# COMPOSITION, STRUCTURE, AND DYNAMICS OF THE ILLINOIS OZARK HILLS FOREST

**Lisa M. Helmig and James S. Fralish[1]**

**Abstract.**—In the mature oak-hickory ecosystem of the Illinois Ozark Hills, forest community composition, dynamics, and structure were studied to examine the extent of conversion to mesophytic species and eventually predict the broad threshold time of complete conversion. Tree, sapling, and seedling data were collected from 87 plots distributed throughout the region. Data for the tree stratum and for the seedling and sapling strata were analyzed by Ecological Land Type (ELT): south slope, ridgetop, north slope, and stream terrace. To compare the vegetation among ELTs and between stand strata, importance values (relative basal area for trees; relative density for seedlings and saplings) were calculated and a composition index [CI = ∑(Species Importance Value x Adaptation Value)] developed for each stratum. On south slope and ridgetop ELTs, CI values near 600 were typical of an oak-hickory dominated overstory (Adaptation Values [AVs] = 4-6.5). Dominant species were white and black oak. On the more mesic north slope ELT, a CI of 774 indicated a mixed overstory dominated by northern red oak, white oak, yellow-poplar, and black oak. The Terrace ELT was dominated by yellow-poplar and a mixture of upland and bottomland species; overstory CI was 747. For all ELTs, sapling CI ranged between 852 and 958, while seedling CI varied between 772 and 921. These CI values indicated an understory moderately to strongly dominated by mesophytes, primarily sugar maple, American beech, and red maple (AVs = 9.1, 9.6, and 10, respectively). Given the universal and extensive development of the understory, the Illinois Ozark Hills seem destined to be the first major ecosystem to convert from a forest dominated by oak-hickory to one dominated by maple-beech.

## INTRODUCTION

Succession is creating a major change in community composition of nearly all North American forests. Succession is defined here as the temporal replacement of a forest community composed of shade- intolerant or shade-intermediate disturbance-dependent (early successional) species by one in which more shade-tolerant mesophytic (late successional) species dominate to form a compositionally stable community (Fralish and others 1991). Within the ecological landscape, stands of early successional species typically have developed after a major period of disturbance, specifically after fire or fire and logging. If a lengthy period of protection or absence of disturbance follows this period, succession often occurs. The process is largely driven by differential shade tolerances among species, and if seed is available, generally proceeds unrestricted in the absence of disturbance and soil moisture deficits (Fralish 1988).

Parallel examples of forests composed of fire-tolerant early successional species are found throughout North America. In the Rocky Mountains, lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands are changing

[1]District Silviculturalist (LMH), Chequamenon-Nicolet National Forests, Park Falls, WI 54552; and Research Ecologist (JSH), Department of Forestry, Southern Illinois University, Carbondale, IL 62901-4411. JSH is corresponding author: to contact, call (618) 521-8006, or email at jfralish@frontier.com.

to Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and Englemann spruce (*Picea engelmannii* Parry ex Engelm.). Large areas of quaking aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) are being replaced by white spruce (*Picea glauca* [(Moench]) Voss) and balsam fir (A*bies balsamea* [L.] Mill.) in Canada. In the Lake states, quaking aspen and jack pine (*Pinus banksiana* Lamb.) are being replaced by white pine (*Pinus strobus* L.) on sand soil and northern hardwoods on loam soil. In the southeastern United States, southern pine (for example, shortleaf pine [*Pinus echinata* Mill.] and loblolly pine [*Pinus taeda* L.]) stands have understories dominated by various species of scrub oak (*Quercus* spp.) and hickory (*Carya* spp.) (Baker and Langdon 1990, Lawson 1990).

On the deep, moist soil of the Central Hardwood Forest Region, the oak-hickory (*Quercus-Carya*) forest community is undergoing a parallel compositional change to mesophytic species, primarily sugar maple (*Acer saccharum* Marsh.) but also including American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and a variety of mesophytic shade-tolerant hardwoods, depending on the region. Invasion has been reported by many researchers working in the oak-hickory dominated communities of Pennsylvania, Indiana, Kentucky and Tennessee, Michigan, Wisconsin, Missouri, Iowa, and Kansas. Refer to Fralish and McArdle (2009) for citations. Most of these studies investigated only present forest condition based on a structure-for-time approach, that is, an oak-hickory overstory canopy and an understory dominated by shade-tolerant mesophytes that eventually will replace the overstory.

Recently, Fralish and McArdle (2009) examined Ozark forest change over a 300-year period characterized by three distinct disturbance regimes. During the last regime, which began about 1930 and continues to the present, the researchers reported a rapid rate of composition change. However, community structure was based on total understory density and was not fully detailed, as estimating the broad threshold time of conversion was not an objective of the research. This broad time or period is defined here as the time at which the biomass of a functional group whose seed is distributed by wind exceeds that of a functional group whose seed is distributed by gravity and animals. The research reported here closely examines community composition change and structure in more detail, and is the first phase in determining the threshold time of conversion from an ecosystem dominated by oak and hickory over the past 4,000-5,000 years (Delcourt and Delcourt 1987, Franklin 1994) to one dominated by sugar maple, American beech, red maple, and other mesophytic species in this century.

The specific objectives of the present study were to do the following for each Ecological Land Type (ELT): (1) determine average composition, density, and basal area for seedling, sapling, and tree strata, and (2) examine forest structure by interfacing data from the seedling and sapling strata with data from several tree size-class strata. The baseline data from objectives (1) and (2), along with growth and mortality data, will be used to estimate the time of conversion. For increased reliability, we doubled the number of plots used by Fralish and McArdle (2009) to more fully document the extent of the successional process in each ELT, and identify any ELT whose community composition might skew or bias the results.

## STUDY AREA

The Illinois Ozark Hills is that portion (approximately 50,000 ha) of the extensive Ozark Plateaus physiographic region that extends into southwestern Illinois. Physiographic regions bordering the region include the sandstone Shawnee Hills on the east, the Mississippi River Alluvial Plain on the west and south, the Till Plain region on the north, and the Coastal Plain on the south/southeast. Schwegman (1973) identified the area as the Southern Section of the Ozark Division. The Illinois Ozark Hills generally outline the western-most section of the Shawnee National Forest. See Fralish and McArdle (2009) for map of area.

Bedrock is Devonian-age cherty limestone uplifted during the Pennsylvanian period. Where chert was exposed on ridgetops and steep slopes, splitting resulted in a subsequent accumulation of fragments on lower slopes and in ravines. Steep slopes and narrow deep valleys characterize the mature dendritic drainage pattern.

The area has been indirectly impacted by Pleistocene glaciation. When the glaciers melted, glacial debris was carried downstream and sorted; a silty flour was deposited in the Mississippi River Alluvial Plain. During dry winter periods for the past 11,000 years, westerly winds lifted particles of this alluvium out of the flood plain and deposited it on the uplands. Near the Mississippi River, these loess deposits are up to 10 m deep on the bluffs and adjacent ridges but as thin as a meter on steep side slopes. Deposit thickness decreases approximately eastward from the Mississippi River across Illinois to near the Ohio River (Fralish and others 2002).

A variety of Alfisols and Entisols occur within the study area. Stookey (fine-silty, mixed, mesic Typic Hapludalf) and Hosmer (fine-silty, mixed, mesic Fragic Hapludalf) types were developed in deep, non-cherty loess deposits of the upper slopes and ridgetops. Hosmer soil has a fragipan and a bisequm profile. Goss soil (clayey-skeletal, mixed, mesic Typic Paleudalf) and Baxter soil (fine, mixed, mesic Typic Paleudalf) are found in thin layers of loess, clay, chert, and limestone on steep mid- to lower slopes. Goss soil contains more chert and has a higher base saturation than Baxter. Elsah (loamy-skeletal mixed, nonacid, mesic Typic Udifluvents) and Wakeland soils (coarse-silty mixed, nonacid, mesic Typic Udifluvents) occur along stream terraces. Elsah soil contains coarse chert fragments in the control section while Wakeland soil is more poorly drained (Natural Resources Conservation Service 2005, 2007).

