ANALYSIS OF HISTORICAL VEGETATION PATTERNS IN THE EASTERN PORTION OF THE ILLINOIS LESSER SHAWNEE HILLS

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Abstract.—We used General Land Office Survey (GLO) records to reconstruct the historical (1806-1810) vegetation of the eastern portion of the unglaciated Lesser Shawnee Hills Ecoregion of the Shawnee National Forest Purchase Area in southern Illinois. Prairies occurred on 0.4 percent of the area and savannah, open forest, and closed forest occupied 14.5 percent, 25.4 percent, and 59.6 percent of the area, respectively. Average tree density and basal area for the area were 102 trees per ha and 13 m^2/ha, respectively. Closed forest occurred at significantly lower elevation than savannah, with average elevation being 139.3 m and 147.1 m for closed forest and savannah, respectively. White oak (*Quercus alba*) and black oak (*Q. velutina*) were the two leading dominant species in all vegetation categories. Savannah had higher importance of xeric species than did closed forest, whereas mesophytic species had higher Importance Values in closed forest. Variation in fire frequency, topography, and moisture availability likely contributed to the landscape vegetation patterns, species composition, and tree density and basal area in the study area. High abundances of oaks and hickories and low tree densities and basal areas throughout the study area indicate that all vegetation types may have experienced periodic fires.

INTRODUCTION

We reconstructed the historical vegetation (1800-1810) of a portion of the Lesser Shawnee Hills in southern Illinois using General Land Office (GLO) survey records. This investigation was part of a larger study that provided information for developing the Shawnee National Forest Plan (Fralish and others 2002).

The Shawnee Hills Natural Division of Illinois (260,620 ha) occurs in an unglaciated portion of Illinois and is divided into two subdivisions, the Greater and Lesser Shawnee Hills. The Greater Shawnee Hills subsection (173,631 ha) is the northern of the two subdivisions and is characterized by a high east-west escarpment of Pennsylvanian-age sandstone. The Lesser Shawnee Hills subsection (86,989 ha) averages 61 m lower in elevation than the more dissected Greater Shawnee Hills, with Mississippian-age limestone as the primary surface bedrock (Willman and Frye 1970, Schwegman and others 1973). Most of the soils were derived from loess that originated primarily from the Mississippi flood plain (Fahrenbacher and others 1967, Willman and Frey 1970). The Lesser Shawnee Hills has thick loess soils along the Mississippi and Ohio rivers and thinner soil in the middle of the state (Willman and Frye 1970, Schwegman and others 1973). Loess deposits vary in depth from more than 7.5 m to 1.2 m or less on scattered rock outcrops (Willman and Frye 1970). The Lesser Shawnee Hills subsection was subdivided into three Land Type Associations (LTAs) based on the thickness

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of the loess deposits: LTA-6 = West Thick Loess, LTA-7 = East Shallow Loess, and LTA-8 = East Thick Loess (Fig. 1). During initial analysis of the witness tree data for the LTAs, the east shallow loess and east thick loess had lower tree density and basal area (88-92 trees/ha and 11-12 m^2/ha, respectively) compared to the other LTA in Lesser Shawnee (235 trees/ha and 32 m^2/ha) and the Greater Shawnee Hills (195 trees/ha and 24 m^2/ha). There were also differences in tree species Importance Values between LTA-7 and LTA-8 compared to the rest of the Shawnee Hills. These two LTAs were studied because of their similarity to each other and the differences between these two LTAs and the remainder of the Shawnee Hills. The GLO witness tree data for LTA-7 and LTA-8 were combined for this study.

The study area is approximately 69,500 ha and was included in the Western Mesophytic region by Braun (1950). The current vegetation is largely characterized by second-growth oak-hickory forest on upland sites and mesic forests dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandiflora*), and yellow poplar (*Liriodendon tulipfera*) in sheltered locations, with a diversity of tree species occupying bottomland sites (Fralish 1976, 1988; Fralish and others 1991; Fralish 1994; Heikens and Robertson 1994; Ozier and others 2006; Chandy and others 2009). Historically, the upland oak-hickory forests were maintained by periodic fire and frequent timber harvests (Fralish and others 1991, Parker and Ruffner 2004). However, with reduced timber harvest and decreased fire frequency beginning near the middle of the past century, shade-tolerant, fire-sensitive mesophytes, including sugar maple and American beech, are replacing the relatively shade-intolerant oaks and hickories (Fralish and others 1991, Fralish 1997, Zaczek and others 2002, Parker and Ruffner 2004, Ozier and others 2006, Chandy and others 2009).

