THE KEYSTONE ROLE OF OAK AND HICKORY IN THE CENTRAL HARDWOOD FOREST

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Abstract—Communities of the central hardwood forest have been dominated primarily by oak and hickory for the past 5000 years. Over this time period, they have become keystone species within the ecosystem and are of major importance in maintaining biodiversity. Not only do the large number of oak and hickory species by themselves contribute to community richness but they are known to provide food and support for a substantial number of wildlife species. Moreover, the structure created by dominance of oak and hickory in the forest community provides an environment for a highly diverse herbaceous understory. Data from oak-hickory stands with a maple-beech understory of saplings and small trees show a 90 percent drop in photosynthetically active radiation (PAR) at ground level accompanied by a 35 percent increase in litter weight compared to stands without an understory. The result is over a 90 percent drop in species richness and cover. This drastic loss of biodiversity, foliage, and fruit has serious implications for insect and bird populations and also suggests a potential for increased soil erosion and loss of nutrients. Extensive research into the loss of biodiversity is advised.

INTRODUCTION

Various oak (*Quercus*) and hickory (*Carya*) species have been the dominant components of the central hardwood forest for the past several millennia. Although the last glacial advance (Wisconsin Stage) did not extend much beyond Wisconsin and Michigan, it had a major influence on forest vegetation. Delcourt and Delcourt (1991) and Franklin (1994) have summarized the research on vegetation change since glacier degradation. Analysis of pollen profiles from bogs and information from geology, archeology, and anthropology indicate that the central states forest went through a progression of vegetation types. When the glacier was still advancing about 16,500 years BP, spruce (*Picea*) and pine (*Pinus*) dominated much of Wisconsin, Illinois, Indiana, and Ohio. From about 13,500 to 11,500 years BP, the forest was a mixture of hemlock (*Tsuga*), pine, spruce, fir (*Abies*), oak, birch (*Betula*), elm (*Ulmus*), ash (*Fraxinus*), maple (*Acer*), and beech (*Fagus*). By 10,000 years BP, mixed hardwoods were dominant within the forest because of the effects of the northward movement of the warm humid tropical airmass.

As the glacier melted between 10-11,000 and 9,000 years BP, a variety of oak species became the dominant forest species. The climate continued to warm and become drier between about 8,700 and 5,000 years BP. This period is known as the Hypsithermal. Concurrent with the warming of the climate was an increase in the occurrence of fire that probably was accentuated by the increased movement and activity of the Early American peoples. During this period, prairie expanded eastward well into Ohio and possibly farther east, and oak and hickory probably were the dominant woodland species. Transeau (1935) noted the existence of the prairie peninsula during the late 1700s and early 1800s. The present plant communities of the Tennessee Barrens are considered by Anderson and Bowles (2000) to be an extension of tall grass prairie. During the Hypsithermal, mixed oak and mesophytic hardwoods were restricted to coves and ravines.

After 5,000 years BP, precipitation levels increased so that oak expanded on uplands while mesophytic hardwoods, such as sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), American Beech (*Fagus grandifolia* Ehrh.), basswood (*Tilia americana* L.), and ash (*Fraxinus*), replaced oak in ravines and stream terraces. At that time, mesophytic species may also have been important on upland sites.

Later, succession to mesophytic species on upland slopes and hills was slowed due to the use of fire and clearing of land by the Woodland (2,500-1,000 years BP), Mississippian (1,000-500 years BP), and Native American Indians (<500 years BP). The Woodland culture depended largely on gathering of nuts, berries, and other wild plant foods such as roots. Southern pines (shortleaf, *Pinus echinata* Miller; Virginia, *Pinus virginiana* Miller) appeared in the forest during this period probably due to increased levels of fire. The Mississippian culture introduced agriculture into the central states; growing of foods such as corn, beans, squash, and pumpkin supplemented fishing and gathering of nuts and berries. Permanent villages often were constructed along major rivers and tributaries. Slash and burn agriculture and sedentary farming were common practices (Franklin 1994). The Native American Indians continued these practices and used fire to clear forest around their camps. Their reasons for use of fire included clearing of brush for improved hunting with bow and arrow, and better visibility for protection against enemy sneak attacks.

At the time of the original land survey in 1806-10, oak and hickory dominated the upland communities of most of southern Illinois including many north slopes and stream terraces (Fralish and others 1991, Fralish and others 2002, Sauer 2002). Forest ecologists universally agree that an active presettlement fire cycle (before ca. 1810) maintained the oak-hickory ecosystem. Abrams (1992) makes a strong case for the relationship between fire and development of oak dominated forests. The writings of early travelers reported relatively open woods and the frequency of fire.

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RECENT DISTURBANCE REGIMES AND OAK HICKORY

A new disturbance regime in the Central Hardwood Forest Region began at the time of settlement around 1810 to 1820. Fralish (1997) reported that the level of forest disturbance was reduced with settlement, and in some of the more eastern populated areas, this reduction probably was necessary to protect farms, towns, and other property including woodlots. However, during the period of European settlement and development in southern Illinois (1810-1930) and probably surrounding areas and states, the general level of disturbance was high as large land areas were cleared for agricultural crops. Fire used to clear land escaped in the woods so that the level of disturbance remained about that of presettlement time or was greater in some areas (e.g., Illinois Ozark Hills) as landowners and farmers continued to disturb the forest by various activities associated with settlement including heavy timber harvesting for buildings, railroad ties, and other construction, and grazing by free roaming cattle and pigs. In 1920, Miller reported that from the top of Bald Knob (a high point in the Illinois Ozark Hills), he could not see the Mississippi River because of smoke from six different wild fires. This level of disturbance maintained the oak-hickory component of the present forest at about that of the presettlement forest. Based on an analysis of presettlement witness tree records of the Land Office survey, McArdle (1991), and more recently, Fralish and others (2002) found that the amount of oak, hickory, and yellow-poplar in the present (Illinois Ozark Hills) forest was somewhat greater than in presettlement time suggesting a slightly greater level of disturbance during the period the present mature forest community was established as seedlings.

