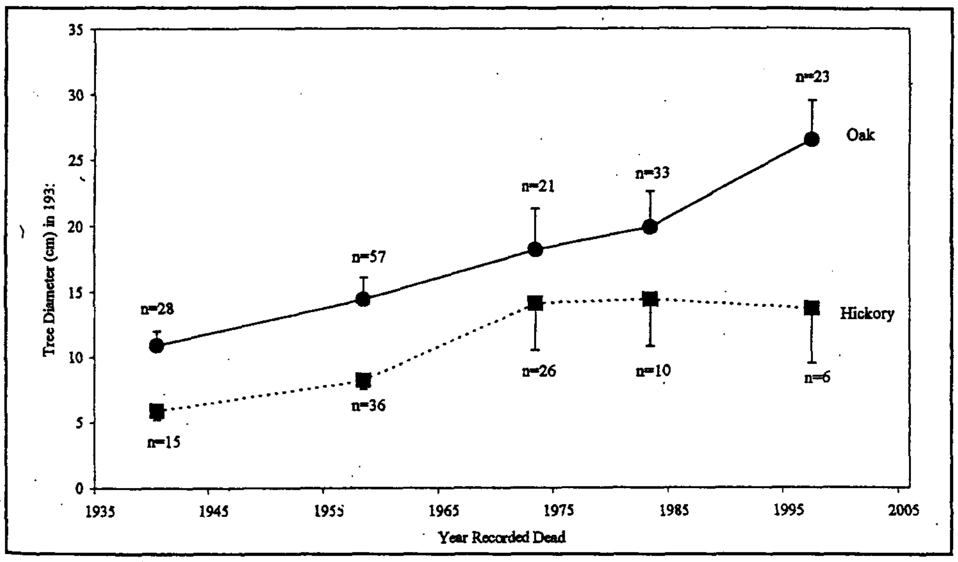

Figure 4. Relationship between mean diameter (cm) in 1935 and year of recorded death of oak and hickory trees in Kaskaskia Woods, Hardin County, Illinois. Data are combined for 1965 and 1973 as well as 1978 and 1983 because of low sample numbers (n). Bars denote standard error of the mean.

present in 1935.

Of the 338 oak and hickory trees ha^{-1} in the stand in 1935, only 81 trees ha^{-1} remained in 1997. These surviving trees tended to be the larger diameter trees in 1935, when they averaged 27.2 cm (SE ±1.63, n=58) and 25.1 cm (SE±3.63, n=23) for oak and hickory, respectively. The smaller trees tended to die sooner (Figure 4).

Of all tree species present in 1935, only 224 of the 892 trees ha^{-1} remained alive in 1997. Including ingrowth, over the course of the study there were 1045 trees ha^{-1} that died (ca. 17 per year). These dead trees had an average diameter of 10.9 $\pm$ 0.36 (SE) cm, which amounted to a cumulative basal area of 19.1 m^2 ha^{-1} over the course of the study—more than half of the amount present in 1997.

Annual gross basal area growth increased slightly over time, whereas net growth fluctuated considerably due to fluctuations in mortality (Figure 5). Gross growth per year (0.47 to 0.63 m^2 ha^{-1}) remained within 2 standard deviations (SD = 0.055 m^2 ha^{-1}) of the mean (0.53 m^2 ha^{-1}) during the study.

Shannon diversity calculated as a function of species density (H'-Den) and basal area by species (H'-BA) declined over the course of the study (Figure 6). Richness also declined from 15 to about 12 tree species per plot. Considering all eight plots together, tree species richness decreased from 26 in 1935 to 20 by 1997.

DISCUSSION

Without a major disturbance in the Kaskaskia Woods for nearly 100 years, large yellow-poplar and oak species still dominate the stand, as measured by relative basal area. However, since 1935, their numbers have been consistently declining, as was true for the majority of other tree species. Conversely, sugar maple density has increased to exceed all other species combined. This was largely a result of survival exceeding mortality of sugar maple ingrowth at nearly every measurement period. Combined with the absence of ingrowth of nearly all other species, it is apparent that this protected old-growth oak stand is succeeding to sugar maple and other shade-tolerant mesophytic species. These results are consistent with previous reports on this stand (Schlesinger 1976, Fralish 1988, Schlesinger 1989) and other undisturbed oak stands on mesic sites throughout the Central Hardwood Forest Region and eastern United States (Lindsey and Schmelz 1964, Schmelz and Lindsey 1965, Parker and Leopold 1983, Barton and Schmelz 1987, Abrams and Downs 1990, Shotola et al. 1992, Fralish 1997, Tyrell et al. 1998).