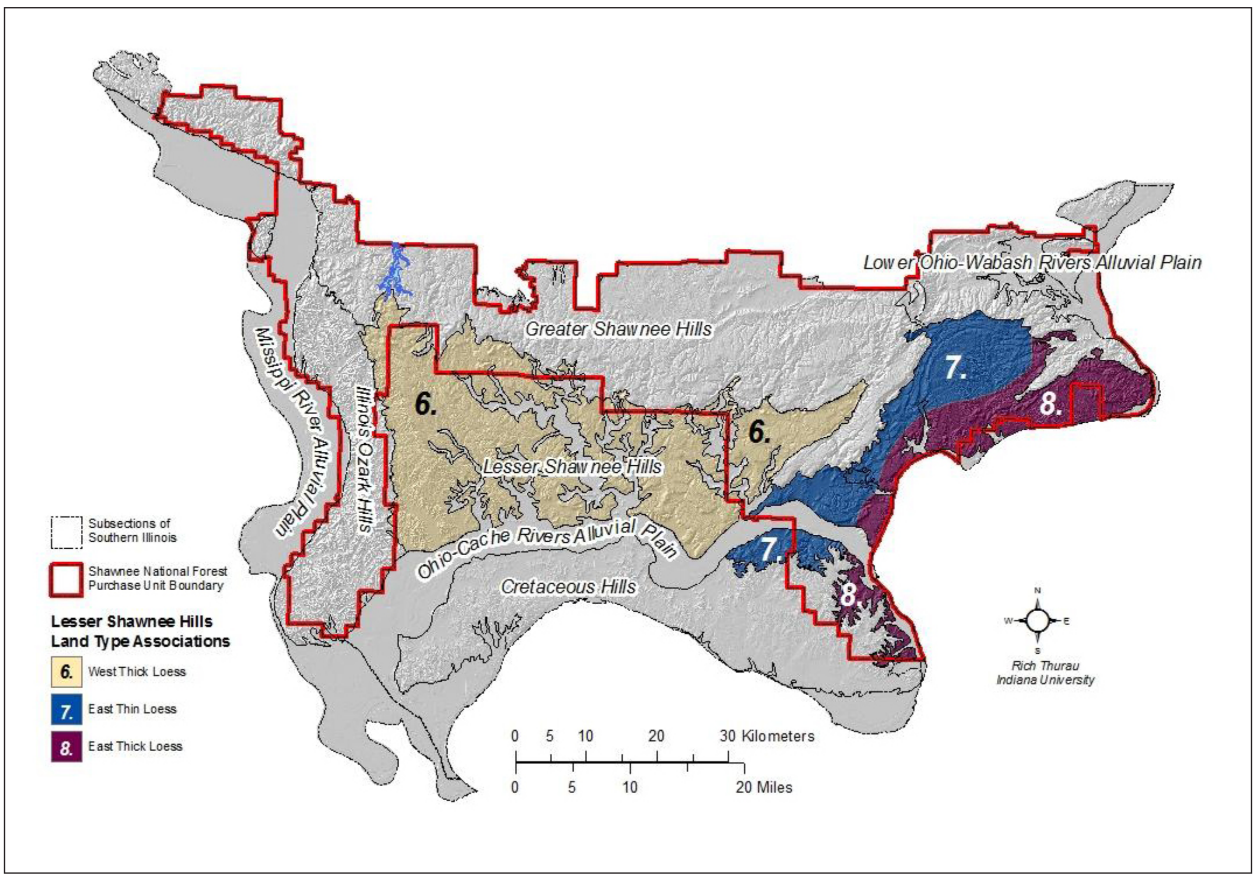

Figure 1.—Land Type Associations (LTA's) for the Shawnee National Forest (Map Produced by Richard Thurau, Indiana University, Bloomington, Indiana). The study areas include LTA7: East Shallow Loess (Lesser Shawnee Hills) and LTA8: East Thick Loess (Lesser Shawnee Hills).

OBJECTIVES

The purposes of this study were to determine: 1) the occurrence of prairie, savannah, open forest, and closed forest vegetation types on the landscape; 2) the composition and abundance of tree species in three vegetation types; and 3) influence of topographic landscape features (slope, aspect, and elevation) on the distribution of three vegetation types.

METHODS

Original survey records are a valuable source of information about historical vegetation. Land surveys were commissioned in 1785 for territories lying northwest of the Ohio River, and were conducted by the GLO before extensive European settlement of the region (Hutchinson 1988). A detailed review of survey instructions and procedures is available in several sources (e.g., Bourdo 1956, White 1983). While some studies have identified limitations in the use of GLO Survey Records for vegetation analysis (Bourdo 1956, Manies and others 2001, Schulte and Mladenoff 2001, Bouldin 2008), it is widely accepted that these records are the best source for historical vegetation data and can be used successfully to determine historical tree density and community composition (Schulte and Mladenoff 2001, Anderson and others 2006).

To calculate the tree densities from the GLO witness tree distance data, the method of Anderson and others (2006) was used. Seven-hundred sixteen points were present in the study area. Outer boundaries of townships are shared with other townships, and to eliminate duplicating measurements, only the southern and eastern boundaries of each township were surveyed. For these survey lines, surveyors tended to select witness trees that were within the township they were surveying rather than in an adjacent one. The average distance for these witness trees was considered to be Qm (average of $Q_1 + Q_2 + Q_3 + Q_4$) of the quarter method and equal to the square root of the mean area. For points with only one tree or one tree and a corner tree and interior points with two witness trees in the same quadrant or missing directions, the single distance or the shorter of the two distances was treated as the Q_1 distance of the quarter method. Points with no witness trees, points with only a corner tree, or points with missing distances were not used in the calculation of tree density.

For data from interior section or quarter section points with two trees, two distances, and two directions in different quadrants were analyzed by modifying the exclusion angle of the random pairs (Anderson and others 2006). Surveyors measured the distance between the point and the tree, but the distance methods assume that the distance is measured to the center of the tree. Because we calculated tree density at each point, and wanted these data to be as precise as possible, one-half of the witness tree diameter was added to the measured distance. Where distances were given, but no tree diameters recorded, one-half of the average tree diameters for the study area (37 cm) was added to the measured distance. Square root of the mean area and tree density were calculated at each point using the appropriate method for that group (Anderson and others 2006).