This disturbance regime abruptly ended and a new one began when fire protection laws were instituted in the late 1920s, and further, after large land areas were purchased for state and federal forests and parks developed in the 1930s and later. Grazing on private property and timber harvesting on national and state forest land continued but the beneficial effect of fire was absent. Since the passage of fire control laws and the cessation of wild fire, and the general protection of the ecosystem beginning in the late 1920s and early 1930s, oak and hickory trees have continued to grow while few seedlings reached sapling size before dying. Because large forested areas have remained undisturbed for the past 70+ years, scattered stems of fire-intolerant but shade tolerant species such as sugar maple, red maple, and American beech have grown to tree size and a become major seed source. Now forest communities are rapidly converting from mid-successional oak and hickory species to shade tolerant climax mesophytes with a concurrent loss of biodiversity.

There is little doubt that near total absence of fire has permitted the development of this classical secondary successional process, particularly on mesic sites in large areas of the central hardwood forest (Interior Low Plateaus, Central Lowlands, and Ozark Plateaus). Replacement of high quality stands of oak and hickory by mesophytes has been reported for stands in Pennsylvania (Downs and Abrams 1991), Ohio (McCarthy and Wistendahl 1988, McCarthy and others 1987, Cho and Boerner 1991,1995), Indiana (Myers and others 1983, Parker and others 1985, Parker and Sherwood 1986, Ward and Parker 1989), Kentucky and Tennessee (Fralish and Crooks 1988, 1989, Kettler 1990, Fralish and others 1993, Franklin and others 1993), Michigan (Host and others 1987, Hammett and Barnes 1989), Wisconsin (Menges and Loucks 1984), Missouri (Kucera and McDermott 1955, Anonymous 1983, Nigh and others 1985a, 1985b, Pallardy and others 1991), Iowa (Countryman and Miller 1989) and as far west as Kansas (Abrams 1986). In the center of the central hardwood region, a similar pattern has been reported for forest communities in northern Illinois (Wilhelm 1991), central Illinois (Boggess 1964, Boggess and Bailey 1964, McClain and Ebinger 1968, Anderson and Adams 1978, Adams and Anderson 1980, Ebinger and Newman 1984, Lehnen and Ebinger 1984, Ebinger 1986, Landes and Ebinger 1991, Edgington 1991), and in southern Illinois (Harty 1978, Schlesinger 1976, 1989, Fralish 1988, 1997, Fralish and others 1991, McArdle 1991, Shotola and others 1992, Schildt 1995, Helmig 1996). For the whole of Illinois, Iverson (1989) reported a 4,119 percent increase in the maple-beech forest type from 24,800 acres to 1,046,400 acres between 1962 and 1985.

Given time, the dense shade created by a closed canopy of shade tolerant mesophytic species will eliminate the oak and hickory by preventing seeding establishment and survival. Because oak and hickory have dominated the forest for thousands of years, the life cycle and ecological requirements of numerous other plant and animal species have become entwined with the existence of oak and hickory. Thus, oak, and to a lesser extent hickory, have become keystone species.

THE KEYSTONE SPECIES CONCEPT

A keystone species has been defined as a species (or group of species) that should be conserved because it makes an unusually strong contribution to community structure, maintains critical or key ecosystem processes, or has a disproportionately large effect on other species (Meffe and Carroll 1991) or on the persistence of other species in the community. A "key process" is a critical ecosystem function that controls ecosystem characteristics (Meffe and Carroll 1991). A keystone species may be of several types, such as a major producer, predator, prey, or mobile link species (e.g., pollinators). Either a single species or a group of species may function as a keystone species. It follows, therefore, that keystone species management is management directed toward ecologically important species as a surrogate for managing for all species in a [forest community or] ecosystem (Meffe and Carroll 1991). One function of a keystone species may be to support other forest species and maintain high biodiversity (species richness). High species diversity may promote stability at the ecosystem level because species usually vary in their tolerance to natural perturbation (e.g., fire) and anthropogenic stressors. Stressors may be single or multiple. As the number of independent stressors with different modes of action increases, there will be fewer resistant species with the potential to survive or increase under the influence of an altered environment (Breitburg and others 1998, Bond 1994). An altered environment includes the absence of fire in the fire-dependent oak-hickory forest.

However, depending on the type of ecosystem, it may be difficult to identify a keystone species in some ecosystems. In the central hardwood forest, there is sufficient evidence to classify oak and hickory species as keystones. A substantial number of wildlife species are not the only biota dependent on these species, but as will be shown later. Although large in number, oak and hickory species are relatively similar in their tolerance to natural and anthropogenic stressors, and thus, as keystone species, the absence of fire combined with invasion by mesophytic species become major stressors for oak-hickory forest both as a community and ecosystem. These two stressors (no fire, succession to mesophytes) are combining to eliminate the once strongly dominant keystone oak and hickory.

KEYSTONE CHARACTERISTICS OF OAK AND HICKORY

In the central hardwood forest, it is apparent that oak and hickory, when viewed in the light of changes that are occurring with invasion of maple, beech and other mesophytes, create a community structure and environment that maintains critical ecosystem processes, and has a disproportionately large effect on other species, particular on the persistence of other species in the community. It is well known that the production of mast (nuts from trees) is important to a substantial number of wildlife species, but for other living organisms, such as the highly diverse herb layer and oak and hickory seedlings and saplings, crown density and canopy structure are important.

Keystone species functions may deal with factors limiting production such as water, light, and nutrients (Vogt and others 1997). In the absence of a canopy created by an invasion by sugar maple, American beech, and other mesophytes, the structure of a mature or nearly mature (age >115 years) oak-hickory forest is typically even-aged with a single high, relatively thin overstory canopy easily penetrated by photosynthetically active radiation (PAR). However, level of PAR (photosynthetic photon flux density) varies with overstory structural characteristics that in turn vary with soil and topographic conditions. Photosynthetic photon flux density decreases rapidly with increasing depth of tree crowns (Kozlowski and Pallardy 1997).