However, conditions in the understory appear to have become inhospitable even for young sugar maple saplings, as evidenced by the low survival (21.1%) of the 1983 ingrowth cohort (Table 2). This coupled with the relatively constant density of sugar maple trees since 1958 may indicate that the stand has become saturated with

Table 2. The fate of sugar maple ingrowth (new stems >4.0 cm dbh) per hectare at Kaskaskia Woods over time.

Year	Ingrowth (trees ha^{-1})	Mean Ingrowth (trees ha^{-1} yr^{-1})	Remaining Alive in 1997 (%)
1940	23.5	4.7	63.2
1958	168.0	9.3	63.2
1965	28.4	4.1	60.9
1973	46.9	5.9	73.7
1978	18.5	3.7	66.7
1983	23.5	4.7	21.1
1997	59.3	4.2	NA

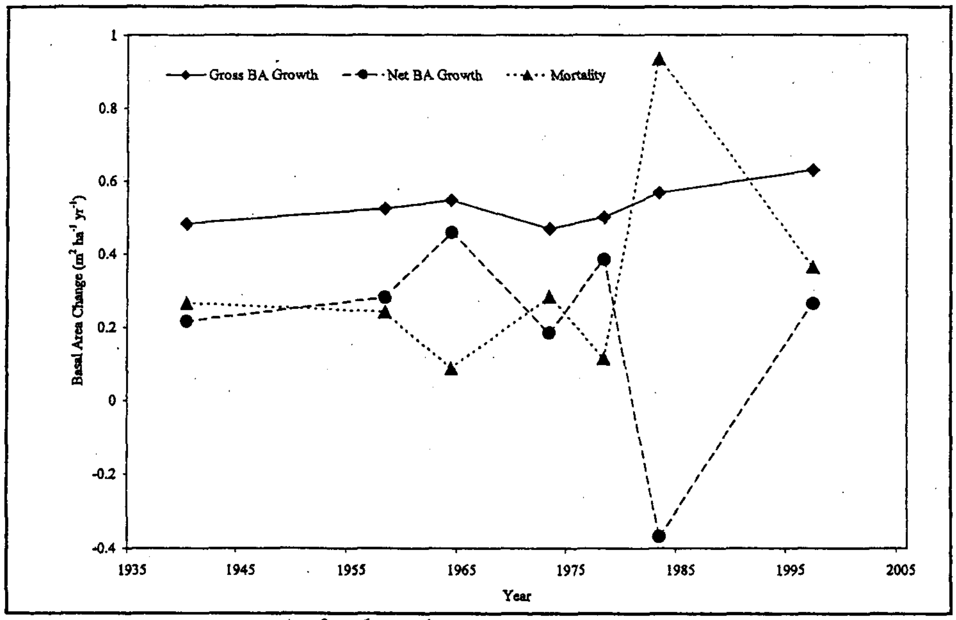

Figure 5. Change in basal area (m^2 ha^{-1} year^{-1}) at Kaskaskia Woods, Hardin County, Illinois, attributable to growth, net growth, and mortaility of trees > 4 cm dbh over time.