Each point was assigned to a vegetation category, based on tree density, according to the categories used by Anderson and Anderson (1975). These vegetation categories were developed by using the GLO survey data from Williamson County, IL and are based on an estimation of the density of average-diameter "open-grown trees" needed to produce canopy cover of <50 percent, >50 percent but <100 percent, and at least 100 percent for savannah, open forest, and closed forest, respectively. In these calculations, it was assumed that the tree crowns do not overlap. The relationship between tree diameter and crown spread was developed by measuring diameter and crown radius of extant open-grown oaks and hickories and using regression analysis to develop a linear relationship between diameter and crown radius, which was used to calculate crown area. Prairies were arbitrarily defined as having less than 0.5 trees/ha. Points with greater than 0.5 but less than 47 trees/ha were categorized as savannah, and points with 47 to 96 trees/ha or more than 96 trees/ha were categorized as open forest or closed forest, respectively. Within each vegetation category, and the study area as a whole, the tree density and basal area per ha, relative density, relative dominance (basal area) and an Importance Value based on the average of the two relative values were calculated for each species (Anderson and Anderson 1975).

Percent similarity (McCune and Grace 2002) was used to compare species' Importance Values of witness trees in the three vegetation categories. To further assess differences in species importance among vegetation types, species were also grouped according to preferred site characteristics into xerophytic, mesophytic, mid-canopy, and bottomland (Fralish and others 2002). There were not enough mid-canopy or bottomland species in all of the vegetation types to include these groups in the analysis. Xerophytic species included white oak, black oak (*Q. velutina*), hickory species (*Carya* species), post oak (*Q. stellata*), red oak (*Q. rubra*), Spanish oak (*Q. falcata*), oak species (*Quercus* species), and blackjack oak (*Quercus marilandica*). Mesophytic species included gum, elm species (*Ulmus* species), yellow-poplar, blackgum (*Nyssa sylvatica*), white ash (*Fraxinus americana*), sugar maple, sweet gum (*Liquidambar styraciflua*), American beech, maple species (*Acer* species), ash species (*Fraxinus* species), black walnut (*Juglans nigra*), sassafras (*Sassafras albidum*), butternut (*Juglans cinerea*), and hackberry (*Celtis occidentalis*).

Shannon diversity index (H') and evenness were calculated for the three vegetation types using tree Importance Values.

GEOGRAPHIC INFORMATION SYSTEMS (GIS) ANALYSIS

The Digital Elevation Model (DEM) for this project was originally provided by the Natural Resource Conservation Service (NRCS), Major Land Resource Area office and modified by NRCS and researchers at Southern Illinois University-Carbondale prior to our use. The DEM of the Lesser Shawnee Hills is projected in the NAD_1983_UTM_Zone_16N coordinate system. This DEM (resolution 10 m) was used to create elevation, slope, and aspect maps for the study area. A file was created containing tree data (tree species, tree density, and vegetation category) and geographical data (including latitude, longitude, elevation, slope, and aspect) for all sample points. These data were used to create the tree density and vegetation cover maps. It was also used for statistical analysis. To better evaluate the study area, the DEM was used to create an elevation map (10-m resolution). Spatial Analyst (ESRI, Redlands, CA) was used to derive slope and aspect from the DEM. Maps (10-m resolution) were also created for slope and aspect.

The latitude and longitude coordinates and the tree density for each sample point were imported into a gridding software (Surfer, Golden Software, Golden, CO). Sample points were located at 0.81-km intervals along a regular grid. Some densities identified as outliers (>1,500 trees/ha) were removed before proceeding. The tree densities were interpolated into a regular surface using Kriging, with linear variogram (Burrough and McDonnell 1998). The interpolated grid was then exported as an ASCII text file, and imported into ArcView (ESRI) as a table from this format. The table was used to add an event theme (i.e., tree density) to the view with the same projection as the DEM. The inverse-distance weighting method was used to interpolate the event theme, recreating the surface that was previously interpolated in the Surfer software. The density categories were reclassified to reflect the density ranges for vegetation categories defined by Anderson and Anderson (1975). Maps were created showing the location of the sample points and their vegetation category, based on the tree density of each sample point, and these data were projected over an elevation map of the study area (Sauer 2002). Digitized soil data were not available to us for this study.

STATISTICAL ANALYSIS

Importance Values for trees, slope, linearized aspect (Beers and others 1966), and elevation data did not have normal distributions and could not be normalized with transformations (logn, square root, arcsine). Consequently, non-parametric tests were used for analyses. Spearman correlations were used to test for similarities in species' Importance Values among vegetation categories. Chi-square analysis was used to assess differences in Importance Values among the vegetation categories for white oak, black oak, and all other species combined, and for xerophytic and mesophytic species grouped separately. Nonparametric Kruskal-Wallace tests were used to determine whether (1) slope, (2) aspect, and (3) elevation were significantly different among vegetation categories. When the test showed a significant difference among vegetation categories, follow-up Kruskal-Wallace tests were used to perform pairwise comparisons between categories. Statistical significance was accepted at $\alpha = 0.05$ that was adjusted using a Bonferroni correction for multiple comparisons. Data were analyzed using SAS (SAS Institute, Cary, NC).