On xeric sites (south, southwest, and west rocky slopes), post oak (*Quercus stellata* Wang.), blackjack oak (*Quercus marilandica* Muench.), southern red (*Quercus falcata* Michx.), scarlet oak (*Quercus coccinea* Muench.), white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.) trees are generally deformed as well as short (maximum height about 45 feet), have large openings in the individual crowns, and are widely spaced so that canopy closure may be only 35-50 percent in these woodlands or barrens (Fralish and others 1999); basal area (25-40 sq.ft. per A.; Fralish 1994), site index (35-50), and total biomass are extremely low. The overall result is that in a xeric post oak-blackjack oak forest, PAR at ground level is, on average, 15 to 20 percent (about 200-250 umol/m^2/sec.) of full sunlight (about 1200 umol/m^2/sec.) with many near full-sun flecks scattered across the forest floor. These sunflecks are essential for survival of many understory plants (Chazdon and Pearcy 1991). In the midcanopy, scattered arborescents such as sparkleberry (*Vaccinium arboreum* Marsh.) and Juneberry [Amelanchier arborea (Michx. f.) Fern.] usually are present but typically there is no oak and hickory sapling stratum; but seedlings may be numerous and a herbaceous layer usually is present (Jones 1974, O'Dell 1978).

On xeric-mesic sites (south, southwest, and west slopes with relatively deep soil), the trees are tall (70-80 feet), relatively straight with more well developed crowns (higher leaf density), and have a higher site index (50-65) and basal area (75-120 sq.ft. per A.; Fralish 1994) compared to oak on xeric sites. The stands on these sites may be dominated by either pure white oak, white oak with several species of the "black oak" group (black, scarlet, southern red), or by species of only the black oak group. There generally is more light penetration in stands dominated by black oak. Because species of the black oak group are more shade intolerant than white oak, they tend to have thinner crown density and a greater distance between crowns to let more light through to the lower leaves. "Black oak" species not only have fewer leaves but leaves in the upper portion of the crowns have large sinuses to permit passage of light. The lower leaves tend to have more green leaf area to capture light with the extreme condition found in the large misshapen black oak seeding leaves that essentially have no sinuses. The sunflecks in these stands are smaller but may comprise up to 80 percent of total light reaching the forest floor (Chazdon and Pearcy 1991). The PAR in black oak stands is about 10-15 percent of full sunlight (Fralish 1997). Scattered arborescents such as Juneberry [Amelanchier arborea (Michx. f.) Fern.] and flowering dogwood (*Cornus florida* L.) may be present but typically there is no oak and hickory sapling stratum; seedlings may be numerous and a herbaceous layer usually is present (Jones 1976, O'Dell 1978).

Form and crown density are further developed in trees on mesic sites (north, northeast and east slopes and stream terraces). These stands generally are dominated by nearly pure white oak or northern red oak (*Quercus rubra* L.); black oak seldom is more than a scattered tree. At maturity, the trees are tall (100-120 feet) and stands have a high site index 96-75) and basal area (130-160 sq. ft. per A.; Fralish 1994). White and northern red oak are shade intermediate and slightly more shade tolerant that other upland oak species. White oak crowns usually are more dense than those of black oak although the crowns seldom touch or overlap in the forest overstory canopy. However, even in a forest of white or northern red oak, crown depth seldom exceeds 1/2 of total tree height. Here PAR probably is 5 to 10 percent of full sun; sunflecks are smaller and more scattered. Flowering dogwood is the most common mid-canopy arborescent and usually is scattered but pawpaw (*Asimina triloba* (L.) Dunal) may form dense thickets.

In contrast to oak and hickory species, the crowns of the shade tolerant species have leaves with small sinuses (sugar and red maple), leaves without sinuses (American beech), densely packed crowns, and a deep crown as shade tolerance permits survival of leaves and branches on the lower half of the trunk (sugar maple and beech). The green cells in the leaves of these shade tolerant species have a special light capturing mechanism that allows them to photosynthesize under extremely low light conditions where PAR may be only one percent of full sunlight. The mechanism may be visualized as a large molecule in which antennae or spokes composed of chlorophyll A, carotinoids, and xanthophyll funnel light energy to chlorophyll B to the hub at the center of the spokes. Oak and hickory do not have this mechanism and are inefficient at photosynthesizing at low light levels.

Light levels are lowest in upland oak-hickory dominated stands where there also is a dense midcanopy of maple and beech. These multi-layered canopies reduce PAR to its lowest levels of less than 0.01 percent. Not only is there a total absence of sunflecks and indirect radiation but the light transmitted through the leaves is highly filtered. These stands also have a high leaf area index (area of leaves/ area of ground), thus the litter layer may be several inches thick and create a smothering effect well into the summer and fall. Oak seedling and herbaceous layers and even sugar maple and beech seedlings usually are absent in this environment (Fralish and others 1991).

FOREST SUCCESSION AND LOSS OF BIOTA

The elimination of natural disturbance such as fire initiated the process of succession which has had and is having several distinctly negative impacts on the forest ecosystem. Succession usually has been viewed as a single lengthy event but in the central hardwood forest some events are distinct, relatively short, and independent and disjunct from other events or processes.

Loss of the Black Oak Species

In the central hardwood forest, the first stage of succession is the loss of “black oak” species (black, blackjack, southern red, scarlet) from post oak dominated stands on xeric sites, or from stands of mixed white oak, “black oak,” and northern red oak on xeric-mesic and mesic sites. On xeric sites where mesophytes seldom invade, the loss of black oak may be considered as part of a compositional change as opposed to the process of succession. The death of “black oak” trees in post and white oak stands has been documented at LBL (Kentucky and Tennessee) and in Illinois. At LBL, data from the 1976 and 1986 remeasurement of permanent plots indicated that high mortality occurred in the black oak group while species of the “white oak” group (white oak, post oak and chestnut oak (*Quercus prinus* L.) and hickory had relatively low mortality (Groton and others 1988). Approximately 70 percent of the stems alive in 1988 were oak with only 20 percent of these in the black oak group, but approximately 45 percent of total mortality was black oak (Wellbaum 1989). On permanent plots at Kaskaskia Experimental Forest in southern Illinois, mortality of scarlet, black and northern red oak was higher than that of white oak with the mortality level of scarlet twice that of black oak (Schlesinger 1989).

However, loss of trees of black oak species on xeric and xeric-mesic sites may only be temporary because mesophytic species usually are not a problem and opening of the canopy may permit the establishment of black oak seedlings. A comparison of 10-12 year old clearcut oak stands at Land Between The Lakes indicates that species of the black oak group have a collective average relative density of 20 to 30 percent (Snyder 1995); however, in many stands, the density was double or triple that of the white oak group or hickory suggesting that there could be a substantial recovery over time.