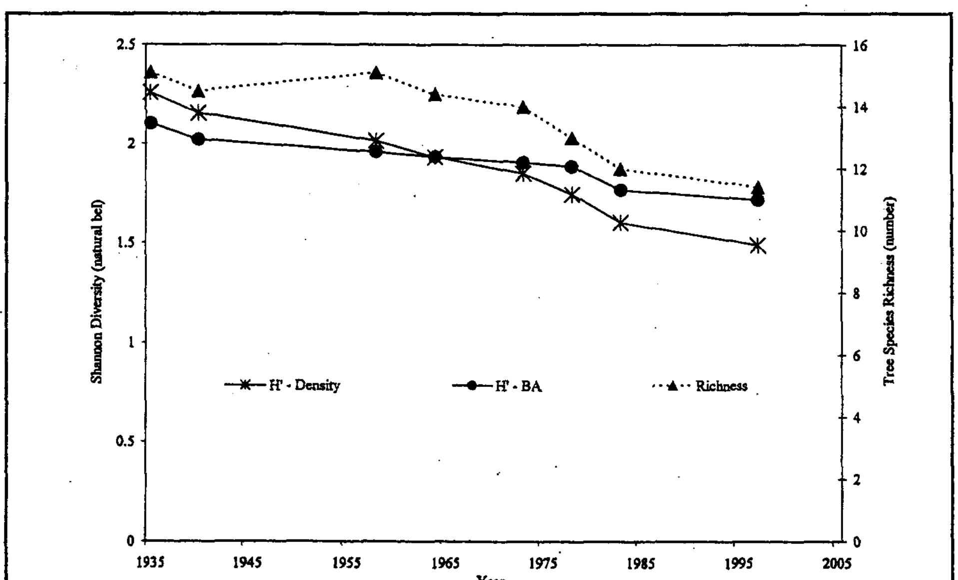

Figure 6. Species diversity based on density (H'-Den), basal area (H'-BA), and richness of live trees > 4 cm dbh since 1935 averaged across all plots within Kaskaskia Woods, Hardin County, Illinois.

sugar maple. Resources such as light and moisture can be in short supply at ground level in mature stands with well-developed midstories and understories (Orwig and Abrams 1995, Oliver and Larsen 1996, Fralish 1997). Therefore opportunities for recruitment may be limited even for this notably shade-tolerant species, at least until more significant autogenic or allogenic disturbances occur in the overstory or midstory.

Even without substantial discrete stand-wide catastrophic disturbance events such as fire, strong winds, or cutting, three-quarters of the trees present in 1935 had died by 1997. In addition, over the years of the study, the cumulative basal area lost due to tree mortality equaled 84% of the amount initially present in 1935. Lacking catastrophic allogenic disturbances, it appears that aging, herbivory, disease, competition among trees, and climatic variation leading to periodic episodes of light, water, and nutrient stress, may be acting as a series of protracted micro-disturbances on the individual-tree scale, and that these have cumulatively manifested into significant successional changes over time at the stand scale.

On average, there were about 17 $\pm$ 1.8 (SE) trees ha^{-1} that died each year, about 2.1% of the total number of trees in an average year. Although losses due to mortality were occurring throughout the study, replacement by ingrowth of primarily sugar maple and ash made up for most of the losses until the 1970s, when tree recruitment ceased.

The density of trees decreased to a low of 588 ha^{-1} in 1997. Based on the 1983 measurements in this stand, Fralish (1997) concluded that the stand may have reached its state of maximum biomass and complete canopy closure. Indeed, the reduction in stand density and the fact that the sugar maple ingrowth cohort of 1983 experienced unprecedented low survival suggest that canopy closure has occurred and further recruitment of new trees may be limited. The 1997 inventory, however, showed an increase in total (or net) stand basal area to 34.3 m^2 ha^{-1}, indicating that the site was able to support additional basal area. Although the basal area is somewhat greater than reported in some other studies (Roovers and Shifley 1997, Shifley et al. 1997, Spetich et al. 1999), it is comparable to the maximum of 35.0 m^2 ha^{-1} reported for an upland forest in a survey of 19 old-growth forests in Illinois, Indiana, and Michigan (Schmelz and Lindsey 1965) and a reported maximum level in the central hardwood forest (Held and Winstead 1975, Fralish 1994). The changes in total basal area in recent decades may reflect the fluctuating pattern around a steady state in the stand (Borman and Likens 1979).

The slight trend toward increasing total basal area (Figure 1) and gross basal area growth (Figure 5) over time may also provide evidence that the stand may be able to support even more total basal area. This trend may be due to increased availability of resources or more full utilization of those resources by the species present. Species-related changes in maximum stand density have been noted in other forest types (Roach 1977). A resource such as sunlight, of which the availability is essentially fixed, may be more fully exploited by the increased presence of shade-tolerant species such as sugar maple in the overstory and understory. Other resources such as nutrients or available water may increase over time with soil developmental processes such as mineralization, deposition, and incorporation of organic matter. It is also possible that atmospheric increases in CO_2, temperature, or rainfall could be partly responsible for increases in gross basal area growth (Saxe et al. 1998, Groninger et al. 1999). Nonetheless, it is interesting to note that despite large fluctuations in basal area lost to mortality and net basal area, gross basal area growth remained fairly consistent. This suggests that resources released when some trees died were readily captured and utilized by remaining trees in the stand.