RESULTS

DISTANCE METHOD APPLICATION-MODIFICATION OF RANDOM PAIRS

Occurrence of witness trees for interior points did not differ significantly from an equal distribution of witness trees in the four quadrants ($\chi^2 = 2.297$, $\chi^2_{0.05,\,3} = 7.815$). There were 264, 278, 252, and 284 trees in the NE, SE, SW, and NW quadrants, respectively. The suitability of using the Point Centered Quarter or the Random Pairs Method with an exclusion angle of 180° to determine tree density from the witness tree distances was tested by determining the distribution of second witness trees (second-closest tree to the point) in quadrants opposite or adjacent to the quadrant of the first witness trees (closest tree to the point) (Anderson and Anderson 1975, Anderson and others 2006). However, analysis of second witness tree distribution showed that 395 second witness trees were located in quadrants opposite to the quadrant of the first tree and 144 were located in adjacent quadrants. There is a significant ($\chi^2 = 386.96$, $\chi^2_{0.05,\,1} = 3.841$) deviation from the expected distribution of twice as many occurrences of witness trees in adjacent than opposite quadrants for application of the Point Centered Quarter Method to the data and to the expected 50 percent in opposite and 50 percent in adjacent quadrants for the random pairs method ($\chi^2 = 116.885$, $\chi^2_{0.05,\,1} = 3.841$). Distribution of second witness trees was found to be 73.3 percent in opposite and 26.7 percent in adjacent quadrants with respect to the quadrant of the first witness tree. When we use the relationship [90° X (proportion of total trees in adjacent quadrants / proportion of total trees in the opposite quadrants] (Sauer 2002, Anderson and others 2006), degrees of azimuth in adjacent quadrants for these data becomes: [90° X (0.267/0.733) = 32.81°], which results in an exclusion angle of 237.19°, (360° - 90° - 32.81°) and a correction factor for the Modified Random Pairs Method of 0.68.

VEGETATION CATEGORIES AND TREE DATA

There were 104 points with tree densities falling within the savannah range. Open and closed forest categories had 182 and 427 points, respectively. The three prairie points, none of which had any witness trees, were excluded from further analysis based on lack of witness tree information and small sample size. Based on the percentage of the points occurring in each vegetation type, excluding the prairie points, the area was 14.6 percent savannah, 25.5 percent open forest, and 59.9 percent closed forest. For the study area as a whole, the most important species were white oak, black oak, and hickory species (Table 1). White oak alone accounted for 44.5 percent of the Importance Value, and together the three species constituted 72.5 percent of the importance. Average tree density and basal area in the study area were 102.4 trees/ha and 13.0 m^2/ha, respectively. Thirty tree taxa (species and genera) were recorded in the study area.

Table 1.—Tree mean diameter, relative density, relative dominance, and Importance Values (IV) by species for the study area. Tree density and basal area were 102.36 trees/ha and 13.03 m²/ha, respectively. Overall mean d.b.h. was 34.41 cm.

Species	No. Trees	Mean d.b.h.(cm)	Relative Density	Relative Dominance	IV
Quercus alba	626	40.92	43.75	45.30	44.52
Quercus velutina	252	48.44	17.61	25.55	21.58
Carya species	111	32.10	7.76	4.94	6.35
Quercus rubra	48	55.86	3.35	6.47	4.91
Cornus species	69	18.48	4.82	1.02	2.92
Quercus stellata	42	37.11	2.94	2.50	2.72
Gum	46	32.03	3.21	2.04	2.63
Ulmus species	43	30.73	3.00	1.75	2.38
Liriodendron tulipifera	29	34.69	2.03	1.51	1.77
Nyssa sylvatica	27	30.29	1.89	1.07	1.48
Fraxinus americana	24	31.62	1.68	1.04	1.36
Acer saccharum	21	33.99	1.47	1.05	1.26
Liquidambar styraciflua	15	44.55	1.05	1.29	1.17
Fagus grandifolia	10	46.04	0.70	0.92	0.81
Morus species	10	31.17	0.70	0.42	0.56
Acer species	9	35.14	0.63	0.48	0.55
Fraxinus species	10	30.73	0.70	0.41	0.55
Platanus occidentalis	3	77.94	0.21	0.79	0.50
Juglans nigra	8	32.65	0.56	0.37	0.46
Quercus falcata	6	37.26	0.42	0.36	0.39
Sassafras albidum	6	23.60	0.42	0.14	0.28
Quercus species	3	32.95	0.21	0.14	0.18
Gleditsia triacanthos	2	44.47	0.14	0.17	0.16
Juglans cinerea	3	22.91	0.21	0.07	0.14
Cercis canadensis	2	24.10	0.14	0.05	0.09
Ostrya virginiana	2	20.95	0.14	0.04	0.09
Celtis occidentalis	1	30.48	0.07	0.04	0.06
Quercus nigra	1	30.48	0.07	0.04	0.06
Acer negundo	1	25.40	0.07	0.03	0.05
Quercus marilandica	1	15.24	0.07	0.01	0.04
Total		34.41	100	100	100

The three leading species in importance in the savannah were white oak, black oak, and hickory species, representing 88.4 percent of importance (Table 2). Post oak was fourth in importance (compared with sixth in the study area), representing 2.8 percent of the Importance Value. Fifteen tree taxa occurred as witness trees in the savannah vegetation. Tree density and basal area were less than the study area as a whole, 19 trees/ha and 3 m²/ha, respectively. In the open forest, white oak, black oak, and hickory species were the three leading species and represented 77.4 percent of Importance Values (Table 3). These species were followed by red oak (*Q. rubra*) and post oak. Average tree density and basal area were low in open forest: 71 trees/ha and 11 m²/ha, respectively. Twenty-two taxa were represented at open forest sites.

The average tree density and basal area for closed forest points was 230 trees/ha and 26 m²/ha, respectively (Table 4). Twenty-eight taxa were represented in the closed forest, with white oak, black oak, and hickory species as the leading three taxa in Importance Value, representing a cumulative Importance Value of 67.6 percent. Post oak was the ninth species in order of importance (Importance Value = 2.11).