The oak-hickory forests of the area generally were established in the mid- to late 1800s and early 1900s, under a regime of relatively heavy disturbance (Fralish and McArdle 2009). The major disturbance that initiated the period was the 1810-11 earthquakes, measuring between 8.4 and 8.7 on the Richter scale (Atkinson 1989). It was the most significant seismic event to occur in the central United States in historic times (Street 1982). These earthquakes severely damaged the forests of the region (Fralish and McArdle 2009) just as settlers began moving into the region. With settlement came extensive cutting of healthy and damaged forests; building of roads, towns, and larger cities; grazing of forests, and development of industries. Moreover, these activities and clearing of land for farms and orchards resulted in many large, frequent, and severe wildfires (van de Gevel and Ruffner 2006) that continued into the early decades of the 1900s (Miller 1920, 1923).

## METHODS

### FIELD PROCEDURES

Data from two sets of plots were used in the study. One set of 42 plots was located within the relatively undisturbed 144-ha Ozark Hills Nature Preserve within Trail of Tears State Forest. Plots were randomly located on sites that had a uniform soil on a ground surface of uniform aspect and steepness. The forest community on an acceptable site was required to have a homogeneous mixture of species, be at least 80 years in age, and lack evidence of disturbance such as fire, cutting, or grazing. These stands appeared to be typical for the Ozark Hills forest ecosystem.

Plots were distributed to obtain data from within four distinct topographic units (south slope, broad ridgetop, north slope, and stream terrace). Following the productivity levels and site index differentials for various aspects (azimuths) reported by Beers and others (1966) and Lloyd and Lemmon (1970), we separated "north" and "south" slopes along a diagonal from southeast (135°) to northwest (315°). The broad ridgetop ELT was differentiated on the basis of the thick loess cap (5-10 m) compared to the thinner deposit of side slopes (1-3 m). It also is differentiated from the "knife edge" ridgetops that are common within the Ozark Hills. The terrace is an area of deposition while the other topographic units are erosional in nature. Terrace environmental conditions and vegetation also interface with bottomland areas.

In keeping with the National Ecological Classification System (U. S. Department of Agriculture 1993, Keys and others 1995) the four topographic units were considered ELTs as more than one site type (i.e., Ecological Land Type Phases [ELTPs]) were found in several units (Fralish and McArdle 2009).

A conduit pipe (permanent marker) was used as the center of three nested circular plots. On a 0.04-ha plot (radius = 11.28 m), trees (stems 9.0 cm and larger) were recorded by genus, species, and diameter at breast height (d.b.h.) to the nearest 0.1 cm. Nomenclature follows Fralish and Franklin (2002). Saplings (stems 1.0 - 8.99 cm d.b.h.) on a 0.012-ha plot (radius = 6.18 m) and seedlings (stems equal <1.0 cm d.b.h. but taller than 10 cm) on the 0.003-ha plot (radius = 3.09 m) were recorded by genus, species, and size class. Aspect in degrees azimuth, slope position, and percent slope were recorded for all plots.

Data also were collected from a set of 46 plots located at randomly selected section and quarter-section corners distributed throughout the region. Prior to field sampling and for each ELT, a pool of 15 potential sampling points (corners) was randomly identified from U.S. Geologic Survey 7.5-minute quadrangle maps. Out of this pool, 10-12 points were sampled. As each corner was visited, stand and site conditions were evaluated for sampling. If the conditions met the criteria established for the first set of plots sampled in the Nature Preserve, data were immediately collected using the same sampling procedures but with one variation. To avoid the possible influence of past disturbance directly at the corner, the center point for the nested sapling and seedling plots was moved in a randomly selected cardinal direction to the midpoint (5.64 m) between the tree plot center and perimeter.

## DATA SUMMARY AND ANALYSIS

Tree diameter was converted to tree basal area (BA) and BA summed by species for all plots within each ELT. These BA values were converted to BA/ha by multiplying by a conversion factor which varied with the number of plots: Basal Area x [10,000 $m^2$/(400 $m^2$ x number of plots)]. Tree densities were calculated in a similar manner. For each species, relative basal area (henceforth referred to as "Importance Value," $IV_{100}$) was calculated by dividing species BA for an ELT by the BA for all species in the ELT and multiplying by 100. These procedures follow Fralish and others (1991; 1993) and Fralish and McArdle (2009). Basal area alone was used as an IV because tree biomass, live sapwood, and leaf area are directly related to basal area (Rogers and Hinckley 1979, Fralish 1994).

Seedling and sapling stem counts were summed by species for all plots within an ELT. Species density (number/ha) was determined for each of the four ELTs by multiplying total stem count by a conversion factor which varied with the number and size of plots: stem count x [10,000 $m^2$/(plot size in $m^2$ x number of plots)]. Seedling and sapling relative densities (henceforth referred to as "Importance Value," $IV_{100}$) were calculated by dividing the density for a species in an ELT by the density for all species in the ELT and multiplying by 100.

Compositional stability of stands in different ELTs was evaluated by comparing a composition index (composition index [CI]; *sensu* Curtis 1959) value for each size class: CI = ∑(Species Adaptation Value x Species Importance Value). Adaptation Values were taken from Fralish (1988) and Fralish and others (1993). Shade-intolerant (early successional) species (for example, chestnut oak [*Q. prinus* L.], post oak [*Q. stellata* Wang.]) have low values (1-3), shade-intermediate species (for example, white oak [*Q. alba* L.], black oak [*Q. velutina* Lam.]) have values between 4 and 7, and shade-tolerant (late successional) species (for example, American beech and sugar maple) have high values (8-10). CI values ranged from 100 to 1000 and provided a means to compare strata within stands (trees vs. saplings vs. seedlings) and between stands (for example, trees vs. trees).

As an additional test of compositional stability, percent similarity (PERSIM) between overstory and understory strata was calculated: PERSIM = 2W/a+b where “a” is the sum of the values in the overstory, “b” is the sum of the values in the understory, and “W” is the sum of the lesser of the two values for species common to both strata. However, when relativized data ($IV_{100}$) are used, as in the present study, the equation reduces to “W”. Similarity values of 55-90 percent indicate relatively similar to strongly similar strata; 45-55 percent, marginally similar strata; and <45 percent, dissimilar strata (Fralish and others 1991, Fralish and McArdle 2009).

# RESULTS

## SOUTH SLOPE ELT

The tree stratum of the south slope ELT community was dominated by white oak (IV = 39.3) and black oak (IV = 23.5), with northern red oak (*Q. rubra* L.) and pignut/red hickory (*Carya glabra* [Mill.] Sweet-*Carya ovalis* [Wang.] Sargent) complex of secondary importance (IV range = 5.1-7.4) (Table 1). Two-thirds of the 20 overstory species on this ELT were oak and hickory species with a combined importance of 88.6 (oak IV = 75.5; hickory IV = 13.1). Collectively, the importance of early successional species (IV = 89.8) was substantially greater than the importance of late successional species (8.6). Only seven late successional mesophytic species appeared in the sample. The CI value of 593 is indicative of a forest overstory dominated by a variety of oak and hickory species whose AVs range from 3.2 to 6.5. Community mean basal area was 24.9 $m^2$/ha.

In contrast to the overstory, the dominant species in the sapling stratum were sugar maple (IV = 26.7), American beech (IV = 20.2), and red maple (IV = 17.2) (Table 2). Collective importance of late successional species was 71.1 and only 27.3 for early successional species. The combined importance of hickory species (total IV = 13.8) was greater than that of oak (9.5). The composition index of 889 indicated the high level of dominance by late successional species, which have AVs of 8-10. Sapling density was 980 stems/ha.