Partial selective cutting of overstory trees during the 1880s and 1910s probably left unmerchantable oak and hickory trees as a seed source to foster the development of a new tree cohort by the time stand protection was initiated. Indeed, there were considerable numbers of oaks and hickories present in the stand in 1935 (338 ha^{-1}). However, less than one-quarter of these had survived by 1997. As illustrated in Figure 4, oak and hickory trees with smaller diameters in 1935 tended to die earlier than larger trees. Early on, smaller individuals of these shade-intolerant species were apparently overtopped and shaded by larger trees in more dominant crown positions, resulting in their mortality. In later years, initially larger diameter and presumably unsuppressed dominant and codominant trees were dying as well, suggesting that age-related mortality is becoming much more important.

Of all tree species, flowering dogwood has seen the greatest decline in density; only 4% of the number of trees present in 1935 remained alive in 1997. About two-thirds of these dogwood stems had died by 1958. Curiously, this decline occurred although the species is classified as an understory tree and very tolerant of shade (McLemore 1990). Since the species may live for 125 years, perhaps these stems were recruited into the stand at the time of the last significant disturbance and had succumbed to age-related factors.

Age alone, however, does not explain why dogwood ingrowth is generally lacking. Dogwood may be less tolerant to shade than previously thought, or at least so in comparison to sugar maple, which more than doubled its density from 1935 to 1958. By 1958, the stand was a mature, closed canopy forest with a well-established maple midstory, which could severely limit light to developing seedlings and saplings. It is possible that availability of other necessary resources such as moisture and nutrients, which are often limited in the understory of mature stands, also may have excluded dogwood, a species characterized by an extensive but shallow root system (McLemore 1990). A relative lack of dogwood was also reported in a Pennsylvania old-growth oak forest with a considerable maple component (Abrams and Downs 1990). It is also possible, although unsubstantiated, that a serious disease such as dogwood anthracnose caused by the fungus (*Discula* sp.) documented in the eastern United States since the 1970s (Daughtrey et al. 1988, Williams and Moriarity 1999), and in Illinois since 1995 (Schwegman et al. 1998), may have been present in the more distant past and contributed to the species decline. Moist conditions associated with old-growth stand structure and mesophyte-dominated understories may further predispose dogwood to anthracnose-induced mortality (Chellemi and Britton 1992, McEwen et al. 2000). These factors and other stresses such as increased herbivory may also have contributed to the dogwood's decline either as single or interacting stresses.

Diversity also declined over the course of the study, whether measured by richness over all plots or per plot, or by Shannon values based on density (H'-Den) or basal area (H'-BA). These values for Kaskaskia Woods fall within a range that is typical for Central Hardwood Forest stands (Hicks and Holt 1999). The decline in H'-Den is largely a result of the greatly increased dominance of sugar maple relative to all other species.

Management of old-growth stands to maintain certain forest types requires careful consideration. Martin (1992) stated that stand manipulations such as thinning to favor certain species, removal of dead coarse woody debris, or removal of diseased trees are neither warranted nor desirable in old-growth hardwood forests. However, it is difficult to determine whether active management such as the reinstitution of fire in a prescribed manner to mimic former patterns of periodicity should be judiciously implemented to restore oak-hickory forest communities. Fire alone may not be sufficient to restore oak stands (Will-Wolf 1991). The exclusion of fire has resulted in forest communities that may be difficult to restore to the desired natural community type using fire alone—that is, without employing other measures such as cutting.

Partial overstory removal is often an effective means of stimulating the generation of a new cohort of oak seedlings in forests of the central hardwoods region (Sander and Graney 1992). Although Kaskaskia Woods was partially cut on two occasions, a new age class of oak failed to develop. Cutting intensity may have been insufficient in terms of canopy removal to permit establishment and continued development of a new age class (Roach and Gingrich 1975, Sander and Graney 1992). Partial cutting may have resulted in the development of oak seedlings and saplings that ultimately perished through competition from the dense overstory and midstory that developed in the absence of further disturbance (Lorimer 1984).