Table 2.—Tree mean d.b.h., relative density, relative dominance, and Importance Values (IV) by species for savannah. Tree density and basal area were 19.28 trees/ha and 2.47 m^2/ha, respectively. Mean d.b.h. for savannah trees was 35.62 cm.

Species	No. Trees	Mean d.b.h. (cm)	Relative Density	Relative Dominance	IV
Quercus alba	98	42.02	59.04	57.76	58.40
Quercus velutina	37	48.36	22.29	28.89	25.59
Carya species	9	33.76	5.42	3.42	4.42
Quercus stellata	5	40.00	3.01	2.67	2.84
Quercus rubra	2	62.84	1.20	2.64	1.92
Cornus species	5	20.22	3.01	0.68	1.85
Acer species	1	63.50	0.60	1.35	0.97
Ulmus species	2	28.06	1.20	0.53	0.87
Acer saccharum	1	45.72	0.60	0.70	0.65
Gum	1	35.56	0.60	0.42	0.51
Platanus occidentalis	1	35.56	0.60	0.42	0.51
Quercus falcata	1	22.86	0.60	0.17	0.39
Liriodendron tulipifera	1	20.32	0.60	0.14	0.37
Morus species	1	20.32	0.60	0.14	0.37
Sassafras albidum	1	15.24	0.60	0.08	0.34
Total		35.62	100	100	100

Table 3.—Tree mean d.b.h., relative density, relative dominance, and Importance Values (IV) by species for open forest. Tree density and basal area were 70.71 trees/ha and 10.66 m^2/ha, respectively. Mean d.b.h. for open forest trees was 37.63 cm.

Species	No. Trees	Mean d.b.h. (cm)	Relative Density	Relative Dominance	IV
Quercus alba	145	42.74	44.75	42.68	43.72
Quercus velutina	72	52.14	22.22	31.54	26.88
Carya species	26	36.55	8.02	5.60	6.81
Quercus rubra	12	54.64	3.70	5.77	4.74
Quercus stellata	15	39.77	4.63	3.82	4.23
Ulmus species	7	32.94	2.16	1.22	1.69
Fagus grandifolia	5	45.11	1.54	1.64	1.59
Gum	8	23.52	2.47	0.71	1.59
Cornus species	8	20.89	2.47	0.56	1.52
Platanus occidentails	1	121.92	0.31	2.40	1.35
Liriodendron tulipifera	5	31.32	1.54	0.79	1.17
Fraxinus americana	4	41.11	1.23	1.09	1.16
Acer saccharum	4	26.00	1.23	0.44	0.84
Nyssa sylvatica	3	29.95	0.93	0.43	0.68
Quercus species	2	36.14	0.62	0.42	0.52
Acer species	1	30.48	0.31	0.15	0.23
Fraxinus species	1	30.48	0.31	0.15	0.23
Morus species	1	30.48	0.31	0.15	0.23
Quercus nigra	1	30.48	0.31	0.15	0.23
Ostrya virginiana	1	25.45	0.31	0.10	0.21
Acer negundo	1	25.40	0.31	0.10	0.21
Juglans nigra	1	20.32	0.31	0.07	0.19
Total		37.63	100	100	100

Table 4.—Mean tree diameter, relative density, relative dominance, and Importance Value (IV) by species for closed forest. Tree density and basal area were 230 trees/ha and 26.09 m^2/ha, respectively. Mean d.b.h. for closed forest trees was 33.14 cm.

Species	No. Trees	Mean d.b.h. (cm)	Relative Density	Relative Dominance	IV
Quercus alba	383	39.92	40.83	43.80	42.31
Quercus velutina	143	46.49	15.25	22.17	18.71
Carya species	76	30.21	8.10	4.98	6.54
Quercus rubra	34	55.85	3.62	7.61	5.62
Cornus species	56	17.95	5.97	1.29	3.63
Gum	37	33.49	3.94	2.98	3.46
Ulmus species	34	30.41	3.62	2.26	2.94
Liriodendron tulipifera	23	35.86	2.45	2.12	2.29
Quercus stellata	22	34.46	2.35	1.87	2.11
Nyssa sylvatica	24	30.33	2.56	1.58	2.07
Liquidambar styraciflua	12	49.81	1.28	2.14	1.71
Fraxinus americana	20	29.36	2.13	1.24	1.68
Acer saccharum	16	34.88	1.71	1.40	1.55
Fraxinus species	9	30.76	0.96	0.61	0.79
Morus species	8	32.35	0.85	0.60	0.73
Juglans nigra	7	34.05	0.75	0.58	0.66
Fagus grandifolia	5	46.96	0.53	0.79	0.66
Acer species	7	29.65	0.75	0.44	0.59
Quercus falcata	5	38.17	0.53	0.52	0.53
Sassafras albidum	5	24.94	0.53	0.22	0.38
Juglans cinerea	3	28.89	0.32	0.18	0.25
Gleditsia triacanthos	2	44.47	0.21	0.28	0.25
Cercis canadensis	2	24.10	0.21	0.08	0.15
Platanus occidentalis	1	38.10	0.11	0.10	0.11
Celtis occidentalis	1	30.48	0.11	0.07	0.09
Quercus species	1	25.40	0.11	0.05	0.08
Ostrya virginiana	1	15.24	0.11	0.02	0.06
Quercus marilandica	1	15.24	0.11	0.02	0.06
Total		33.14	100	100	100

Shannon Diversity Index (H') and evenness (J) increased from savannah to open and closed forests (H' = 1.31, 1.79, and 2.09; J = 0.48, 0.58, and 0.70 for savannah, open and closed forests, respectively).