Similar to the sapling stratum, the seedling stratum also was strongly dominated by late successional species (collective IV = 61.8) but had a larger component of early successional species (Table 3). The most important species were red maple (IV = 17.4), American beech (IV = 14.6), black oak (IV = 16.6), sugar maple (IV = 8.8), white oak (IV = 7.6), and white ash (IV = 5.8). Twenty-five species were recorded. Density was 9,064 stems/ha and CI was 789.

**Table 1.—Tree species' adaptation and importance values in four Ecological Land Types of the Illinois Ozark Hills region. Species with importance values >5 are in bold format. Adaptation values are from Fralish (1988) and Fralish and others (1993). The letter W indicates the adaptation value for the mesic to hydric section of the moisture gradient. Species number in the north slope ELT based on 20 plots.**

| | | Ecological Land Type | | | |
|---|---|---|---|---|---|
| Species | Adaptation Value | South Slope | Broad Ridgetop | North Slope | Stream Terrace |
| **Early Successional Xeric and Xeric-Mesic Species** | | | | | |
| Chestnut Oak | 1.0 | 0.1 | 3.3 | | |
| Winged Elm | 2.1 | | 0.1 | | |
| Post Oak | 3.2 | 1.4 | 2.2 | | |
| Black Hickory | 3.5 | 0.4 | 0.8 | | |
| Scarlet Oak | 4.7 | 2.3 | 2.3 | 1.2 | |
| Southern Red Oak | 4.8 | 3.8 | | | |
| Black Oak | 5.0 | **23.5** | **27.3** | **10.8** | |
| Mockernut Hickory | 5.0 | 1.8 | 0.4 | 0.6 | 1.6 |
| White Oak | 5.4 | **39.3** | **30.5** | **15.8** | 2.9 |
| Chinkapin Oak | 6.5 | | | 0.5 | 1.5 |
| Shagbark Hickory | 6.5 | 3.1 | 1.3 | 2.2 | 0.1 |
| Pignut/Red Hickory | 6.5 | **7.4** | **11.1** | **7.2** | 1.0 |
| Northern Red Oak | 8.0 | **5.1** | **7.0** | **17.0** | **5.3** |
| Yellow-Poplar | 9.5 | 1.6 | **7.5** | **11.9** | **22.0** |
| SUBTOTAL | | 89.8 | 93.8 | 67.2 | 34.4 |
| **Late Successional Mesophytic Species** | | | | | |
| Blackgum | 7.2 | 1.9 | 0.2 | 1.1 | |
| White Ash | 8.7 | 1.6 | 2.2 | 2.3 | 0.9 |
| Hackberry | 8.8 | | | 0.3 | 1.8 |
| Black Cherry | 8.8 | | | 0.4 | 2.7 |
| Red Maple | 9.1 | 0.2 | 0.3 | 1.0 | |
| Cucumber-Tree | 9.5 | 0.2 | 0.6 | 2.7 | 0.4 |
| Bitternut Hickory | 9.5 | 0.4 | | 0.3 | **9.4** |
| Slippery Elm | 9.5 | 1.8 | | 2.3 | **8.2** |
| American Beech | 9.6 | 2.5 | | **14.7** | 0.4 |
| Sugar Maple | 10.0 | | 2.7 | **5.6** | **11.0** |
| Blue-Beech | 10.0 | | | | 0.7 |
| KY Coffee-Tree | 10.0 | | | | 1.0 |
| Black Walnut | 10.0 | | | 1.2 | 3.1 |
| SUBTOTAL | | 8.6 | 6.0 | 31.8 | 39.6 |
| **Early Successional Mesic-Hydric and Hydric Species** | | | | | |
| American Elm | 9.5W | | | 0.1 | 0.3 |
| Boxelder | 7.0W | | | | 3.9 |
| Swamp Chestnut Oak | 6.0W | | | | 2.0 |
| Sweetgum | 4.0W | 1.6 | 0.2 | 0.8 | **6.9** |
| Eastern Sycamore | 5.0W | | | | **12.9** |
| SUBTOTAL | | 1.6 | 0.2 | 0.9 | 26.0 |
| TOTAL | | 100.0 | 100.0 | 100.0 | 100.0 |
| Number of Plots | | 20 | 20 | 28 | 20 |
| No. of Species | | 18 | 19 | 20 | 22 |
| Basal Area ($m^2$/ha) | | 24.9 | 21.7 | 27.1 | 27.2 |
| Density (Stems/ha) | | 403 | 380 | 239 | 392 |
| Composition Index | | 593 | 593 | 774 | 747 |

**Table 2.—Species' importance values for saplings in the communities of four Ecological Land Types in the Illinois Ozark Hills region. Species with importance values >5 are in bold format. Adaptation values are from Fralish (1988) and Fralish and others (1993). The letter W indicates the adaptation value for the mesic to hydric section of the moisture gradient. Number of species in the north slope ELT based on 20 plots.**

| | | Ecological Land Type | | | |
|---|---|---|---|---|---|
| Species | Adaptation Value | South Slope | Broad Ridgetop | North Slope | Stream Terrace |
| **Early Successional Xeric and Xeric-Mesic Species** | | | | | |
| Chestnut Oak | 1.0 | 2.0 | 0.5 | | |
| Persimmon | 1.5 | 0.7 | 0.5 | | |
| Winger Elm | 2.1 | 3.3 | 2.5 | | |
| Post Oak | 3.2 | 2.3 | | | |
| Black Oak | 5.0 | 2.1 | 1.0 | | |
| Chinkapin Oak | 6.0 | | | | 1.8 |
| White Oak | 5.4 | 3.1 | 3.5 | 1.2 | 0.9 |
| Pignut/Red Hickory | 6.5 | **8.0** | **10.9** | 2.3 | |
| Shagbark Hickory | 6.5 | **5.8** | 1.0 | 0.8 | |
| SUBTOTAL | | 27.3 | 19.9 | 4.3 | 2.7 |
| **Late Successional Mesophytic Species** | | | | | |
| Blackgum | 7.2 | 1.6 | 1.0 | 1.6 | 8.1 |
| White Ash | 8.7 | 0.8 | 2.0 | 1.2 | 0.9 |
| Black Cherry | 8.8 | | 1.0 | | |
| Red Maple | 9.1 | **17.2** | **6.4** | **9.0** | |
| Cucumber-Tree | 9.5 | | | | 0.9 |
| Slippery Elm | 9.5 | 0.9 | | 0.8 | **9.0** |
| Bitternut Hickory | 9.5 | 2.9 | 1.5 | 1.2 | **6.3** |
| American Beech | 9.6 | **20.2** | **22.2** | **29.9** | **11.7** |
| Sugar Maple | 10.0 | **26.7** | **46.0** | **46.5** | **28.9** |
| Ohio Buckeye | 10.0 | | | | 1.8 |
| Blue-Beech | 10.0 | 0.8 | | 0.4 | **28.8** |
| SUBTOTAL | | 71.1 | 80.1 | 90.6 | 96.4 |
| **Early Successional Mesic-Hydric and Hydric Species** | | | | | |
| American Elm | 9.5W | 1.6 | | 4.7 | |
| Sweetgum | 4.0W | | | 0.4 | 0.9 |
| SUBTOTAL | | 1.6 | 0.0 | 5.1 | 0.9 |
| TOTAL | | 100.0 | 100.0 | 100.0 | 100.0 |
| Number of Plots | | 20 | 20 | 27 | 20 |
| No. Species | | 16 | 15 | 11 | 12 |
| Density (Stems/ha) | | 980 | 779 | 973 | 580 |
| Composition Index | | 889 | 852 | 958 | 948 |