The growth rates and species composition of Kaskaskia Woods suggest that this stand occupies a type of site where long-term maintenance of oak species typically presents a formidable challenge to silviculturists (Sander et al. 1984, Abrams and Downs 1990). Even the heavier and more frequent cuttings typically favoring oak sometimes fail to prevent successional replacement by shade-tolerant species such as sugar maple and American beech (*Fagus grandifolia* Ehrh.) (Sander and Graney 1992). The use of prescribed fire, in conjunction with partial cutting followed by complete overstory removal, appears to be a promising means to perpetuate the oak component in similar stands (Brose et al. 1999). Although effective silvicultural methods are being developed, the most daunting aspect of regenerating oak in natural areas may concern the social implications of replicating the conditions under which this and similar stands developed.

After over 60 years of protection from large-scale disturbance, Kaskaskia Woods dramatically changed in species composition, structure, and diversity. By 1997, the stand had relatively few but large and mature oaks and hickories, no oak and hickory saplings, and a dramatically increased presence of sugar maple. This loss of oak and hickory with an increase of mesophytic species is typical of many oak forests in the eastern deciduous forest biome (Lindsey and Schmelz 1964, Parker et al. 1985, Fralish 1988, Abrams and Downs 1990, Abrams 1996, Fralish 1997, Spetich and Parker 1998). With continued protection from disturbance, especially fire, it is likely that the coming decades will bring a continuing decline or perhaps total loss of oak, hickory, dogwood, and associated species in this southern Illinois forest.

ACKNOWLEDGMENTS

We would like to acknowledge the cooperation of Clark Ashby, Steve Hupe, Dick Johnson, Nick Giannettino, Tom Neal, Elizabeth Shimp, Jody Shimp, Dan Spivey, and Sharon Suchecki, in assisting with logistics, data collection, and re-tagging of trees in this study. We thank Steven R. Shifley and the anonymous reviewers for their helpful suggestions.

James Zaczek is Assistant Professor of Forest Ecology in the Department of Forestry at Southern Illinois University. His interests include regeneration ecology of hardwood forests, riparian forest restoration, and plant propagation.

John Groninger is Assistant Professor of Silviculture in the Department of Forestry at Southern Illinois University. His interests include forest restoration and stand dynamics.

Jerome Van Sambeek is Research Plant Physiologist with the USDA Forest Service in Columbia, Missouri. His interests include hardwood propagation and the use of herbaceous and woody legumes to enhance forest productivity.

LITERATURE CITED

Abrams, M.D. 1996. Distribution, historical development, and ecophysiological attributes of oak species in the eastern United States. Annales des Sciences Forestieres 53:487-512.

Abrams, M.D., and J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwest Pennsylvania. Canadian Journal of Forest Research 20:1864-1870.

Barton, J.D., and D.V. Schmelz. 1987. Thirty years of growth records in Donaldson's Woods. Proceedings of the Indiana Academy of Science 96:209-213.

Borman, F.H., and G.E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York. 253 pp.

Braun, E.L. 1950. Deciduous Forests of Eastern North America. Hafner Publishing, New York. 596 pp.

Brose, P., D. Van Lear, and R. Cooper. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. Forest Ecology and Management 113:125-141

Campbell, J.J. 1987. Gradients of tree species composition in the central hardwood region. Pp. 325-345 *in* R.L. Hay, F.W. Woods, and H. DeSelm, eds., Proceedings of the Sixth Central Hardwood Forest Conference, Knoxville, Tenn.

Chellemi, D.O., and K.O. Britton. 1992. Influence of canopy microclimate on incidence and severity of dogwood anthracnose. Canadian Journal of Botany 70:1093-1096.

Clark, F.B. 1976. The central hardwood forest. Pp. 1-8 *in* J.S. Fralish, G.T. Weaver, and R.C. Schlesinger, eds., Proceedings of the First Meeting of the Central Hardwood Forest Conference, Carbondale, Ill.

