SPECIES REPLACEMENT PATTERNS IN CENTRAL ILLINOIS WHITE OAK FORESTS

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ABSTRACT

In central Illinois white oak is presently being replaced by more shade tolerant species in forests in which it is a dominant tree. Nine of 37 stands sampled in a gradient analysis study of the region had white oak as a first or second dominant. These stands were examined to determine species replacement patterns. The two leading tree species in the nine stands were either white oak, black oak, black cherry, or sugar maple. White oak seedlings occurred in only three of the nine stands and at low densities (123 to 146 stems/ha). Leading species in the seedling stratum were white ash, sugar maple, red elm, and black cherry. Dominant species in the sapling stratum were sugar maple, white ash, ironwood, paw paw, and American elm. White oak saplings were sampled in only two stands.

Species diversity, measured by the Shannon-Wiener function or by the number of species present, tended to decrease from larger to small strata, except for drier sites, suggesting a successional trend towards fewer tree species with greater shade tolerance.

Structural diagrams prepared using witness tree data, Government Land Office records for McLean County, Illinois, indicate that white oak was probably successful in reproducing itself in presettlement times. In the past white oak may have maintained dominance through occassional disturbances, such as periodic fires, that permitted its successful reproduction and eliminated more shade tolerant, but less fire resistant, competitors.

INTRODUCTION

During a gradient analysis study of the forest of central Illinois it became apparent that the oak species as a group had low levels of reproductive success in stands in which they were the dominant canopy tree. This was particularly evident for white oak (Quercus alba L.) an important tree species on upland sites. A search of the literature revealed that this pattern of low reproductive success for white oak was found in several studies conducted in central Illinois (Calef 1953, Boggess and Geis 1966). In contrast Auclair and Cottam (1971) concluded that many of the oak forests in southern Wisconsin will maintain themselves, because the droughty sites they occupy limit the invasion of more shade tolerant species.

Ebinger et al. (1977) reported that white oak was successfully reproducing on an upland site in Douglas County, Illinois; however, their data does not support this conclusion. They report that white ash (Fraxinus americana L.) and red elm (Ulmus rubra Muhl.) had a total of 4,440 and 3,950 stems/acre respectively, in their two smallest size classes: < 1 ft. tall and > 1 ft. tall, but < 1 in. dbh. White oak had only 190 stems/acre in these classes.

An objective of this work was to document the pattern of species diversity and replacement patterns across the range of environmental conditions in which white oak occurs as a dominant tree. A second objective was to develop a hypothesis that accounts for the low number or lack of white oak seedlings and saplings in present day forests, but its apparently greater reproductive success in the past.

METHODS

The study area was limited to sites within a radius of about 113 km (70 mi.) of Bloomington-Normal, Illinois. This encompasses an area primarily occurring in the Grand Prairie Division as delineated by Schwegman (1973). The stands varied in size from .3 to .8 ha and were relatively homogenous in terms of vegetation and site characters such as slope, aspect and topographic position. They were free of recent cutting and grazing, except that a few sites had an occasional black walnut (Juglans nigra L.) removed within recent times.

In each stand five sampling points were located that served as the center for three nested circular quadrats which were .04, .01, and .004 ha in size to sample trees, saplings and seedlings, respectively. Trees were defined as stems at least 9.0 cm dbh. Seedlings were stems greater than 20 cm tall, but less than 1 cm dbh. The seedlings were further divided into three size classes, (1) > 20 cm tall, but < .5 cm in diameter at 20 cm, (2) $\geq$ .5 cm in diameter at 20 cm, but less than breast height (1.37 m), and (3) $\geq$ 1.37 m tall, but < 1.0 cm dbh. Saplings were also divided into three classes (4, 5 and 6) by dbh intervals ($\geq$ 1.0 cm but < 3.5 cm), ($\geq$ 3.5 cm but < 6.0 cm), and ($\geq$ 6.0 cm but < 9.0 cm).