**Table 3.—Species' adaptation and importance values for seedlings in the communities of four Ecological Land Types of the Illinois Ozark Hills region. Species in each group are listed from lowest to highest adaptation value (AV). Adaptation values are from Fralish (1988) for the Shawnee Hills, IL, and Fralish and others (1993) for Land Between the Lakes, KY and TN. Importance values greater than 5 percent in bold. The letter W indicates the adaptation value for the mesic to hydric section of the moisture gradient. Species number for north slope ELT based on 20 plots.**

| | | Ecological Land Type | | | |
|---|---|---|---|---|---|
| Species | Adaptation Value | South Slope | Broad Ridgetop | North Slope | Stream Terrace |
| **Early Successional Xeric and Xeric-Mesic Species** | | | | | |
| Chestnut Oak | 1.0 | | 1.7 | | |
| Persimmon | 1.5 | 1.6 | 2.2 | 0.7 | 0.6 |
| Winged Elm | 2.1 | 1.2 | 0.7 | | 0.4 |
| Post Oak | 3.2 | 0.6 | | | |
| Scarlet Oak | 4.7 | 0.2 | 0.2 | | |
| Black Oak | 5.0 | **16.6** | **13.9** | 1.5 | 0.6 |
| Mockernut Hickory | 5.0 | | 0.5 | | |
| White Oak | 5.4 | **7.6** | **6.2** | **5.7** | 0.6 |
| Chinkapin Oak | 6.5 | 0.4 | 0.2 | 0.4 | 2.7 |
| Shagbark Hickory | 6.5 | 3.5 | **6.0** | 1.3 | |
| Pignut/Red Hickory | 6.5 | 1.8 | 3.3 | 1.9 | |
| Northern Red Oak | 8.0 | 2.9 | 1.9 | **5.0** | 1.2 |
| Yellow-Poplar | 9.5 | 0.6 | 1.4 | **7.0** | 0.6 |
| SUBTOTAL | | 37.0 | 38.2 | 23.5 | 6.7 |
| **Late Successional Mesophytic Species** | | | | | |
| Blackgum | 7.2 | 1.6 | 2.9 | 2.2 | 0.4 |
| White Ash | 8.7 | **5.8** | **9.8** | **9.6** | **11.2** |
| Hackberry | 8.8 | 0.2 | | | 0.2 |
| Black Cherry | 8.8 | 1.2 | **5.0** | 0.6 | **5.6** |
| Red Maple | 9.1 | **17.7** | **17.0** | **12.0** | |
| Cucumber-Tree | 9.5 | 0.2 | | 1.3 | 0.2 |
| Bitternut Hickory | 9.5 | 2.9 | 2.4 | 4.8 | **11.1** |
| Slippery Elm | 9.5 | **7.3** | 3.6 | 4.3 | **40.1** |
| American Beech | 9.6 | **14.6** | **14.6** | **21.7** | **6.6** |
| Sugar Maple | 10.0 | **8.6** | **6.5** | **16.3** | **5.8** |
| Black Walnut | 10.0 | | | 0.2 | 0.2 |
| Butternut | | | | 0.2 | 1.9 |
| Blue-Beech | 10.0 | 1.9 | | 0.7 | 1.3 |
| American Basswood | 10.0 | | | 0.4 | |
| SUBTOTAL | | 62.0 | 61.8 | 74.3 | 84.6 |
| **Early Successional Mesic-Hydric and Hydric Species** | | | | | |
| American Elm | 9.5W | | | 2.0 | **5.8** |
| Boxelder | 7.0W | | | | 1.9 |
| Swamp Chestnut Oak | 6.0W | | | | 0.4 |
| Shellbark Hickory | 5.5W | 1.0 | | | 0.2 |
| Sweetgum | 3.0W | | | 0.2 | 0.4 |
| SUBTOTAL | | 1.0 | | 2.2 | 8.7 |
| TOTAL | | 100.0 | 100.0 | 100.0 | 100.0 |
| Number of Plots | | 20 | 20 | 28 | 20 |
| No. of Species | | 18 | 19 | 20 | 22 |
| Basal Area ($m^2$/ha) | | 24.9 | 21.7 | 27.1 | 27.2 |
| Density (Stems/ha) | | 403 | 380 | 239 | 392 |
| Composition Index | | 593 | 593 | 774 | 747 |

An average community structure graph shows the extent of mesophyte invasion into oak-hickory dominated forest (Fig. 1A). The cohort invasion appears more as a wave pattern rather than continuous input. The graph shows that in general there is little similarity between the sapling and tree strata, and particularly with the 60+ cm tree size class.

## BROAD RIDGETOP ELT

The ridgetop ELT overstory was strongly dominated by early successional species (combined IV = 93.8). The most important species were white oak (IV = 30.5) and black oak (IV = 27.3), followed by pignut/red hickory (IV = 11.1), yellow-poplar (*Liriodendron tulipifera* L.) (IV = 7.5), and northern red oak (IV = 7.0) (Table 1). Oak and hickory species had a combined importance of 86.2 (oak IV = 72.6; hickory IV = 13.6). The five mesophytic species had a combined importance of only 6.0. The CI value of 593 was identical to that of the south slope ELT. Community mean basal area was 21.7 $m^2$/ha, somewhat higher than the basal area for the south slope ELT.

The sapling stratum was dominated by mesophytic species. Sugar maple was the major species (IV = 46.0), along with American beech (IV = 22.2) (Table 2). The strong dominance by sugar maple and beech is reflected in the CI value of 852. Oak species had a combined IV of only 5.0 and hickory an IV of 11.9. Early successional species formed only 21.4 percent of the community. Only 14 species were present.

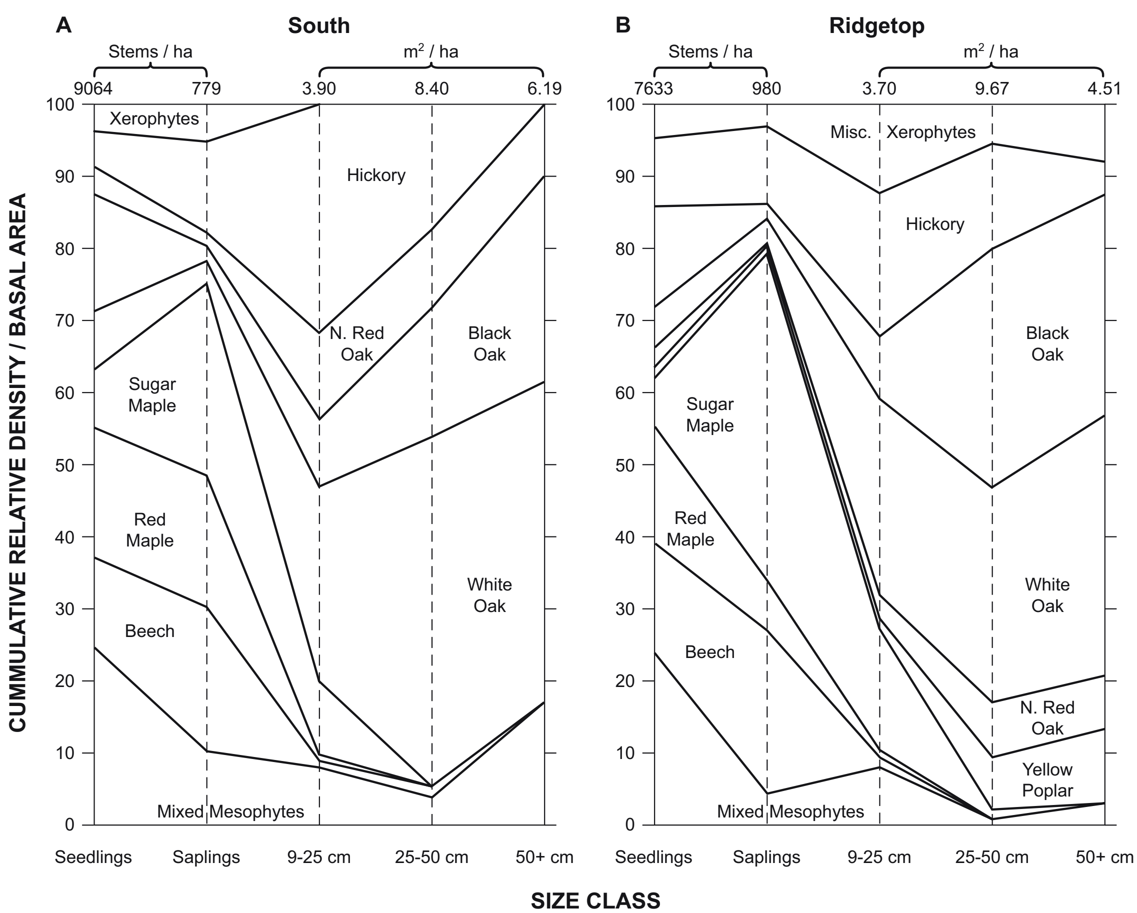


Figure 1.—Forest community structure diagrams for the south slope and ridgetop Ecological Land Types.