Crow, T. R. 1988. Reproductive strategy and mechanisms for self-replacement of northern red oak (*Quercus rubra* L.)—a review. Forest Science 34:19-40.

Daughtrey, M.L., C.R. Hibben, and G.W. Hudler. 1988. Cause and control of dogwood anthracnose in the northeastern United States. Journal of Arboriculture 14:159-164.

Fralish, J.S. 1988. Predicting potential stand composition from site characteristics in the Shawnee Hills forest of Illinois. American Midland Naturalist 120:79-101.

Fralish, J.S. 1994. The effect of site environment on forest productivity in the Illinois Shawnee Hills. Ecological Applications 4:134-143.

Fralish, J.S. 1997. Community succession diversity and disturbance in the Central Hardwood Forest. Pp. 234-266 *in* M.W. Schwartz, ed., Conservation in Highly Fragmented Landscapes. Chapman and Hall, New York.

Fralish, J.S., F.B. Crooks, J.L. Chambers, and F.M. Harty. 1991. Comparison of pre-settlement, second growth, and old-growth forests on six site types in the Illinois Shawnee Hills. American Midland Naturalist 125:294-309.

Groninger, J.W., K.H. Johnsen, J.R. Seiler, R.E. Will, D.S. Ellsworth, and C.A. Maier. 1999. Elevated carbon dioxide in the atmosphere: What might it mean for loblolly pine plantation forestry? Journal of Forestry 97(7):4-10.

Held, M.E., and J.E. Winstead. 1975. Basal area and climax status in mesic forest systems. Annals of Botany 19:1147-1148.

Hicks, R.R., Jr., and J. Holt. 1999. Comparison of ecological characteristics of three remnant old-growth woodlots in Belmont County, Ohio. Pp. 51-59 *in* J.W. Stringer and D.L. Loftis, eds., Proceedings of the 12th Central Hardwood Forest Conference, Lexington, Ky. General Technical Report SRS-24, U.S. Department of Agriculture, Forest Service, Asheville, N.C.

Keys, J., Jr., C. Carpenter, S. Hooks, F. Koenig, W.H. McNab, W. Russell, and M.L. Smith. 1995. Ecological units of the eastern United States—first approximation. U. S. Department of Agriculture, Forest Service, Atlanta, Ga. 80 pp.

Lindsey, A.A., and D.V. Schmelz. 1964. Comparison of Donaldson's Woods in 1964 with its 1954 forest map of 20 acres. Proceedings Indiana Academy of Science 73:169-177.

Lorimer, C.G. 1984. Development of the red maple understory in north-eastern oak forests. Forest Science 30:3-22.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, N.J. 179 pp.

Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natural Areas Journal 12:127-135.

McEwan, R.W., R.N. Muller, M.A. Arthur, and H.H. Housman. 2000. Temporal and ecological patterns of flowering dogwood mortality in the mixed mesophytic forest of eastern Kentucky. Journal of the Torrey Botanical Society 127:221-229.

McGee, G.G., D.J. Leopold, and R.D. Nyland. 1999. Structural characteristics of old growth, maturing and partially cut northern hardwood forests. Ecological Applications 9:1316-1329.

McLemore, B.F. 1990. *Cornus florida* L. flowering dogwood. Pp. 278-283 *in* R.M. Burns and B.H. Honkala, eds., Silvics of North America. Vol. 2: Hardwoods. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Oliver, C.D. and B.C. Larsen. 1996. Forest Stand Dynamics. John Wiley and Sons, New York. 520 pp.

Orwig, D.A., and M.D. Abrams. 1995. Dendroecological and ecophysiological analysis of gap environments in mixed-oak understoreys of northern Virginia. Functional Ecology 9:799-806.

Parker, G.R. 1989. Old-growth forests of the central hardwood region. Natural Areas Journal 9:5-11.

Parker, G.R., and D.J. Leopold. 1983. Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of the Torrey Botanical Club 110:482-488.

Parker, G.R., D.J. Leopold, and J.K. Eichenberger, 1985. Tree dynamics in an old-growth deciduous forest. Forest Ecology and Management 11:31-57.

Roach, B.A. 1977. A stocking guide for Allegheny hardwoods and its use in controlling intermediate cuttings. Research Report NE-373, U.S. Department of Agriculture, Forest Service, Radnor, Penn.