On mesic sites in the central hardwood forest region, death of black oak species is the only beginning of a more extensive loss of biodiversity as species richness (number) decreases concurrently with purification (reduced equability) as white oak temporarily assumes greater dominance. Small trees {< 8 inches in diameter at breast height (d.b.h.)] with poorly developed crowns and the largest trees (70-100 cm in d.b.h.) of the shorter lived (150-175 years) “black oak” species have been or are being phased out while trees of the longer lived (300-350 years) white oak and hickory remain. Individuals of “black oak” reach physiological maturity and the end of their life span at about 150-170 years. At 125-150 years or earlier for some species such as scarlet oak, trees begin to show the typical signs of old age: heart rot, presence of large dead branches, patches of dead bark, large broken branches and/or tops, reduced number of leaves (thin crown) and a weak root system (frequent wind thrown trees). The relatively high density and increased competition in forest stands in addition to the drought and insect attacks of the 1980s may have reduced tree vigor which subsequently resulted in increased mortality due to secondary causal agents such as Hypoxylon canker.

Loss of White Oak and Hickory

The loss of white oak and hickory is probably the last event to occur as mesophytes totally occupy the site. On mesic sites, white oak (specifically *Quercus alba*) and hickory (extreme life expectancy = 300-400 years) will be replaced by the more long lived (450-500 years) sugar maple and American beech. Because of the extensiveness of mesic sites, the effect of succession will be to create “islands” of remaining white oak and post oak stands on xeric and xeric-mesic sites in some regions (e.g., Shawnee Hills; LBL) or to completely blanket the landscape with a near monoculture of sugar maple or American beech in others (e.g., Illinois Ozark Hills, Illinois Coastal Plain, Tipton Till Plain).

Reduced Productivity/Mast

Forest productivity will decrease as oak and hickory trees are systematically eliminated from the forest. In a high light environment (direct sunlight on the upper crowns), they grow faster than maple and beech. In a shaded environment, maple and beech seedlings, saplings, and midcanopy trees survive better and grow faster. The physiological basis for the growth differential between these two groups is reviewed by Hale and Orcutt (1987), Kozlowski and others (1991), and Kozlowski and Pallardy (1997).

There is an interesting paradox regarding the rate of oak growth and rate of succession. It would be reasonable to expect that slow-growing oak and hickory stands on xeric and xeric-mesic sites should be easily replaced by invading species, while their high growth rate on mesic sites would permit them to dominate indefinitely. The reverse situation actually occurs. The lack of soil moisture which results in slow oak growth on xeric sites also prevents succession to mesophytic (moisture requiring) species. High soil moisture on mesic sites permits a rapid oak growth rate but creates an environment suitable for invasion and development of a community dominated by shade tolerant mesophytes. In terms of resource management, the most productive oak and hickory stands are being replaced by slower growing mesophytic species while the least productive stands remain intact. The amount of mast produced for wildlife parallels that of tree growth.

Loss of Animals

The importance of oak and hickory nuts to wildlife is well known and documented. Nationwide, oak is used by 96 animals (Martin and others 1951); however, for eastern United States (land west of the prairie zone), the number is considerably lower (table 1). Of the 44 animals listed, the majority are birds (28) and of these only seven are considered game animals; the remainder (21) are small birds.

Succession impacts stand productivity by reducing the amount of mast (nuts, buds, twigs) produced for wildlife as oak and hickory are replaced by mesophytes. Thus, loss of animals will start to occur as the black oak are lost but the major impact will come decades or more latter when white oak trees die. While beech is a mast producer, the soft tissues of maple seed quickly decompose if the seed does not germinate.

However, the impact of succession on wildlife populations is going to be greater than that suggested by the number of species listed in table 1. The somewhat more indirect influence will be on herbaceous plants which support various neotropical migrant birds and insect populations.

Loss of Herbaceous Plants

The present high density of seedlings, saplings and small trees of mesophytic species within the central states oak-hickory forest is having a major deleterious effect on the herbaceous layer. This loss is the most important unreported impact resulting from forest succession. The loss in herb richness can be considerable as Jones (1974) and Harty (1978) reported between 50 and 75 herbaceous plants for both spring and summer/fall guilds.

Data collected from Trail of Tears State Forest in the Illinois Ozark Hills region indicates that as photosynthetically active radiation decreases and the amount of ground litter increases, there is a major decrease in the number of herbaceous species (table 2). Species richness increased 200 percent from an average of 10 species/10 m^2 sample in a forest composed of black and white oak and hickory with a closed canopy of smaller sugar maple trees (d.b.h. of 10-20 cm) to an average of 31.5 species/10 m^2 in open stands dominated by black oak, white oak, and hickory without maple. There is little difference in species richness between the open black/white and post oak stands although post oak occurs on drier sites and has considerably higher PAR levels. In dense sugar maple dominated forest of the Ozark Hills region, few seedlings or herbs can be observed.

Wilhelm (1991) also reported a decrease in the number of summer and fall flowering species between 1980 and 1988 and related this decrease to the increase in sugar maple importance in the tree canopy. At Land Between The Lakes (LBL) in Kentucky and Tennessee, Close (1996) recorded cover for herbaceous in uncut post oak, black oak, and white oak dominated stands. By comparison, Glickauf (1998) found about twice the number and double the cover of species in shelterwood cut stands at LBL, suggesting that even in oak dominated stands, the light resource prevents full development of understory herbs. Therefore, it should be of no surprise that the added layers of branches and leaves, due to a midcanopy of mesophytic species, impoverishes the herbaceous stratum.

In a related experiment on a common oak-hickory forest herb, pots containing dittany [*Cunila origanoides* (L.) Britt.] plants were placed in the open and in the same four community/structural types as listed in table 2: post oak, black oak/white oak without a sugar maple understory, black oak/white oak with a thin maple understory, and black oak/white oak with a dense maple understory. The amount of light decreased with increasing overstory and understory density. The plants in the two open areas (no shade) were healthy and robust (high dry weight) and produced copious flowers in the fall. The plants in the post oak and black oak/white oak stands (minimum shade) without maple grew well, were slightly taller than the open grown plants, and flowered in the fall, but were less robust (smaller dry weight). One-half of the dittany plants in the black oak/white oak forests with a thin maple midcanopy (moderate shade) and all but one plant under the dense maple midcanopy (heavy shade) were dead by July or August. The one plant that survived under heavy shade did not flower. Across the light levels (table 2), plants grown in shade were taller and thinner than those grown in the open, and the heavier the shade, the taller and thinner the stem such that under the two lowest light levels, the plants were unable to maintain an upright orientation, fell over and died.