As in the south slope ELT, red maple was the leading dominant (IV = 17.0) in the seedling stratum, followed closely by American beech (IV = 14.6), black oak (IV = 13.9), and white ash (*Fraxinus americana* L.) (IV = 9.8) (Table 3). Importance values for shagbark hickory (*Carya ovata* [Mill.] K. Koch), sugar maple, and black cherry (*Prunus serotina* Ehrh.) ranged between 5.0 and 6.5.

Compared to the sapling stratum, the stronger importance of oak and hickory species and a reduced importance of sugar maple resulted in a lower CI (722). The number of species (21) was greater than in the tree and sapling strata primarily because of the increased number of oak and hickory species. Density was 7,633 stems/ha. The general structure of the ridgetop ELT community (Fig. 1B) is similar to that of the south slope ELT community.

## NORTH SLOPE ELT

The tree stratum of the north slope community was dominated by a mixture of species, including northern red oak (IV = 17.0), white oak (IV = 15.8), American beech (IV = 14.7), yellow-poplar (IV = 11.9), black oak (IV = 10.8), and sugar maple (IV = 5.6) (Table 1). Compared with the community on south and ridgetop ELTs, dominance shifted to a more equitable balance among species. However, oak dominated the community with a combined IV of 45.3. Three hickory species had a total IV of 10.3 for a total oak and hickory importance of 55.6. Thirteen mesophytic species were present. The CI (774) indicates the presence of a combined component of early and late successional species (IVs = 7.1-10).

The sapling stratum had a larger mesophytic component and less equitability than the mixed overstory canopy. Sugar maple (IV = 46.5), beech (IV = 29.9), and red maple (IV = 9.0) had a combined importance of 90.6 (Table 2). Oak and hickory had a combined IV of only 4.3, the total importance for early successional species. The CI of 958 (maximum 1,000) reflects the composition of nearly pure late successional species.

Compared to the sapling stratum, the seedling layer was somewhat less strongly dominated by mesophytic species (CI = 892) but had a greater equitability among four species: American beech (IV = 20.8), sugar maple (IV = 17.3), red maple (IVN=12.0), and white ash (IV = 9.7) (Table 3). The combined IV of early successional species is only 23.5 while that of late successional species is 74.3.

Compared to the south slope or ridgetop ELT communities, the general structure of the north slope ELT community (Fig. 2A) reflected a more rapid invasion by mesophytes. Both sugar maple and beech have a strong wave-form invasion pattern although the two patterns are not synchronized.

## STREAM TERRACE ELT

A mixture of upland early and late sucessional species and bottomland species dominated the stream terrace ELT community in approximately equal numbers (combined IV = 34.4, 39.9, and 25.7, respectively) (Table 1). Oak and hickory had a collective IV of 18.5. Yellow-poplar was the only single major early successional species (IV = 22.0), and it is considered more of a mesophyte than a species of dry sites (Beck 1990). Dominance by the late successional species was nearly equal among sugar maple (IV = 11.0), bitternut hickory (*C. cordiformis* [Wangenh.] K. Koch) (IV = 9.4), and slippery elm (*Ulmus rubra* Muhl.) (IV = 8.2). Sycamore (*Platanus occidentalis* L.) (IV = 12.9) and sweetgum (*Liquidambar styraciflua* L.) (IV = 6.9) are bottomland species that commonly invade mesic sites after disturbance. Compared to upland sites, this community had the highest basal area (27.2 m/ha), with a CI value of 747, reflecting the mixture of early

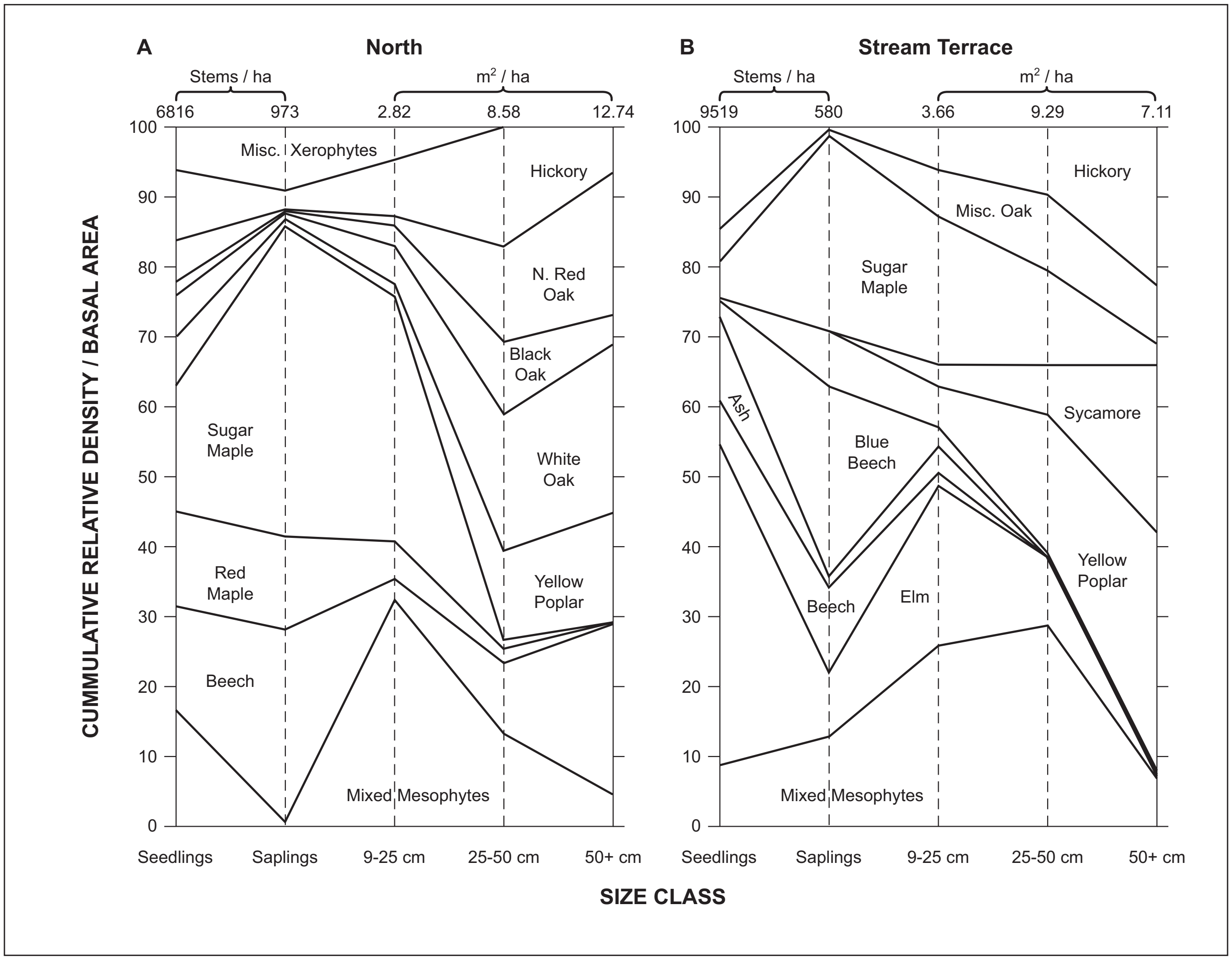


Figure 2.—Forest community structure diagrams for the north slope and stream terrace Ecological Land Types.

and late successional species and bottomland species. Species richness was 22, of which about 75 percent was mesophytic species and 25 percent was oak and hickory species.