Importance values (Curtis and McIntosh 1951) for each species in a stand were computed by stratum (seedling, sapling and trees) by summing relative frequency, density and dominance and dividing by three. Species diversity was examined by computing the Shannon-Wiener function (Shannon and Weaver 1949) for the tree and sapling strata in each stand (P_i = a species IV as a proportion), and also tabulating the number of species in the seedling, sapling and tree strata.

Using the slope position and exposure information a protection-slope index value was derived for each stand. The criteria used in preparing the index are given in table 1. The index ranges from a low value of one to a maximum value of fifteen and is scaled so low values reflect xeric site conditions and high values more mesic ones.

A total of 37 stands were sampled on sites ranging from the driest to the wettest capable of supporting forest vegetation within the study region. Nineteen stands occurred on upland sites with silt loam soils. These stands were ordinated using Gaussian Ordination (Gauch et al. 1974). The fifteen stands containing white oak were then ordered by their x-vector values. Environmental and phytosociological data were then examined across the compositional gradient delineated by the ordination.

Table 1. Criteria used in deriving the protection-slope index

I. SLOPE POSITION

Condition	Value
Upper	1
Ridge Top	2
Middle	3
Level	4
Lower	5

II. PROTECTION

Condition	Value
1. Exposed	
Protection from adjacent topography or vegetation on one side or less	0
2. Moderate	
Protection on two or three sides	5
3. Protected	
Protection on all sides	10

RESULTS

The importance values of the five dominant tree species in the white oak stands are plotted over the stand x-vector values in figure 1. The lines for each species are generalized optimum values along the compositional gradient delineated by the ordination. Compositionally the stands grade from those dominated by black oak (Quercus velutina Lam.), to white oak dominated stands, to sugar maple (Acer saccharum Marsh.) dominance on the far right. Black oak achieves its highest dominance in central Illinois on sandy areas along the Illinois River. However, white oak does not occur on these sandy sites and they are not included in this study. Sugar maple dominates more protected locations such as high river and stream terraces with silt loam soils and decreases in importance on wetter sites. Thus, the compositional gradient delineated by the ordination reflects environmental conditions varying from dry mesic sites dominated by black oak to mesic sites where sugar maple achieves prominance. Red oak (Quercus rubra L.) has its highest importance values in sites intermediate to those dominated by white oak and sugar maple. Its importance decreases on wetter sites as does sugar maple. The dominance pattern of white ash as a tree is similar to that of red oak across the compositional gradient, however, its maximum importance value is somewhat less than red oak and it is more successful on drier sites.

In figure 2A the protection-slope index value for each stand is plotted over its x-vector. Black oak dominated stands have low index values indicating the xeric site conditions, whereas the sugar maple dominated sites have high index values reflecting the more mesic character of these sites. The stands on the far left end of the horizon axis (black oak stands) occupy ridge tops and the stands on the opposite end of the axis (sugar maple stands) occur on sheltered locations on lower slopes and high stream terraces. White oak, as a tree, has relatively high dominance on sites intermediate between those dominated by black oak and sugar maple, with respect to the protection-slope index. The three stands in which black oak was the leading dominant had soils with fragipans. The bulk densities of fragipans (B_{2tx}) in these three stands were 1.61, 1.55 and 1.60 g/cc. In all cases the soil was mottled in the fragipan and in the horizon immediately beneath it. Fragipans also occurred in stands in which sugar maple was the leading dominant, but the bulk densities of the fragipans were somewhat less. Of the six sugar maple dominated stands shown in figure 2B, four had fragipans. The bulk densities of the fragipans in these stands were 1.42, 1.54, 1.58 and 1.60 g/cc. In all but one case, the fragipan was less well developed than in the black oak stands.