As described earlier, the amount of PAR on the forest floor is a function of crown and stand density (structure). The adaptive geometry of oak trees (Horn 1971) permits light penetration through the canopy and increases photosynthesis not only in lower leaves but permits survival of herbaceous plants on the forest floor. Because of oak species have thin crowns and there is space around each crown, the relatively low amount of leaf biomass produces only a thin leaf litter layer in the fall, and this layer is decomposed by early summer.

Conversely, extremely shade tolerant species such as sugar maple and American beech have a high stem density, overlapping crowns and thick crowns of multiple leaf layers as lower branches remain alive. These characteristics produce a high leaf biomass. In autumn, the leaves create a thick (3-5 cm deep) litter layer that often remains throughout the growing season and smothers the new growth of herbaceous plants. The litter appears to be of sufficient thickness that new seedlings will not survive because the extending radical cannot reach mineral soil and water before desiccation occurs. Bazzaz (1979, 1996) describes these and additional relationships.

Although the invasion of mesophytes reduces the number of oak forest herbs, the herbaceous layer of maple/beech

Table 1—Amount of oak (*Quercus*) species used as food by bird and animal species in eastern United States

Type of animal	Percent of diet	Region
	Upland game birds (*acorns, buds*)	
Grouse, ruffed	**	E
Pheasant, ringed-necked	*	NE
Prairie chicken, greater	*	Wisc
Prairie chicken, lesser	*	Okla
Quail, bobwhite	**	NE
	Songbirds (*acorns*)	
Blackbird, rusty	+	NE
Crow, common	*	E
Flicker, yellow-shafted	+	E
Grackle, purple	***	E
Grosbeak, rose-breasted	+	E
Jay, blue	****	E
Meadowlark	+	SE
Nuthatch, white-breasted	***	E
Sapsucker, yellow-bellied	+	E
Starling	+	NE
Thrasher, brown	**	E
Titmouse, tufted	**	E
Towhee, red-eyed	**	NE
Woodpecker, downy	+	E
Woodpecker, red-bellied	***	E
Woodpecker, red-cockaded	+	SE
Woodpecker, red-headed	***	E
Wren, Carolina	+	E
	Waterfowl (*acorns*)	
Mallard duck	*	E
Pintail duck	+	SE
Wood duck	*****	NE
Wood duck	***	SE
	Marsh birds (*acorns*)	
Rail, clapper	+	SE
	Fur and game animals (*acorns, buds, bark*)	
Bear, black	****	NE
Beaver	+	NE
Fox, gray	+	S
Fox, red	+	NE
Muskrat	+	NE
Opossum	*	E
Rabbit, cottontail	*	NE
Rabbit, mearns	+	NE
Raccoon	++++	E
Squirrel, flying	**	NE
Squirrel, fox	****	E
Squirrel, gray	****	E
Squirrel, red	**	E
Small mammals (acorns)		
Chipmunk, eastern	**	NE
Mouse, meadow	+	E
Rat, wood	++	S
	Hoofed browser (*twigs, foliage, acorns*)	
Deer, white-tailed	****	E

Data summarized from Martin and others (1951). The star ranking system for percent of diet is: + = 0.5–5 percent; * = 2-5 percent; ** = 5–10 percent; *** = 10–25 percent; **** = 25–50 percent; ***** = > 50 percent. Location is designated by region: E = eastern United States; NE = central hardwood forest region including most of the Appalachian Mountains and the northern hardwood-conifer forest of the Lake States and New England; SE = southern pine-hardwood forest.

Table 2—The relationship between number of species, photosynthetically active radiation, and litter weight under four forest canopy/community types on southeast, south, and southwest slopes in the Illinois Ozark Hills region

	Canopy/community type			
	Open		Closed	
	Post oak	Black oak	Black oak	Oak/maple
PAR (umol m^{-1} s^{-1})	233.8	138.4	51.7	8.85
Litter weight (kg/m^2)	0.75	0.66	0.97	1.10
Species/10 m^2	31.5	31.5	25.0	10.0

PAR = photosynthetically active radiation.
Unpublished data collected in 1996. All the oak communities include some white oak, southern red oak, and scarlet oak.

dominated communities has high species richness in some regions (Curtis 1959) and some mesic sites in the central hardwood forest (Jones 1974, Harty 1979, Close 1996). Small stems of sugar maple, American beech and other mesophytes indicate the advance of this forest, but the gap between time of elimination of oak-hickory forest herbs and time of invasion of mesophytic forest herbs may be 50 to 100 years or longer and may not occur on more xeric sites. During this gap, insect populations are likely to be reduced and soil surface erosion increased depending on seedling density. These aspects of herb importance should be the thrust of future research.

A dense herbaceous layer is important for production of flowers and seeds and of leaf material for insects, all of which are used by various neotropical bird species. The above ground herbaceous layer also protects the soil from erosion by heavy rains as roots assist in holding soil is place. Herbaceous plants also store nutrients and reduce the loss of nutrients from the site and ecosystem.

OAK MANAGEMENT

It would appear that near complete loss of the oak-hickory forest component is eminent. Given another 75-100 years, there will be few stands dominated by oak and hickory species although a few scattered trees may remain. Moderate disturbances that would regenerate oak and hickory remain absent or restricted, and at this time, there appears to be limited opportunity to reintroduce fire into the ecosystem. Non-scientists have suggested that oak regeneration will appear when large individual trees die as is occurring with the black oak component. These large individuals may be standing dead or on the ground as windfalls. Standing dead typically lose progressively larger branches over a period of five to ten years and then fall as a single pole-like structure. A windfall, where the entire tree tips and falls, will typically leave intact the midcanopy of mesophytic species where it was standing but may disrupt the midcanopy under adjacent large trees. In either case of individual tree death, or under a silvicultural program of individual tree selection where sugar maple and American beech have formed a sufficiently mid-canopy, no canopy gap for light penetration is formed, or if formed, it is rapidly closed by the crowns of mesophytes. The death of or removal of individual trees works strongly to the advantage of sugar maple and beech and to the detriment of oak and hickory seedlings and saplings which need direct solar radiation throughout their entire life.