The sapling stratum was dominated equally by two mesophytes—sugar maple (IV = 28.9) and blue-beech (*Carpinus caroliniana* Walt.) (IV = 28.8)—but American beech (IV = 11.7) and slippery elm (IV = 9.0) also were important (Table 2). However, blue-beech does not have the genetic potential to grow into the large-size tree classes (30+ cm d.b.h.). Excluding blue-beech from the potential overstory canopy, the IVs of the major mesophytes were sugar maple, 40.4; American beech, 16.2; blackgum, 11.1; slippery elm, 9.9; and yellow-poplar, 8.7. Collectively, the combined importance of mesophytes in the sapling stratum was more than 90.5 percent. When yellow-poplar is included as a cross-over mesophyte (it is also early successional), the IV is 96.4.

Species composition of the seedling stratum was distinctly different from that of the tree and sapling strata. Seedlings were dominated by slippery elm (IV = 40.1), with white ash (IV = 11.2) and bitternut hickory (IV = 11.1) as secondary species (Table 3). The importance of maple and American beech was relatively low (IV = 5.8 and 6.6, respectively). Composition index was high (846) although sugar maple and beech did not have high importance values.

Structurally, sugar maple and other mesophytes have already progressed well into the tree canopy, with diameters of a few trees exceeding 50 cm (Fig. 2B). Sugar maple, slippery elm, and other mesophytes are also invading in wave-form patterns that are not synchronized.

### COMMUNITY AND STRATA SIMILARITY

The three upland ELTs (south slope, ridgetop, and north slope) are relatively similar in composition and structure. The tree strata of the south slope and ridgetop communities were most similar in composition (PERSIM = 76.5 percent) although there also was high similarity between the ridgetop and north slope (PERSIM = 69.3 percent). The south slope and north slope tree strata were marginally similar (PERSIM = 53.0 percent). For these upland ELTs, the sapling strata also are similar to each other (PERSIM = 66.6-75.9 percent), as are the seedling strata (PERSIM = 64.1-79.4 percent).

In contrast, there is little similarity between the tree overstory and the understory for the upland ELTs. Percent similarity between the tree and sapling strata for these three ELTs ranged from 25.1 to 30.4 and between the tree and seedling strata from 35.4 to 44.9. Similarity between the tree and seedling strata was greater than between the tree and sapling strata because of seedlings (established and ephemeral) of early successional species. Here "ephemeral" refers to seedlings produced from recently germinated seed; most of these seedlings are not likely to live more than a few months or a year.

Similarity values between the seedling and sapling strata were not consistent. The composition of these strata was similar for the south slope ELT (PERSIM = 72.2) and the north slope ELT (PERSIM = 58.4), but was dissimilar for the ridgetop (PERSIM = 42.4). The dissimilarity between the strata for the ridgetop is primarily attributed to the high importance of sugar maple in the sapling stratum compared to its low importance in the seedling stratum.

The composition of the stream terrace tree canopy was extremely dissimilar (PERSIM = 11.6-25.2 percent) from the canopies of the other ELTs. Similarly, the stream terrace sapling stratum and seedling stratum are relatively dissimilar from their counterparts on the upland ELTs (PERSIM = 44.9-46.4 percent and 37.2-38.8 percent, respectively). The sapling and seedling strata of the stream terrace also are dissimilar (PERSIM = 27.6 percent). This low similarity is attributed to the wide difference in IVs for slippery elm and blue-beech (Table 3).

## DISCUSSION

In the early 1930s, large areas of land in the Ozark Hills were abandoned and subsequently purchased by the U.S. Department of Agriculture, Forest Service (Shawnee National Forest) and the State of Illinois (Trail of Tears State Forest). Since that time and with the establishment of homes in the region, fire is no longer a factor influencing forest community composition. Timber harvesting also has been minimal and generally absent on public land for the past 30+ years. The result is that in the absence of disturbances, major composition changes are occurring within this regional forest (Osier and others 2006, van de Gevel and Ruffner 2006, Fralish and McArdle 2009).

Data from plots concentrated within the 144-ha Ozark Hills Nature Preserve and from plots systematically located on section and quarter-section corners distributed throughout the region leave little doubt that succession—that is, the replacement of overstory oak and hickory by mesophytic species—is rapidly occurring

(Helmig 1997). In related studies in the Ozark Hills, Groninger and others (2002) and Osier and others (2006) reported a substantial change from an oak-dominated forest toward a maple-dominated forest based on data from plots established in 1980 and remeasured in 2000. Nearby, Weaver and Ashby (1971) and Shotola and others (1992) found a similar pattern over a 36-year period in Weaver's Woods.

The analysis of forest community data by size class strata (Figs. 1 and 2) outlines the present similar encroachment pattern in the upland ELT communities, which would be expected to continue over time (structure-for-time analysis) and in the absence of active forest management or a major disturbance. The forest overstory on south, ridgetop, and north slopes is presently dominated by oak and hickory (CI = 593-774) while dominance is about equally shared with mesophytic species on the stream terrace. Composition index values from near 800 to more than 950 in both the sapling and seedling strata indicate the strong dominance by mesophytic species that ultimately will be the next forest as the overstory trees die or are cut.

## MOISTURE-ELT COMMUNITY RELATIONSHIPS

An implied soil moisture-evapotranspiration gradient is expressed by the sequence of ELTs from the mesic south slope and ridgetop ELTs to the relatively more mesic north slope and strongly mesic stream terrace ELTs. Fralish and McArdle (2009) split out a southwest ELT, but there was no observable difference in composition between it and the south ELT. However, the basal area of the southwest slope community was the lowest for all ELT communities, suggesting the southwest slope may be somewhat less productive.

In the Ozark Hills, the south slope ELT often is relatively steep (30-60 percent), with only 100-200 cm of soil depth although the soil often is deeper. The south slope and ridgetop ELTs receive the full impact of the growing season sun and rapidly lose soil moisture. The ridgetop ELT may have up to a 10-m loess deposit for buffering this loss, but frequently a fragipan at a depth of 60-70 cm limits tree root penetration. Because of the angle of incoming solar radiation, the north ELT has a reduced solar radiation load compared to the south slope, and often experiences topographic shading during early and late daylight hours. Stream terraces often have deep soil; receive runoff from adjacent slopes; and are shaded for various parts of the day, making them moist and relatively cool.

The importance of early successional species in the tree stratum generally follows the moisture-ELT gradient. The importance of early successional species decreases from an IV of 89.8 and 93.8 on the south slope and ridgetop, respectively, to 67.2 on the north slope and 34.4 on the terrace. The heavy disturbance by wildfire and timber harvesting during the mid- to late 1800s and early 1900s generally opened sites for establishment of the oak-hickory community across the gradient (Fralish and McArdle 2009).

The pattern for late successional species' importance is the reverse of that for early successional species. On the drier south and ridgetop ELTs, late successional tree species have been slow to invade or survive and thus have low importance (IV = 8.6 and 6.0, respectively) (Table 2). The heavy disturbance, probably combined with high soil surface temperatures, apparently had a substantial impact on mesophytic species. On the cool, moist north and alluvial ELTs, IVs for mesophytes increase to 31.9 and 39.9, respectively. On mesic sites, survival rates apparently have been higher and invasion more rapid. The result of these two reverse patterns for early and late successional species is that overstory CI increases from 593 on the south slope to 747 on the terrace ELT.