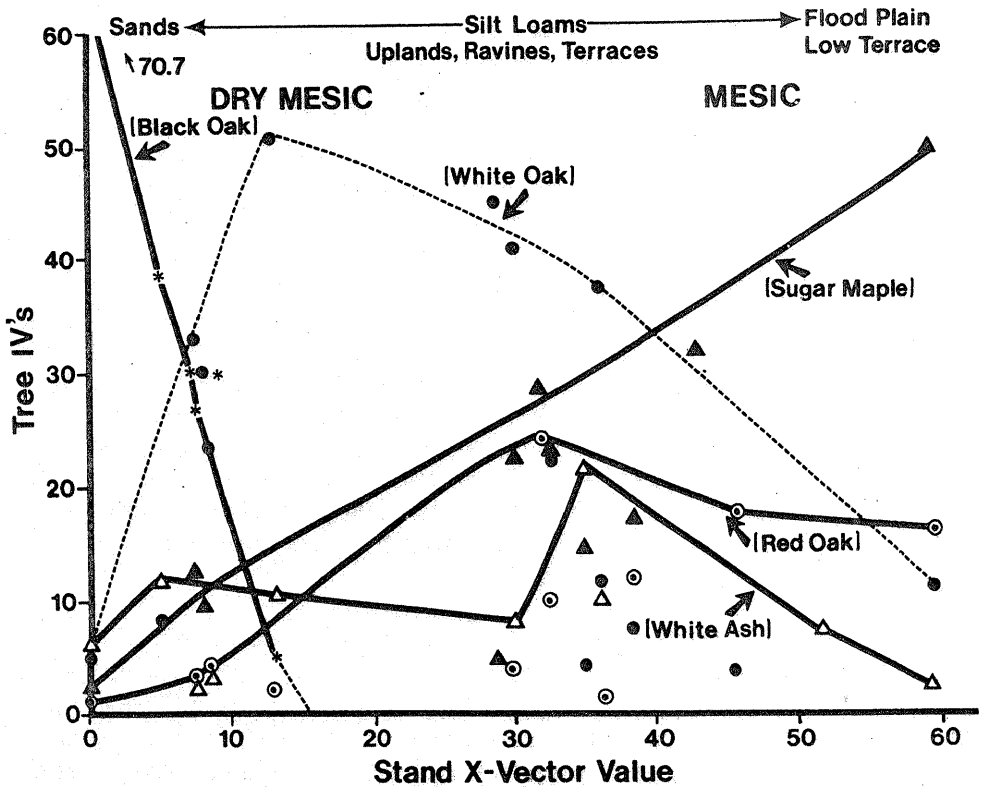

Figure 1. Generalized species success curves for four tree species along a compositional gradient in central Illinois.