Conversely, data from 80 permanent plots in the Illinois Ozark Hills have shown that clearcutting is not the answer to regenerating oak on moist sites. This case study by Presmyk (1987) examined four contiguous areas: 1981 clearcut, 1975 clearcut burned (wildfire) in 1981, mature forest burned (wildfire) in 1981, unburned forest. The original overstory on these areas was black, white, and northern red oak with yellow-poplar and beech as secondary species. The plots were resampled in mid 1990. In the 1981 clearcut (no fire), the north slopes converted immediately to beech, red maple, yellow-poplar, black gum and sassafras; a small amount of oak was present. In the 1975 clearcut that burned in 1981, the beech, maple, and other tree species on north slopes were killed and the area reverted into a tangle of brush [devil's walking stick, *Aralia spinosa* L.; sassafras, *Sassafras albidum* (Nutt.) Nees; mulberry, *Morus rubra* L.; grape, *Vitis* spp.]. Few stems of oak were present. However, on the drier south slopes, white and black oak were major regenerating species along with red maple, yellow-poplar (*Liriodendron tulipifera* L.), black gum (*Nyssa sylvatica* Marsh.), and sassafras. The burned mature forest had a similar understory as did the unburned forest but the burned forest had larger amounts of sassafras, white oak, yellow-poplar, and black gum. The conclusion is that clearcutting alone does not regenerate oak, post harvest fire may reduce a forest to non-productive status for a lengthy period, and that fire in mature forest increases the amount of oak regeneration. It would appear that on moist sites in particular, fire prior to harvesting is necessary to establish oak regeneration. In the absence of fire after cutting, the forest will immediately convert to mesophytic hardwoods if they are the major understory component. In the clearcuts of these watersheds, erosion of tributaries to the main intermittent stream was evident and substantial.

Based on research, it would appear that in stands where stems of the invading mesophytes are still relatively small (saplings), several prescribed fires followed by partial harvesting using an even-aged approach such as shelterwood would permit the establishment of oak and hickory seedlings, maintain mast production at a reasonable level, and develop the herbaceous layer while protecting the site.

CONCLUDING REMARKS

For many years, mast production for wildlife has been considered one of the most important attributes of oak and hickory dominated communities. However, due to the length of time (centuries) oak and hickory have dominated the central hardwood forest region, and because of the low density of their crowns and overstory canopy, they have become of major importance to the herbaceous stratum and the wildlife that depend on herb foliage and seed for survival. In terms of supporting mammals, birds, herbs, and insects, oak and hickory have become keystone species. In the central hardwood forest, loss of these dominant keystone species through succession will result is loss of biota ecologically and evolutionarily associated with oak-hickory forest.

In recent years, new attitudes developed jointly with new available scientific information have directed forest management away from timber production and toward other forest ecosystem values such as preservation of rare or endangered species, development of old growth characteristics, and maintenance of species diversity to the level thought to be present in presettlement communities (before ca. 1810). Unfortunately, it is too often believed that total protection will permit the forest to maintain or restore these values. This belief is in error because oak and hickory are shade intolerant keystone species subject to successional replacement, and thus, their response is similar to other communities composed of disturbance dependent, pioneer species of the southwest (e.g., longleaf pine, *Pinus palustris*), the north (quaking aspen, *Populus tremuloides*), and west (lodgepole pine, *Pinus contorta*).

Disturbance plays an important role in ecosystem development. Fire in particular reduces invasion of mesophytes in oak stands, and with a less dense overstory, white and black oak stands can be maintained to old growth with a full complement of understory herbs. Conversely, the extremely dense, multi-layered mesophytic forest is viewed by many as the epitome of old growth (primeval forest), yet according to early land survey records, it was rare to nonexistent in most areas of the central hardwood forest (Crooks 1988; Fralish and others 1991, 2002).

LITERATURE CITED

Anonymous. 1983. Sugar maple takeover threatens state forests. Missouri Farm News 80: 49.

Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65: 29-37.

Abrams, M.D. 1992. Forest and the development of oak forests. BioScience 42: 346-53.

Adams, D.; Anderson, R.C. 1980. Species response to a moisture gradient in central Illinois. American Journal of Botany 67: 381-392.

Anderson, R.C.; Adams, D. 1978. Species replacement patterns in central Illinois white oak forests. In: Pope, P.E., ed. Proceedings of the second central hardwood conference; 1978 November 14-16; West Lafayette, IN: Department of Forestry, Purdue University: 284-301.

Anderson, R.C.; Bowles, M.L. 2000. Deep-soil savanna and barrens of the midwestern United States. In: Anderson, R.C.; Fralish, J.S.; Baskin, J.M, eds. Savannas, Barrens, and Rock Outcrop Communities of North America. Cambridge, United Kingdom: Cambridge University Press: 155-170.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. In: Johnston, R.F.; Frank, P.W.; Michener, C.D., eds. Vol. 10. Annual Review of Ecology and Systematics. Palo Alto, CA: Annual Reviews, Inc.: 351-371.

Bazzaz, F.A. 1996. Plants in changing environments. Cambridge, UK: Cambridge University Press.

Boggess, W.R. 1964. Trelease Woods, Champaign County, Illinois: woody vegetation and stand composition. Illinois Academy of Science 57: 261-271.

Boggess, W.R; Bailey, L.W. 1964. Brownfield Woods, Illinois: woody vegetation and change since 1925. The American Midland Naturalist 71: 392-401.

Bond, W.J. 1994. Keystone species. In: Schultz, E.D.; Mooney, H.A. eds. Biodiversity and Ecosystem Function: 237-53. New York: Springer-Verlag.

Breitburg, D.L.; Baxter, J.W.; Hatfield, C.A. [and others]. 1998. Understanding effects of multiple stressors: ideas and challenges. In: Pace, M.L.; Groffman, P.M., eds. Successes, limitations, and frontiers in ecosystem science. New York, NY: Springer-Verlag: 416-431.