Community basal area also is related to ELT environment, with moderate values on the more xeric ELTs (24.9 and 21.7 $m^2$/ha) and higher values on the moist ELTs (27.1 and 27.2 $m^2$/ha). Because of the deep, moist soil and/or low evapotranspiration on cool slopes, the basal area is likely to increase to as high as 35 $m^2$/ha, a level similar to that reported for several stands on mesic sites in the Shawnee Hills (Fralish 1976, 1988, 1994; Fralish and others 1991) and for the central states in general (Held and Winstead 1975). For permanent plots on a mesic site in the Kaskaskia Experimental Forest of southern Illinois, basal area increased from 19.8 $m^2$/ha in 1935 to 31.1 $m^2$/ha in 1973 (Schlesinger 1976) to 32.0 $m^2$/ha in 1978; by 1983, the basal area decreased slightly to 30.2 $m^2$/ha as several large oak trees died (Fralish 1988). In 1997, basal area was 34.3 $m^2$/ha (Zaczek and others 2002). However, basal area is likely to continue to increase somewhat as the stand is becoming progressively dominated by sugar maple.

In the tree stratum, species richness generally increases across the sequence of sites from south slopes and ridgetops to mesic north slopes and terraces. This pattern can be attributed to various combinations of early and late successional and bottomland species. No similar patterns exist for either the sapling or seedling strata. Vertically, however, there is a distinct pattern of species richness. Lowest species richness is found in the sapling stratum (11-16 species), with the highest richness in the seedling stratum (21-25 species) and intermediate values in the tree stratum (18-23 species). A number of species in the tree stratum (scarlet oak [*Q. coccinea* Muenchh.], southern red oak [*Q. falcate* Michx.], northern red oak, black hickory [*Carya texana* Buck.], and mockernut hickory [*Carya tomentosa* (Poir.) Nutt.]) are not found in the sapling layer but reappear here in small numbers in the seedling stratum along with stems of nearly all mesophytic species. The large species number in the seedling stratum results from a combination of older established seedlings and a continuous influx of recently established seedlings of shade-intolerant and -intermediate tree species that are likely to live only a short while (ephemerals). The tree stratum probably was initiated under relatively open (moderately disturbed) conditions, which allowed a large number of species to survive and grow to become trees. The saplings developed under the present forest overstory and with sufficient stress to reduce the number of species.

## DISTURBANCE EFFECTS

Oak and hickory have dominated the Central States forest for about the past five centuries (Delcourt and Delcourt 1987, Franklin 1994). Given the deep soil, high water availability, lack of disturbance, and a long time period, the entire Ozark Hills forest will eventually be dominated by mesophytes to the near-exclusion of early successional species. Ecologists believe that fire and fire interacting with microclimate and topography were the factors that allowed forest stands to be dominated by oak and hickory and prevented domination of the overstory canopy by sugar maple, red maple, and beech. Thus, we agree with Van Lear (1988), Abrams (1992), Olson (1996), Ruffner and Groninger (2004), and Nowacki and Abrams (2008) that fire was a major factor in the development of early and present oak-hickory communities.

Forests protected from disturbances such as fire, grazing, and logging will change over time as a result of small-scale disturbances, such as the death of dominant or codominant trees, which create canopy gaps. Sugar maple is an extremely competitive species in the gap-phase replacement process, as demonstrated in various studies (Parker and others 1985, Parker and Sherwood 1986, Ward and Parker 1987, Parker and Ward 1987, McCarthy and others 1987, McCarthy and Wistendal 1988, Spetich and Parker 1998). Edgington (1991) came to a similar conclusion and Lin and Augsburger (2008) found a population explosion of sugar maple in Brownfield Woods (Illinois), where permanent plots were established in 1925 (Telford 1926). Shade-tolerant species such as sugar maple and beech can withstand long periods of suppression in the understory (Burns and Honkala 1990, Cho and Boerner 1991). Abrams and Downs (1990) studied the successional change of an old-growth white oak forest in Pennsylvania and reported that logging operations during the 1930s and 1940s released understory mesophytic species.

## CONCLUSIONS AND RECOMMENDATIONS

In the absence of disturbance, the forest communities of the Illinois Ozark Hills ultimately will be dominated by mesophytic species. However, with the well developed midcanopy of mesophytic species, any disturbance that creates gaps in the overstory is likely to accelerate the successional process. The recent severe windstorm (derecho of 8 May 2009) with maximum wind velocity in excess of 100 mph is an example of such a disturbance. Many large overstory trees were blown over in the northern section of the Ozark Hills. The development of the forest in these patches should be monitored.

Conversion is likely to be a long, continuous process as the mesophytic component of the oak-hickory forest is still developing. However, it should be of interest to resource managers and scientists to have an estimate of the threshold time of conversion. In a preliminary analysis, Helmig (1997) used stand table projection and basal area values for early and late successional species. The analysis indicated that the time of conversion may be between 2040 and 2050, but additional analysis is necessary.

From now until the basal area (biomass) of mesophytic species equals and exceeds that of oak and hickory, there will be important changes in the forest ecosystem. More than 45 years ago, Voigt and Mohlenbrock (1964) strongly suggested that the tree and floristic diversity of the Illinois Ozark Hills was comparable to that of the Great Smoky Mountains. An important question is what effect succession and conversion will have on maintaining an ecosystem of exceptional biodiversity. Fralish (1997, 2004) and Fralish and McArdle (2009) have expressed major concern regarding the loss of herbaceous species resulting from a multi-layered overstory, increased leaf area, low light levels at the forest floor, and a deeper litter layer. It is our opinion that the successional process for the entire region has advanced beyond control; moderate fire and physical removal of larger trees of mesophytic species would be required to regenerate oak. In view of the situation, changes in tree, shrub, and herbaceous species and density should be carefully monitored in the Illinois Ozark Hills, which we maintain probably will be the first large-scale oak-hickory ecosystem to convert to one dominated by maple and beech.

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## LITERATURE CITED


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

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

Atkinson, W. 1989. **The next New Madrid earthquake.** Carbondale, IL: Southern Illinois University Press. 224 p.

Baker, J.B.; Langdon, O.G. 1990. ***Pinus taeda* L., loblolly pine.** In Burns, R.M.; Honkala, B.H., tech. coord. Silvics of North America. Agric. Handbk. No. 465. Volume 2: Conifers. Washington, DC: U.S. Department of Agriculture, Forest Service: 497-512.

Beck, D.E. 1990. ***Liriodendron tulipifera* L., yellow-poplar.** In Burns, R.M.; Honkala, B.H., tech. coord. Silvics of North America. Agric. Handbk No. 465. Volume 1: Hardwoods. Washington, DC: U.S. Department of Agriculture, Forest Service: 406-416.

Beers, T.W.; Dress, P.E.; Wensel, L.C. 1966. **Aspect transformation in site productivity research.** Journal of Forestry. 64: 691-92.

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.

Curtis, J.T. 1959. **The vegetation of Wisconsin: an ordination of plant communities.** Madison, WI: The University of Wisconsin Press. 657 p.

Delcourt, H.R.; Delcourt, P.A. 1987. **Pre-Columbian Native American use of fire on southern Appalachian landscapes.** Conservation Biology. 11: 1010-1014.

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

Fralish, J.S. 1976. **Forest site-community relationships in the Shawnee Hills region, southern Illinois.** In: Fralish J.S.; Weaver, G.T.; Schlesinger, R.C., eds. Proceedings 1st central hardwood forest conference. Carbondale, IL: Department of Forestry, Southern Illinois University: 76-87.

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.** In: Schwartz, M.W., ed. Conservation in highly fragmented landscapes. New York, NY: Chapman & Hall: 234-266.