Spearman correlation showed that species' Importance Values were correlated between the vegetation categories in the closed and open forests (df = 28, Rho = 0.733, $p < 0.0001$); open and savannah (df = 22, Rho = 0.698, p = 0.0002); and savannah and closed (df = 27, Rho = 0.651, p = 0.0001); Bonferroni adjustment = alpha significant at 0.017. Differences between the groups did not occur because of dominant species, but rather were the result of differences in importance occurring among the less-abundant species. Percent similarity between vegetation types was high: 83.4 percent and 75.7 percent between savannah and open and closed forests, respectively, and 84.8 percent between open and closed forest.

Chi-square analysis showed differences in Importance Values of white oak, black oak combined, and all other species combined among the three vegetation types (χ^2 = 14.382, df = 4, p = 0.0062). Open forest showed no significant difference between closed forest or savannah (open vs. closed χ^2 = 2.831, df = 2, p = 0.243; open vs. savannah χ^2 = 6.087, df = 2, p = 0.048; Bonferroni adjustment = alpha significant < 0.017), but there was a significant difference between closed forest and savannah (χ^2 = 12.206, df = 2, p = 0.0005). While white oak and black oak were the first and second most important species in closed forest and savannah, they had higher importance in the savannah than in the closed forest (white oak 42.3 in closed forest vs. 58.4 in savannah; black oak 18.7 in closed forest vs. 25.6 in savannah). The "other species" category had higher combined importance in the closed forest (40.0) than in the savannah (16.0).

A significant difference was found among the vegetation categories for Importance Values of xerophytic and mesophytic species groups (χ^2 = 13.198, df = 2, p = 0.0014). While there was no significant difference between the closed forest and open forest (χ^2 = 4.1, df = 1, p = 0.0429; Bonferroni adjustment = significant alpha < 0.017) or open forest and savannah (χ^2 = 2.668, df = 1, p = 0.102), there was a significant difference in Importance Values of xerophytic and mesophytic species when closed forest and savannah (χ^2 = 12.2061, df = 1, p = 0.0005) were compared. Xerophytic species were somewhat more important in savannah than in open forest and mesophytic species were more important in the open forest sites than in savannahs (Fig. 2). While not statistically significant, there was a pattern showing higher importance of mesophytic species in closed forest compared to open forest, and greater importance of xerophytic species in the open forest compared to the closed forest (Fig. 2).

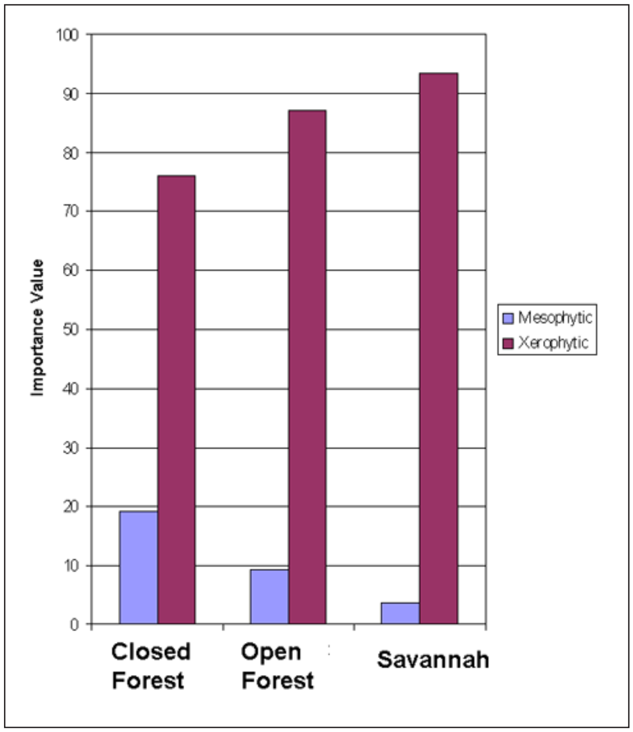

Figure 2.—Sum of Importance Values for mesophytic and xerophytic species in closed forest, open forest, and savannah vegetation categories.

GIS MAPPING AND VEGETATION AND ELEVATION PATTERNS

The study area is not highly dissected, so the slope map showed few steep ridges and there were weak relationships between slope and aspect and vegetation patterns as described later. Historically, the study area was a mosaic of savannah, open forest, and closed forest with the three prairie points located in the extreme southern portion of the study area, as shown in Figure 3.

There were no significant differences among vegetation categories for slope (χ^2 = 2.979, df = 2, p = 0.2255) or aspect (χ^2 = 0.269, df = 2, p = 0.8741). There was a weak significant difference in elevation among vegetation categories (χ^2 = 5.893, df = 2, p = 0.052) (Table 5). Savannah elevations were significantly different from those in closed forest (χ^2 = 5.456, df = 1, p = 0.019), but open forest elevations were not statistically different from elevations either in savannah (χ^2 = 1.927, df = 1, p = 0.165) or in closed forest (χ^2 = 1.136, df = 1, p = 0.286). Savannah occurred at significantly higher elevations (147.1 m) than closed forest (139.5 m) but not open forest (142.6 m); open and closed forests were not significantly different (Table 5).