Chazdon, R.L.; Pearcy R.W. 1991. The importance of sunflecks for forest understory plants. BioScience 41: 760-766.

Cho, D.S.; Boerner, R.E.J. 1991. Canopy disturbance patterns and regeneration of Quercus species in two Ohio old-growth forests. Vegetatio 93: 9-18.

Cho, D.S.; Boerner, R.E.J. 1995. Dendrochronological analysis of the canopy history of two old-growth forests. Vegetatio 120: 173-183.

Close, D.D. 1996. Evaluation of herbaceous diversity and differential species in mature forest stands at Land Between The Lakes, Kentucky and Tennessee. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Countryman, D.W.; Miller, H.R. 1989. Investment analysis of upland oak stands with sugar maple understories: management for oak vs. conversion to sugar maple in Iowa and Missouri. Northern Journal of Applied Forestry 6: 165-169.

Crooks, F.B. 1988. Comparison of presettlement and old growth forest communities in the Shawnee Hills, Illinois. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Delcourt, H.R.; Delcourt, P.A. 1991. Quaternary ecology: a paleoecological perspective. New York, NY: Chapman & Hall.

Downs, J.A.; Abrams, M.D. 1991. Composition and structure of an old-growth versus a second-growth white oak forest in southwestern Pennsylvania. In: McCormick, L.H.; Gottschalk, K.W., eds. Proceedings of the eighth central hardwood forest conference; 1991 March 2-6, University Park, PA. Gen. Tech. Rep. NE-148. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 207-223.

Ebinger, J.E. 1986. Sugar maple, a management problem in Illinois forests? Transactions of the Illinois Academy Science 79: 25-30.

Ebinger, J.E.; Newman, J.A. 1984. Woody vegetation of a dry-mesic upland forest in Cumberland County, Illinois. Transactions of the Illinois Academy Science 77: 187-192.

Edgington, J.M. 1991. Brownfield Woods, Illinois: present composition and changes in community structure. Transactions of the Illinois Academy Science 84: 95-112.

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

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

Fralish, J.S. 1997. Community succession, diversity, and disturbance in the Central Hardwood Forest. In: Schwartz, M.W., ed. Conservation in Highly Fragmented Landscapes. New York, NY: Chapman and Hall: 234-66.

Fralish, J.S.; Carver, A.D.; Anderson, R.C. [and others]. 2002. Presettlement, present, and projected forest communities of the Shawnee National Forest. Report Submitted to the U.S. Department of Agriculture, Shawnee National Forest, Harrisburg, IL. Carbondale, IL: Department of Forestry, Southern Illinois University.

Fralish, J.S.; Crooks F.B. 1988. Forest communities of the Kentucky portion of Land Between The Lakes: a preliminary assessment. In: Snyder, D.H. ed. Proceedings of the first annual symposium on the natural history of lower Tennessee and Cumberland River valleys. 1966 March 11-12. Clarksville, TN: Center for Field Biology, Austin Peay State University: 74-75.

Fralish, J.S.; Crooks, F.B. 1989. Forest composition, environment, and dynamics at Land Between The Lakes in northwest middle Tennessee. Journal of the Tennessee Academy of Science 64: 107-111.

Fralish, J.S.; Crooks, F.B.; Chambers, J.L.; Harty, F.M. 1991. Comparison of presettlement, second-growth, and old-growth forest on six soil types in the Illinois Shawnee Hills. The American Midland Naturalist 125: 294-309.

Fralish, J.S.; Franklin, S.B.; Close, D.D. 1999. Open woodland communities of southern Illinois, western Kentucky, and middle Tennessee. In: Anderson, R.C.; Fralish, J.S.; Baskin J.M., eds. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge, United Kingdom: Cambridge University Press: 171-189.

Fralish, J.S.; Franklin, S.C.; Robertson, P.A. [and others]. 1993. An ordination of compositionally stand and unstable forest communities at Land Between The Lakes, Kentucky and Tennessee. In: Fralish, J.S.; McIntosh, R.P.; Loucks, O.L. eds. John T. Curtis: Fifty Years of Wisconsin Plant Ecology. Madison, WI: Wisconsin Academy of Science, Arts and Letters: 247-267.

Franklin, S.B. 1994. Late Pleistocene and Holocene vegetation history of Land Between The Lakes, Kentucky and Tennessee. Transactions of the Kentucky Academy of Science 55: 6-19.

Franklin, S.B.; Robertson, P.A.; Fralish, J.S.; Kettler, S.M. 1993. Overstory vegetation and successional trends of Land Between The Lakes, U. S. A. Journal of Vegetation Science 4: 1-12.

Glickauf, S.P. 1998. The effect of shelterwood cutting on the woody and herbaceous understory. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Groton, E.S.; Field, R.J.; Pullin, B.P. 1988. Land Between The Lakes forest and wildlife resources: twenty year trends. Internal report. Norris, TN: Tennessee Valley Authority.

Hale, M.G.; Orcutt, D.M. 1987. The physiology of plants under stress. New York: John Wiley & Sons.

Hammitt, W.E.; Barnes, B.V. 1989. Composition and structure of an old-growth oak-hickory forest in southern Michigan over 20 years. In: Rink, G.; Budelsky, C.A., eds. Proceedings of the seventh central hardwood forest conference. Gen. Tech. Rep. NC-132. St. Paul, MN, U.S. Forest Service, North Central Forest Experiment Station: 247-253.

Harty, F.M. 1978. Tree and herb species distribution, and herbaceous vegetation as an indicator or site quality for disturbed upland forest stands in the Greater Shawnee Hills region of southern Illinois. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Helmig, L.M. 1996. Predicting the threshold time of conversion from *Quercus-Carya* to mesophytic forest in the Illinois Ozark Hills. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Horn, H.S. 1971. The adaptive geometry of trees. Princeton, NJ: Princeton University Press.

Host, G.E.; Pregitzer, K.S.; Ramm, D.W. [and others]. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern lower Michigan. Forest Science 33: 445-457.

Iverson, L.R.; Oliver, R.L.; Tucker, D.P. [and otherts]. 1989. The forest resources of Illinois: an atlas and analysis of spatial and temporal trends. Special Publication 11. Champaign, IL: Illinois Natural History Survey.