Fralish, J.S. 2004. **The keystone role of oak and hickory in the Central Hardwood Forest.** In: Spetich, M.A., ed. Proceedings: Upland oak ecology symposium: history, currents conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: U. S. Department of Agriculture, Forest Service. Southern Research Station: 78-87.

Fralish, J.S.; Franklin, S.B. 2002. **Taxonomy and ecology of woody plants in North American forests.** New York, NY: John Wiley & Sons. 612 p.

Fralish, J.S.; McArdle, T.G. 2009. **Forest dynamics across three century-length disturbance regimes in the Illinois Ozark Hills.** American Midland Naturalist. 162: 418-449.

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

Fralish, J.S.; Franklin, S.B.; Robertson, P.A.; Kettler, S.M.; Crooks, F.B. 1993. **An ordination of compositionally stable 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.

Fralish, J.S.; Carver, A.D.; Anderson, R.C.; Thurau, R.G.; Sauer, S.L.; Ruffner, C.M.; Close, D.D.; Swigart, R.; White, E.M. 2002. **Presettlement, present, and projected forest communities of the Shawnee National Forest, Illinois.** Report prepared for the U.S. Department of Agriculture, Forest Service. Carbondale, IL: Department of Forestry, Southern Illinois University. 145 p.

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.; Ketter, S.M. 1993. **Overstory vegetation and successional trends of Land Between The Lakes, USA.** Journal of Vegetation Science. 4: 509-520.

Groninger, J.W.; Ozier, T.B.; Ruffner, C.M. 2002. **Stand compositional dynamics in mature Illinois Ozarks forest: Implications for management.** In: Van Sambeek, J.W.; Dawson; J.O.; Ponder, F., Jr.; Loewenstein, E.F.; Fralish, J.S., eds. Proceedings, 13th central hardwood forest conference. Gen. Tech. Rep. NC-234. St. Paul, MN: U.S. Department of Agriculture, Forest Service. North Central Research Station: 296-302.

Held, M.E.; Winstead, J.E. 1975. **Basal area and climax status in mesic forest ecosystems.** Annals of Botany. 39: 1147-1148.

Helmig, L.M. 1997. **Predicting the threshold time of conversion from *Quercus-Carya* to *Acer-Fagus* forest in the Illinois Ozark Hills.** Carbondale, IL: Department of Forestry, Southern Illinois University. 84 p. Master of Science thesis.

Keys, J.E., Jr.; Carpenter, C.A.; Hooks, S.L.; Koening F.G.; McNab, W.H.; Russell, W.E.; Smith, M-L. 1995. **Ecological units of eastern United States-first approximation.** Map and booklet. Atlanta, GA: U.S. Department of Agriculture, Forest Service.

Lawson, E.R. 1990. ***Pinus echinata* Mill., shortleaf pine.** In: Burns, R.M.; Honkala, B.H., tech. coord. Silvics of North America. Agric. Handbk No. 465. Volume 2: Conifers. Washington, DC: U.S. Department of Agriculture, Forest Service: 316-326.

Lin, Y.; Augsburger, C.K. 2008. **Long term spatial dynamics of *Acer saccharum* during a population explosion in an old-growth remnant forest in Illinois.** Forest Ecology and Management. 256: 922-928.

Lloyd, W.J.; Lemmon, P.E. 1970. **Rectifying azimuth (of aspect) in studies of soil-site relationships.** In: Youngberg, C.T.; Davey, C.B., eds. Proceedings, Third North American forest soils conference. 1968 August; Raleigh, NC: North Carolina State University. Corvallis, OR: Oregon State University: 435-448.

McCarthy, B.C.; Wistendahl, W.A. 1988. **Hickory (*Carya* spp.) distribution and replacement in a second-growth oak hickory forest of southeastern Ohio.** American Midland Naturalist. 119: 156-64.

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.

Miller, R.B. 1920. **Fire prevention in Illinois Forests.** Forestry Circular No. 2. Urbana, IL: Illinois Natural History Survey. 13 p.

Miller, R.B. 1923. **First report on a forestry survey of Illinois.** Bulletin XIV. Urbana, IL: Illinois natural history survey. 377 p. + illustrations and map.

Natural Resources Conservation Service. 2005. **Soil survey of Union County, Illinois.** Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service.

Natural Resources Conservation Service. 2007. **Soil survey of Alexander County, Illinois.** Washington, DC: U.S. Department of Agriculture, Natural Resources Conservation Service.

Nowacki, G.J.; Abrams M.D. 2008. **The demise of fire and "mesophication" of forests in the eastern United States.** BioScience. 58: 123138.

Olson, S.D. 1996. **The historical occurrence of fire in the Central Hardwoods, with emphasis on southcentral Indiana.** Indiana Natural Areas Journal. 16: 249-256.

Osier, T.B.; Groninger, J.W.; Ruffner, C.M. 2006. **Community composition and structural changes in a managed Illinois Ozark Hills forest.** American Midland Naturalist. 155: 253-269.

Parker, G.R.; Ward, J.S. 1987. **Woody vegetation of Davis-Purdue research forest.** Indiana Academy of Science. 97: 263-268.

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

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.

Rogers, R.; Hinckley, T.M. 1979. **Foliar weight and area related to current sapwood area in oak.** Forest Science. 25: 298-303.

Ruffner, C.M.; Groninger, J.W. 2004. **Oak ecosystem restoration and maintenance in southern Illinois.** In: Spetich, M.A., ed. Upland oak symposium: history, current conditions, and sustainability. Gen. Tech. Rep. SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 177-181.

Schwegman, J.E. 1973. **Natural divisions of Illinois.** Rockford, IL: Illinois Nature Preserves Commission.

Schlesinger, R.C. 1976. **Hard maples increasing in an upland hardwood stand.** In: Fralish, J.S.; Weaver, G.T.; Schlesinger, R.C., eds. Proceedings, 1st central hardwood forest conference. Carbondale, IL: Southern Illinois University, Department of Forestry: 175-185.

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.** American Midland Naturalist. 127: 125-38.

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

Street, R. 1982. **A contribution to the documentation of the 1811-12 Mississippi valley earthquake sequence.** Earthquake Notes 53.

Telford, C.J. 1926. **Brownfield Woods: a remnant of the original Illinois forest.** Urbana, IL: Illinois Natural History Survey. Bulletin XVI.

U.S. Department of Agriculture. 1993. **National hierarchical framework of ecological units.** Unpublished Report. ECOMAP. Washington, DC: Forest Service.

van de Gevel, S.L.; Ruffner, C.M. 2006. **Land-use history and resulting forest succession in the Illinois Ozark Hills.** In: Buckley, D.S.; Clatterbuck, W.K., eds. Proceedings, 15th central hardwood forest conference. Gen. Tech. Rep. SRS 101. Asheville, NC: U.S. Department of Agriculture, Forest Service: 719-726.

Van Lear, D.H. 1988. **Fire and oak regeneration in the southern Appalachians.** In: Nodvin, S.C.; Waldrop T.A., eds. Fire and the environment: ecological and cultural perspectives. Asheville, NC: U.S. Department of Agriculture, Forest Service: 15-21.

Voigt, J.W.; Mohlenbrock, R.H. 1964. **Plant communities of southern Illinois.** Carbondale, IL: Southern Illinois University Press. 202 p.

Ward, J.S.; Parker, G.R. 1987. **Fifty-five years of association and diversity dynamics in an old-growth forest in Indiana: Davis-Purdue Research Forest 1926-1981.** In: Hay, R.L.; Woods, F.W.; DeSelm, H., eds. Proceedings, 6th central hardwood forest conference. Knoxville, TN: The University of Tennessee: 369-376.

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

Zaczek, J.J.; Groninger, J.W.; van Sambeek, J.W. 2002. S**tand dynamics in an old-growth hardwood forest in southern Illinois.** Natural Areas Journal. 22: 211-219.