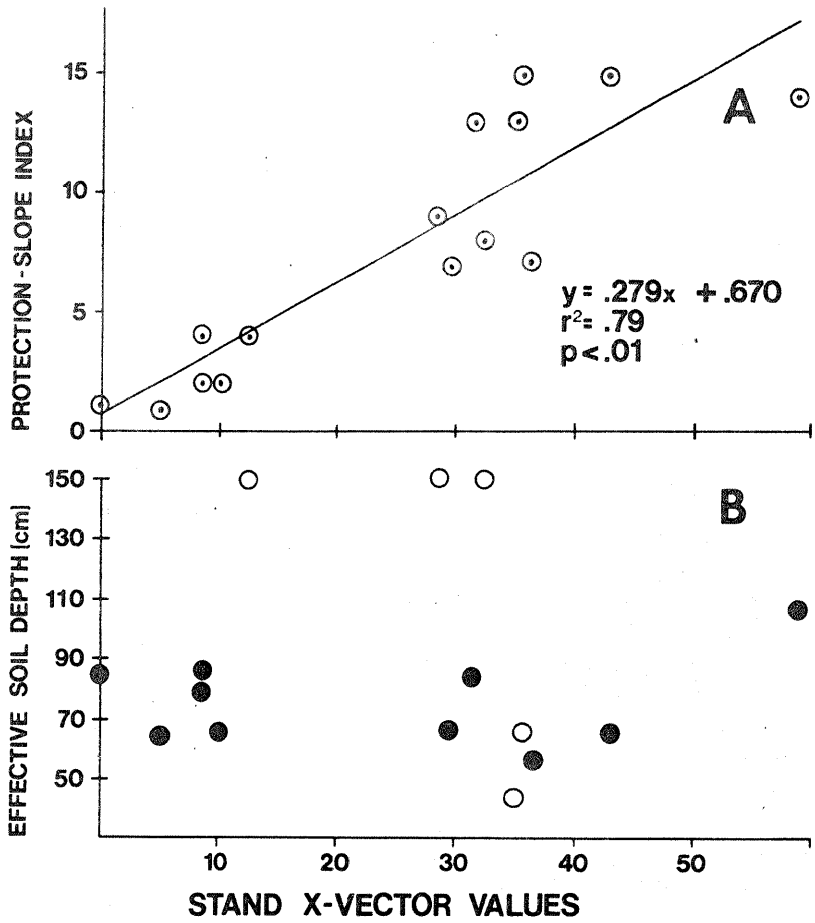

Figure 2A. A plot of stand protection-slope index values over stand x-vector values derived using Gaussian ordination.

2B. The relationship between effective soil depth and stand x-vector values. Solid circles are for stands with fragipans and open circles indicate the absence of fragipans.

The importance values for the three leading tree species in the nine white oak stands (white oak the leading or second dominant) is given in table 2. The stands are arranged by increasing x-vector values from left to right and are therefore along a gradient of decreasing dryness of the site from left to right. Black oak shares dominance with white oak on the drier sites in the tree strata and there is a gradual increase in the dominance of sugar maple towards the mesic end of the gradient. American elm (Ulmus americana L.) is a third leading dominant on the dry end and black cherry (Prunus serotina Ehrh.), ironwood (Ostrya virginiana [Mill.] K.), red oak, and white ash are second or third leading species on more mesic sites.

In none of the nine stands, in which white oak was the first or second dominant in the tree strata, was it among the three leading species in the sapling category, table 3. White oak saplings occurred in only two of the stands with densities of 20 and 60 stems/ha. Black oak was the dominant tree species in both of the stands that occurred on the dry end of the gradient. Ironwood and white ash were important on the drier end of the gradient reaching maximum densities of 620 and 740 sapling/ha, respectively. On the mesic end of the gradient Ohio buckeye (Aesculus glabra Willd.) was the third leading dominant in one stand and paw paw (Asimina triloba [L.] Dunal.) was the most important sapling species in a single stand with 400 stems/ha. Sugar maple was the leading species in the sapling stratum in five of the nine stands.

The dominance pattern in the seedling stratum (table 4) was similar to that of the sapling stratum. White ash, ironwood, and elms were important on the drier sites, whereas sugar maple, white ash and black cherry were important on more mesic sites. Mesophytic and shade tolerant species such as basswood (Tilia americana L.), yellowbud hickory (Carya cordiformis [Wang.] K. Koch.) and blue ash (Fraxinus quadrangulata Michx.) were more important in the seedling than in the sapling stratum.

Tree diversity, as measured by the Shannon-Wiener H′ (Shannon and Weaver 1949) (table 5), was similar across the compositional gradient that was delineated using Gaussian Ordination. However, if diversity in the tree stratum is compared with that of the sapling stratum, there is a trend of decreasing diversity in the sapling stratum on mesic sites. The reverse is generally true on drier sites. If the number of species (rather than H′) is used to characterize diversity, the diversity also generally decreases from larger to smaller strata on mesic sites. However, on the drier sites the number of species tends to increase from the largest to the smallest stratum.

Table 2. Quantative information about the tree stratum in white oak forests.

IV'S TREES (THREE LEADING SPECIES)

Stand x-vector	8.2	8.5	9.8	12.7	28.6	29.7	31.7	32.5	36.3
Species									
Black oak	30.4	27.2	29.5						
White oak	23.7	25.3	33.2	50.8	45.4	41.2	29.2	22.6	14.9
American elm	9.9	12.5							
Sugar maple			13.0			23.2	29.4	23.2	37.9
Black cherry				10.2					
Ironwood				8.1					
Shagbark					24.4			15.9	
Red oak					18.0		24.2		
White ash						8.3			10.2
Basal area M^2/ha	29.7	40.0	32.8	32.0	30.8	25.6	31.4	33.5	37.9
Trees/ha	435	475	310	400	206	375	419	470	280

Table 3. The importance values and densities of the three leading sapling species.