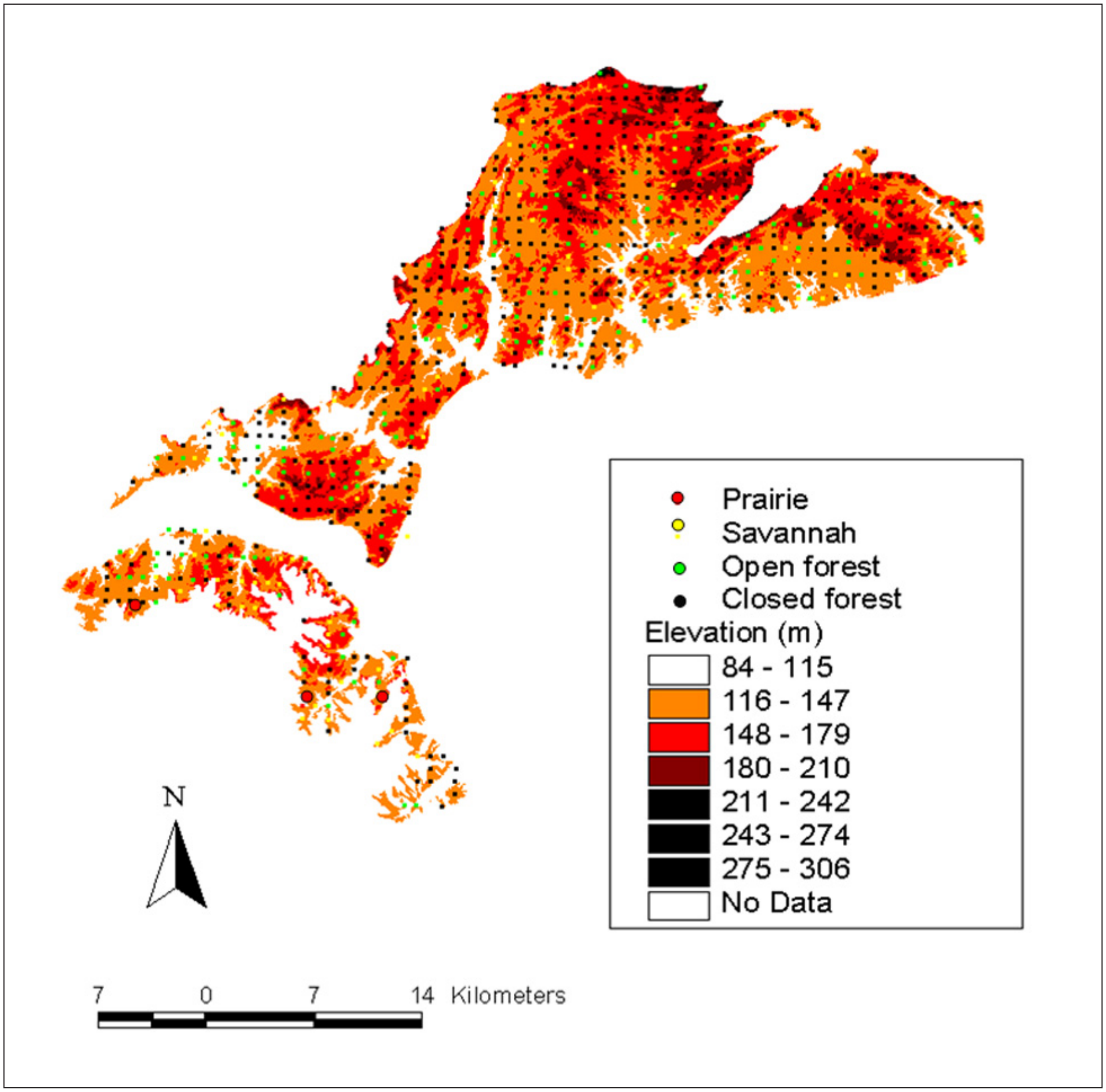

Figure 3.—The distribution of survey points by vegetation categories (prairie, savanna, open forest, and closed forest) in relation to elevation.

Table 5.—Mean values and standard error for slope, elevation, and aspect in each vegetation category.

	Savannah (n=104)	Open Forest (n=182)	Closed Forest (n=427)
Slope (percent)	8.7 ± 0.5	8.8 ± 0.4	9.7 ± 0.4
Elevation (m)	147.1 ± 2.0	142.6 ± 1.7	139.5 ± 1.1
Aspect (degrees)	175.3 ± 10.4	186 9 ± 8.1	181.1 ± 4.9

DISCUSSION

We selected this study area for analysis primarily because of its lower historical (1806-1810) tree densities and basal areas than the rest of the Lesser Shawnee Hills or Greater Shawnee Hills subsection (Fralish and others 2002). Historic vegetation and topography patterns within the study area suggest factors that may have influenced the lower tree density in the area. The average tree density for this study area was 102 trees/ha, which is just within the closed forest category of 96 trees/ha. Forty percent of the points in the area had tree densities within the savannah and open forest ranges, again indicating that open woodlands and savannahs were an important component of vegetation of the area. Post oak, which is characteristic of barrens (Taft 1997) and dry sites (Fralish 1976), has slightly higher Importance Values in the study area than in Greater Shawnee Hills, where tree density is higher (Fralish and others 2002). The study area, especially savannah and open forest sites, was dominated by oak-hickory vegetation rather than species characteristic of more mesic, mixed woodlands. The tree density (303 to 631/ha) and basal area (15 to 29 m^2/ha) reported by Fralish and others (1991) for current forests in the Shawnee Region occurring on north- and south-facing slopes and ridgetops are greater than we found for the historic forests. Three interrelated factors would have likely contributed to maintaining this low tree density and basal area: fire, site topography, and moisture availability.