Jones, S.M. 1974. Herbaceous vegetation as an indication of site quality and potential stand composition for upland forests in southern Illinois. Carbondale, IL: Department of Forestry. Southern Illinois University. [Not paged]. M.S. thesis.

Kettler, S.M. 1990. The effect of soil and topography on forest successional patterns at Land Between The Lakes, KY and TN. Carbondale,IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Kozlowski, T.T.; Kramer, J.P.; Pallardy, S.G. 1991. The physiological ecology of woody plants. New York: Academic Press.

Kozlowski, T.T.; Pallardy, S.G. 1997. Physiology of woody plants. New York, NY: Academic Press.

Kucera, C.L.; McDermott, R.E. 1955. Sugar maple-basswood studies in the forest-prairie transition of central Missouri. The American Midland Naturalist 54: 495-503.

Landes, J.M.; Ebinger, J.E. 1991. Woody understory of Baber Woods, Edgar County, Illinois. Erigenia 11: 18-26.

Lehnen, L., Jr.; Ebinger, J.E. 1984. Woody vegetation at Burgner Acres, east-central Illinois: composition and changes since 1964. Transactions of the Illinois Academy of Science 77: 35-42.

Martin, A.C.; Sim, H.S.; Nelson, A.L. 1951. American wildlife & plants: a guide to wildlife food habits. New York, NY: Dover Publications.

McArdle, T.G. 1991. Comparison of presettlement and present forest communities by site type in the Illinois Ozark Hills. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

McCarthy, B.C.; Hammer, C.A.; Kauffman, G.L.; Cantino, P.D. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. Bulletin of the Torrey Botanical Club 114: 33-45.

McCarthy, B.C.; Wistendahl, W.A. 1988. Hickory (*Carya* spp.) distribution and replacement in a second-growth oak hickory forest of southeastern Ohio. The American Midland Naturalist 119: 156-164.

McClain, W.E.; Ebinger, J.E. 1968. Woody vegetation of Baber Woods, Edgar County, Illinois. The American Midland Naturalist 79: 419-428.

Meffe, G.K.; Carroll, C.R. 1994. Principles of conservation biology. Sunderland, MA: Sinauer Associates, Inc.

Menges, E.S.; Loucks, O.L. 1984. Modeling a disease-caused patch disturbance: oak wilt in the Midwestern United States. Ecology 65: 487-498.

Miller, R.B. 1920. Fire prevention in Illinois. Forestry Circular No. 2. Springfield, IL: Illinois Natural History Survey.

Myers, C.C.; Roth, P.L.; Weaver, G.T. 1983. Pioneer Mothers Memorial Forest: baseline data. Technical Bulletin 1. Carbondale, IL: Department of Forestry, Southern Illinois University.

Nigh, T.A.; Pallardy, S.G.; Garrett, H.E. 1985a. Changes in upland oak-hickory forests of central Missouri. In: Dawson, J.O.; Majerus, K.A. eds. Proceedings of the fifth central hardwood forest conference. Urbana, IL: Department of Forestry, University of Illinois: 170-177.

Nigh, T.A.; Pallardy, S.G.; Garrett, H.E. 1985b. Sugar maple-environmental relationships in the River Hills and central Ozark Mountains of Missouri. The American Midland Naturalist 114: 235-251.

O'Dell, R.K. 1978. A study of the mid-canopy strata in upland forest communities of the Shawnee Hills of southern Illinois. Carbondale, IL: Department of Forestry. Southern Illinois University. [Not paged]. M.S. thesis.

Pallardy, S.G.; Nigh, T.A.; Garrett, H.E. 1991. Sugar maple invasion in oak forests of Missouri. In: Burger, G.V.; Ebinger, J.E.; Wilhelm, G.S., eds. Proceedings of the oak woods management workshop. Charleston, IL: Eastern Illinois University: 21-30.

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

Parker, G.R.; Sherwood, P.T. 1986. Gap phase dynamics in a mature Indiana forest. Indiana Academy of Science 95: 217-223.

Presmyk, C.J. 1987. The effect of a wildlife and clearcutting on woody species regeneration in a southern Illinois Ozark Hills forest. Carbondale, IL: Department of Forestry. Southern Illinois University. [Not paged]. M.S. thesis.

Sauer, S. 2002. Analysis of historic vegetation using General Land Survey records in the Shawnee National Forest, Illinois, U.S.A.. Normal, IL: Department of Biological Sciences. Illinois State University. [Not paged]. M.S. thesis.

Schildt, A.L. 1995. A study of presettlement, present, and future forest in the coastal region of southern Illinois. Carbondale, IL: Southern Illinois University. [Not paged]. M.S. thesis.

Schlesinger, R.C. 1976. Hard maples increasing in an upland forest stand. In: Fralish, J.S.; Weaver G.T.; Schlesinger, R.C., eds. Proceedings of the first central hardwood conference. Carbondale, IL: Department of Forestry, Southern Illinois University: 177-185.

Schlesinger, R.C. 1989. Dynamics of the sugar maple component of a white oak-yellow-popular community. In: Rink, G.; Budelsky, C.A., eds. Proceedings of the seventh central hardwood forest conference. Gen. Tech. Rep. NC-132. St. Paul, MN: U.S. Department of Agriculture, Forest Service. North Central Forest Experiment Station: 262-266.

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

Snyder, P.R. 1995. Forest regrowth in 10-12 year old clearcuts at Land Between The Lakes, Kentucky and Tennessee. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Transeau, E.N. 1935. The prairie peninsula. Ecology 16: 423-37.

Vogt, K.A.; Gordon, J.C.; Wargo, J.P. [and others]. 1997. Ecosystems: balancing science with management. New York, NY: Springer-Verlag.

Ward, S.W.; Parker, G.R. 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70: 1279-85.

Welbaum, E.M. 1989. Site, stand and tree characteristics associated with oak decline and mortality. Carbondale, IL: Department of Forestry, Southern Illinois University. [Not paged]. M.S. thesis.

Wilhelm, G.S. 1991. Implications of changes in floristic composition of the Morton Arboretum's East Woods. In: Burger, G.V.; Ebinger, J.E.; Wilhelm, G.S., eds. Proceedings of the oak woods management workshop. Charleston, IL: Eastern Illinois University: 31-48.