IV'S SAPLINGS (THREE LEADING SPECIES)

Stand x-vector	8.2	8.5	9.8	12.7	28.6	29.7	31.7	32.5	36.3
Species									
White Ash	39.0	6.9		26.9	7.5	6.5	9.6		
Ironwood	24.1	47.5		23.1	9.1		28.8	46.1	22.6
American elm	13.1		15.4						
Sugar maple		12.1	48.3		70.3	80.0	61.6	49.7	31.0
Shagbark hickory			12.0			4.3			
Black cherry				13.5					
Ohio buckeye								4.2	
Paw paw									31.4
Total stems/ha x 10^{-2}	10.0	11.0	20.8	24.0	27.5	25.0	13.5	6.4	10.4

Table 4. The importance values and densities of the three leading seedling species.

IV'S SEEDLINGS (THREE LEADING SPECIES)

Stand x-vector	8.2	8.5	9.8	12.7	28.6	29.7	31.7	32.5	36.3
Species									
White ash	48.7	37.6	11.4	56.4	12.0		26.2	14.4	
American elm	10.8								
Ironwood	17.1	20.6		10.3					
Sugar maple		15.1	15.3		70.3	70.4	59.6	19.3	55.7
Red elm			44.8	11.8	6.6				
Black cherry				10.3		10.0		50.0	
Yellowbud hickory					6.6				
Ohio buckeye						10.9			
Basswood							7.8		
Paw paw									16.5
Blue ash									7.3
Total stems/ha x 10^{-2}	32.5	54.5	128.5	77.5	19.3	81.5	125.0	98.5	119.0

Table 5. Diversity patterns in white oak stands.

Stand x-vector	8.2	8.5	9.8	12.7	28.6	29.7	31.7	32.5	36.3
H_1' tree	1.91	2.00	1.79	1.67	1.40	1.84	1.55	1.95	2.03
H′ sapling	2.11	2.09	1.55	1.87	1.10	0.87	0.88	0.84	1.43
No. of species									
Seedling	12	10	12	9	5	5	7	7	12
Sapling	8	11	9	7	7	7	3	3	5
Tree	9	13	12	9	6	12	6	9	13

[1] H′ is the Shannon-Wiener function.

DISCUSSION

In this study white oak was found not replacing itself on sites where it is a canopy dominant. Species replacement patterns in white oak dominated sites is a function of site conditions. On drier sites white ash, ironwood and American elm are important replacement species, whereas on mesic sites sugar maple and white ash are prominent in the seedling and sapling strata. The status of white oak as a successional species has previously been noted. However, many studies have concluded that white oak is intermediate in shade tolerance. For example, Curtis (1959) gave white oak a climax adaptation value of 3.5 where a value of 10 indicates maximum shade tolerance. In contrast bur oak (Quercus macrocarpa Michx.) and black oak were assigned climax adaptation values of 1.0 and 2.5 respectively. Peet and Loucks (1977) separated the continuum gradient for southern Wisconsin into moisture and successional gradients, as the original Curtis and McIntosh (1951) continuum combined these two gradients. Species were assigned separate successional and moisture adaptation values ranging from zero to ten. A moisture adaptation value of zero indicates adaptation to mesic conditions and 10 adaptation to xeric conditions. Successional adaptation values also ranged from 0 to 10, with pioneer species having low values and climax species high ones.

For the oak species presented in figure 1, black, white, and red oak, the moisture adaptation values assigned by Peet and Loucks (1977) were 10.0, 6.2 and 2.9, respectively. The successional adaptation values for these species were all relatively low 2.5, 3.1 and 0.0, for black, white and red oak respectively. Their work indicates that the three oak species are successional species occupying different portions of the moisture gradient. The data presented in this paper also support this hypothesis. Black oak appears to be capable of maintaining itself only on sandy sites in central Illinois, where more shade tolerant species can not withstand the droughty conditions.