Fire was likely an important factor in maintaining the low tree densities and basal areas of this area. Oaks and hickories, in particular, are resistant to fire and dependent upon periodic fire for their maintenance (Abrams 1992, Heikens and Robertson 1994, Nowacki and Abrams 2008). Fire hinders the growth of non fire-tolerant species, like beech and sugar maple, and reduces the overall tree density. Several studies have shown that fire was an important factor in maintaining oak savannahs and open woodlands (Reich and others 1990, Abrams 1992, Delcourt and Delcourt 1997, Anderson and Bowles 1999, Nowacki and Abrams 2008). Native Americans used fire (Fralish 1997, Parker and Ruffner 2004), as did early European settlers in southern Illinois (Miller 1920, Parker and Ruffner 2004) as a means of clearing land for farming and increasing forb and grass growth. One of the reasons for the lack of a strong relationship between elevation, aspect, and slope with tree density or historic vegetation type could be the landscape homogeneity of the study area. The topography of the study area differs from much of the Shawnee Hills in that it is more rolling and less dissected. While sheltered narrow ravines in the Greater Shawnee Hills would have supported mesic communities, it is likely that the moderately rolling topography of this study area would have allowed fire to travel across most of the landscape (Anderson 1991). Widespread occurrence of fire could account in part for the lower tree density and basal area of the study area compared to the Greater Shawnee Hills.

While variation in fire frequency on the landscape could account for differences in tree density and species composition availability, species composition and dominance can be strongly influenced by moisture availability. However, we presented no evidence for soil moisture as a factor in determining vegetation patterns within our study area. Nevertheless, the distribution of tree species and vegetation communities has been shown to be related to a soil moisture gradient in the Shawnee Hills (Fralish 1976, 1988, 1994). In our study, savannahs occurred on average at higher elevations and slightly more level topography than closed forests. Savannahs appeared to be more common on ridge tops than were closed forests, which were associated more with ravine and valley habitats. For example, 21.1 percent of closed forest points occurred at elevations less than 120 m in elevation, compared with 18.2 percent for open forest and 6.6 percent for savannah. In contrast, 8.7 percent of savannah points were at elevations greater than 180 m, compared to 5.5 percent and 4.5 percent of open and closed forest points, respectively. Higher moisture availability along the lower slopes, in ravines, and along riparian areas may account for areas of higher species diversity and tree densities, as well as for the presence and importance of mesic and bottomland species in closed forests. Lower moisture would have been associated with upper hilltops and ridges, where soil depth was shallow and favored low-density forests with a higher proportion of xerophytic species than in lower-elevation closed forests (Fralish 1976).

The vegetation mosaic that occurred on the study site at the time of the GLO surveys was likely the result of a combination of interacting factors, including soil moisture, fire, and topography. However, the fire disturbance regime in southern Illinois has changed in the past 55-65 years after the establishment of the Shawnee National Forest and institution of fire control practices (Heikens and Robertson 1994, Fralish 1997, Anderson and others 2000, Parker and Ruffner 2004, Fralish and McCardle 2009). Barrens were present in the study area at the time of the survey, especially at the southern end (Hutchinson and others 1986), and remnants can still be seen today. Nevertheless, studies conducted during the past 40 years have shown that these open forest and barrens undergo transition to closed forest unless fire is used consistently as a management tool (Anderson and others 2000). Similarly, numerous studies have shown that the fire-tolerant oak-hickory community shifts to a community where mesic species like sugar maple increase in importance after fires are suppressed (Lorimer 1985, Abrams 1992, Shotola and others 1992, Zaczek and others 2002, Nowacki and Abrams 2008). For example, Chandy and others (2009) reported that sugar maple in the understory of forests in the Shawnee Region increased (mean ± SE) from 36 ± 116 to 775 ± 1387 stems/ha over a 3- to 6-year period and sugar maple was the third most abundant tree (basal area = 2.6 ± 4.5 m^2/ha), although white oak was the dominant tree species (5.9 ± 10.9 m^2/ha). We found that the basal area of sugar maple was 0.1 m^2/ha and white oak basal area was 5.9 m^2/ha.

The total basal area for all species was 17.9 ± 1.7 m^2/ha in the current forest (Chandy and others 2009), whereas we found a total basal area of 13.0 m^2/ha in the historic forest. Similarly, in a protected old-growth forest sampled in permanent plots established in 1935, sugar maple density increased from 156 stems/ha to 346 stems/ha and basal area increased from 1.0 m^2/ha to 6.8 m^2/ha between 1935 and 1997, whereas white oak density declined from 111 to 28 stems/ha and basal area increased from 4.7 to 5.5 m^2/ha (Zaczek and others 2002). The authors concluded that the old-growth forest without disturbance for 100 years is succeeding to sugar maple and other shade-tolerant species, even though yellow-poplar and white oak are the two leading species based on relative dominance.

In a process termed "mesophication," by Nowacki and Abrams (2008), the increased abundance of mesophytic species alters the landscape in such a way that the fire regime is changed so that fires occur less frequently and the microclimate is changed to favor shade-tolerant mesophytic species. This pattern has been documented in the Shawnee Hills and other portions of southern Illinois (Fralish and others 1991, Shotola and others 1992, Ozier and others 2006, Chandy and others 2009). Mesophication has progressed on some portions of the landscape to the point where fire management in the absence of other silvicultural practices, such as cutting, is no longer an effective tool to restore historic conditions (Anderson and others 2000, Zaczek and others 2002, Ozier and others 2006).

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