Roach, B.A., and S.F. Gingrich. 1975. Even-aged silviculture for upland central hardwoods. Agriculture Handbook 355, U.S. Department of Agriculture, Forest Service, Upper Darby, Penn. 38 pp.

Roovers, L.M., and S.R. Shifley. 1997. Composition and dynamics of Spitler Woods, an old-growth remnant forest in Illinois (USA). Natural Areas Journal 17:219-232.

Sander, I.L., and D.L. Graney. 1992. Regenerating oaks in the central states. Pp. 174-183 *in* D.L. Loftis and C.E. McGee, eds., Oak Regeneration: Serious Problems, Practical Recommendations Symposium Proceedings. General Technical Report SE-84, U.S. Department of Agriculture, Forest Service, Asheville, N.C.

Sander, I.L., P.S. Johnson, and R.R. Rogers. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. Research Paper NC-251, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. 16 p.

Saxe, H., D.S. Ellsworth, and J. Heath. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. New Phytologist 139:395-436.

Schlesinger, R.C. 1976. Hard maples increasing in an upland hardwood forest stand. Pp. 177-185 *in* J.S. Fralish, G.T. Weaver, and R.C. Schlesinger, eds., Proceedings of the First Meeting of the Central Hardwood Forest Conference, Carbondale, Ill.

Schlesinger, R.C. 1989. Dynamics of the sugar maple component of a white oak–yellow-poplar community. Pp. 262-267 *in* G. Rink and C.A. Budelsky, eds., Proceedings of the 7th Central Hardwood Forest Conference, Carbondale, Ill. General Technical Report NC-132, U. S. Department of Agriculture, Forest Service, St. Paul, Minn.

Schmelz, D.V., and A.A. Lindsey. 1965. Size-class structure of old-growth forests in Indiana. Forest Science 11:258-264.

Schwegman, J.E., W.E. McClain, T.L. Esker, and J.E. Ebinger. 1998. Anthracnose-caused mortality of flowering dogwood (*Cornus florida* L.) at the Dean Hills Nature Preserve, Fayette County, Illinois, USA. Natural Areas Journal 18:204-207.

Shifley, S.R., B.L. Brookshire, D.L. Larsen, and L.A. Herbeck. 1997. Snags and down wood in Missouri old-growth and mature second-growth forests. Northern Journal of Applied Forestry 14(4):165-172.

Shotola, S.J., G.T. Weaver, P.A. Robertson, and W.C. Ashby. 1992. Sugar maple invasion in an old growth oak-hickory forest in southwestern Illinois. American Midland Naturalist 127:125-138.

Spetich, M.A., and G.R. Parker. 1998. Distribution of biomass in an Indiana old-growth forest from 1926 to 1992. American Midland Naturalist 139:90-107.

Spetich, M.A., G.R. Parker, and E.J Gustafson. 1997. Spatial and temporal relationships of old-growth and secondary forests in Indiana, USA. Natural Areas Journal 17:118-130.

Spetich, M.A., S.R. Shifley, and G.R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in midwestern old-growth forests. Forest Science 45:302-313.

Tyrell, L.E., G.J. Nowacki, T.R. Crow, D.S. Buckley, E.A. Nautertz, J.N. Niese, J. Rollinger, and J.C. Zasada. 1998. Information about old growth for selected forest type groups in the eastern United States. General Technical Report NC-197, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. 507 pp.

Weaver, G.T., and W.C. Ashby. 1971. Composition and structure of an old-growth forest remnant in unglaciated southwestern Illinois. American Midland Naturalist. 86:46-56.

Will-Wolf, S. 1991. Role of fire in maintaining oaks in mesic oak maple forests. Pp. 27-33 *in* S.B. Laursen and J.F. DeBoe, eds., The oak resource in the upper Midwest: implications for management. Publication NR-BU-5663-S, Minnesota Extension Service, University of Minnesota, St. Paul.

Williams, C.E., and W.J. Moriarity. 1999. Occurrence of flowering dogwood (*Cornus florida* L.), and mortality by dogwood anthracnose (*Discula destructiva* Redlin), on the northern Allegheny Plateau. Journal of the Torrey Botanical Society 126: 313-319.