White oak does not occur on the sandy sites and appears to be limited to the silt loam soils with relatively high water storage capabilities. Shade tolerant mesophytes are capable of invading these sites and replacing white oak and other oak species. However, on drier silt loam sites dominated by black oak, this replacement is slower than on more mesic sites where white and red oak are important.

Changes in species diversity also suggest a pattern of rapid replacement of white oak by shade tolerant mesophytes on mesic sites. Diversity of the sapling and seedling layer is considerably less than that of the trees on mesic sites. However, the reverse is true for drier sites. This pattern of diversity along a moisture gradient was also reported by Auclair and Goff (1971). On mesic sites pioneers are unable to compete in the seedling and sapling strata with the few species of invading shade tolerant species and they quickly disappear from these strata. On drier sites replacement of intolerant oaks is by species such as white ash and elm that are less shade tolerant than sugar maple. Under these conditions oaks and other less shade tolerant and less competitive species persist, although at low densities. The greater number of species and a more equitable distribution of dominance results in higher diversity on the more xeric sites than on the mesic ones in the seedling and sapling strata.

During presettlement times in central Illinois (1822), using McLean County as an example, forests occurred on more rugged topography associated with river valleys and glacial moraines. The areas of less topographic relief were dominated by tallgrass prairie (Anderson 1970, Rodgers 1978). White oak was the most important species in the presettlement forests of McLean County with importance values of 34.2, 31.3 and 26.9 (Σ IV's for all species = 100) in savannah, open and closed forest communities, respectively. While the importance of white oak decreased as the forest became more closed (savannah to closed forest), the reverse was true for more mesophytic species such as elm, sugar maple, and basswood. The prairies were not completely treeless and the three leading species occurring in the prairie, or perhaps prairie edges, were black oak, white oak and bur oak (IV = 50.5, 17.3, and 13.7; respectively). The importance of bur oak decreased rapidly as the forest became more closed and its importance value in the closed forest community was only 0.34.

A hypothesis regarding the conditions needed to maintain white oak can be derived from a knowledge of presettlement forests and current trends in species replacement patterns. In presettlement times fire was an important factor in the vegetation of the Midwest (Gleason 1923, Cottam 1949, Curtis 1959, Anderson 1970, Loucks 1970, Auclair 1976). In central Illinois the areas of rugged topography were probably subjected to fire less frequently than the level areas supporting tallgrass prairies (Wells 1970, Rodgers 1978). A lessened frequency of fire permitted the maintenance of forest vegetation on the moraines and along the valleys of river systems.

It has been noted by several workers that white oak is less fire resistant than black and bur oak (Cottam 1949, Auclair 1976). This would account for the decline in importance of white oak in the prairie as compared to the other two oak species. On the other hand white oak is more fire resistant than the more shade tolerant sugar maple, elms and ashes. On sites that were protected from fire, perhaps high stream terraces and similar sites, sugar maple, elms, ash and other similarly adapted species may have dominated the vegetation. On less protected sites, that had occasional fires (perhaps 4 or 5 times per century) white oak might have achieved dominance (Loucks 1970). Occasional fires eliminated the more shade tolerant but less fire resistant species and permitted white oak to replace itself. In the past 40 or more years the virtual elimination of fire has allowed the shade tolerant species to invade the white oak dominated sites.

Structural diagrams prepared using the witness trees recorded in the Government Land Office records, and the data from three white oak stands sampled in McLean County in 1977, revealed that forty percent of the stems occurred in the smallest size class (4 in., 10.2 cm) in present forest, whereas the presettlement forest had only eight percent of its stems in this class. The dominant species in the smallest class in the present forest were sugar maple, American and red elm, and white ash, no white oak stems occurred in this size class. However, white oak stems occurred in the smallest class in the presettlement vegetation, although elms were the dominant species (Rodgers 1978).

It appears as if sugar maple may eventually gain dominance over most if not all of the sites that white oak currently is a dominant tree species. The soil depth is apparently sufficiently deep so that there is enough moisture storage to support species with higher moisture requirements than white oak. The minimum effective soil depth encountered in this study was 46 cm which is 6 cm deeper than the York Woods site in southern Wisconsin where McIntosh (1957) found white oak being replaced by sugar maple. The apparently more rapid replacement of oaks by sugar maple on protected sites may be a function of availability of seeds than of better site condition. Perhaps, only on the exposed sites with shallow soils, that are presently dominated by black oak, do site conditions limit the rapid invasion of sugar maple.

Perhaps fire, clear cutting, or a combination of both may be necessary for successful regeneration of white oak. Some experimental burns should be conducted on a limited scale to document patterns of species replacement in oak forest following fire. The data presented here and numerous literature references suggest that white oak and other oak species will diminish in importance in the next fifty to one hundred years without the application of silvicultural techniques designed to enhance their reproduction and discourage that of the shade tolerant mesophytes.

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LITERATURE CITED

Anderson, R. C. 1970. Prairies in the prairie state. Trans. Ill. State Acad. Sci. 63:214-221.

Auclair, Allan N. 1976. Ecological factors in the development of intensive-management ecosystems in the midwestern United States. Ecology 57:431-444.

Auclair, Allan N. and Grant Cottam. 1971. Dynamics of black cherry (Prunus serotina Erhr.) in southern Wisconsin oak forests. Ecol. Monogr. 41:153-177.

Auclair, Allan N. and F. Glen Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. Amer. Natur. 105:499-528.

Boggess, W. R. and J. W. Geis. 1966. The Funk Forest Natural Area, McLean County, Illinois: woody vegetation and ecological trends. Trans. Ill. Acad. Sci. 59:123-133.

Calef, Robert T. 1953. Flora and ecological analysis of the Funk Forest Natural Area, McLean County Illinois. Trans. Ill. Acad. Sci. 46:41-55.

Cottam, Grant. 1949. The phytosociology of an oak woods in southwestern Wisconsin. Ecology 30:271-287.

Curtis, John T. 1959. The vegetation of Wisconsin. The Univ. of Wisconsin Press, Madison, pp. 657.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476-496.

Ebinger, John E., Phillippe, Philip E. and Loy R. Phillippe. 1977. Woody vegetation of an upland forest in Douglas County, Illinois. Castanea 42:285-293.

Gauch, Hugh G., Gene B. Chase, and Robert H. Whittaker. 1974. Ordination of vegetation samples by Gaussian species distributions. Ecology 55:1382-1390.

Gleason, H. A. 1923. The vegetational history of the Middle West. Ann. Assoc. Am. Geogr. 12:39-85.

Loucks, Orie L. 1970. Evolution of diversity, efficiency and community stability. Am. Zoologist 10:17-25.

McIntosh, Robert P. 1957. The York Woods, a case history of forest succession in southern Wisconsin. Ecology 38:29-37.

Peet, Robert K. and Orie L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58:485-499.

Rodgers, Cassandra Sue. 1978. The presettlement vegetation of McLean and Mason Counties, Illinois. MS. thesis, Dept. of Biological Sciences, Ill. State Univ., Normal, 110 pp.

Schwegman, John. 1973. Comprehensive plan for the Illinois Nature Preserves System. Part 2. The Natural Divisions of Illinois. Illinois Nature Preserves Commission, Rockford, Ill.

Shannon, C. E. and W. Weaver. 1949. The mathematical theory of communication. Univ. Ill. Press, Urbana, Ill., 117 pp.

Wells, Philip V. 1970. Historical factors controlling vegetation patterns and floristic distribution in the central plains region of North America. Pleistocene and Recent Environments of the Central Great Plains, Ed. W. Dort and J. K. Jones. Univ. of Kansas Special Pub. No. 3, Univ. of Kansas Press, Manhattan, pp. 211-221.