Vegetation-Site Relationships in the Lake Katharine State Nature Preserve, Ohio: A Northern Outlier of the Mixed Mesophytic Forest[1]

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ABSTRACT. **Eighteen 0.1-ha plots were sampled for woody vegetation in the Lake Katharine State Nature Preserve in southeastern Ohio. These plots were selected to cover a great variety of topographic positions. Ordination (DECORANA) and classification (TWINSPAN) techniques were used to group the plots into seven site-types: ridge tops, slope edges, upper slopes, lower slopes, flood plains by small creeks, coves, and terraces by large creeks. Soil nutrients generally were higher for the lower slopes and terraces. Vegetation varied from oak-dominated upland sites to mixed mesophytic coves to floodplain stands of *Platanus occidentalis, Betula nigra,* and *Ulmus americana.* The distributions of species suggest that soil moisture is primarily responsible for determining where species occur. The low level of soil nutrients may limit the occurrence of the more nutrient-demanding mesophytic species in the area.**

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INTRODUCTION

The rich mesophytic forests of the Cumberlands and the southern Appalachians have long attracted the attention of botanists. Much of the high plant diversity of those areas can be attributed to their great topographic relief. For instance, in the rugged west-facing Pottsville Escarpment or the "cliff section" of the Cumberland Plateau, "rich mesophytic forests in the gorges alternate with pine-clad promontories and dry oak uplands" (Braun 1950). From the Cumberland Plateau, this resistant Pottsville series continues north locally along the western edge of the unglaciated Allegheny Plateau to southern Ohio. Although it is not as rich floristically as its southern counterparts, the rugged Pottsville conglomerate area of Jackson County, Ohio contains an assemblage of species (e.g. *Magnolia macrophylla, M. tripetala, Rhododendron maximum, Betula lutea, Euonymus americanus, Chionanthus virginicus,* and *Viburnum cassinoides*) unique to southern Ohio (Beatley 1959, Braun 1961).

The Lake Katharine State Nature Preserve, a 600-ha reserve administered by the Ohio Department of Natural Resources, is located in Liberty Township, Jackson County, in southeastern Ohio. It encompasses some of the best exposures in Ohio of the massive Sharon conglomerate, the basal member of the Pottsville series (Beatley 1959). The objectives of the present study were to provide an initial quantification of the major patterns of variation in plant species composition within the Preserve, and to relate these patterns to some of the more broad-scale determinants (e.g., topography and substrate) of vegetation in the mixed mesophytic forest region.

DESCRIPTION OF STUDY AREA

Jackson County has a temperate, humid, continental climate with long hot summers (Beatley 1959, Miller 1969, Critchfield 1983). Annual precipitation averages 105 cm and is well distributed throughout the year. Severe droughts do occur occasionally (8 times from 1929-1968), however. In hilly sections of the county, cool air drainage down the slopes and into the valleys is pronounced, occasionally resulting in large differences in surface temperatures between valley floors and hilltops. The growing season in Jackson County averages 154 days, with 80% of the years falling between 132 and 176 days.

Soils of the uplands and slopes of the Lake Katharine Preserve are predominately well-drained hapludults of the Clymer and Rigley series. The Clymer series is a silt loam formed in residuum derived from sandstone; the Rigley series is a sandy loam formed in colluvium at the base of the slopes. Moderately well-drained fluvaquents of the Orville series dominate the floodplains of the smaller coves and creeks, whereas well-drained dystrochrepts of the Pope series characterize the flood plains of Little Salt Creek. These upland and lowland soils are often connected by the Rigley-rock outcrop association, which has slopes of 40-70% and cliffs up to 46 m in height (Kerr 1983, Brown et al. 1984). Bedrock is the Sharon conglomerate and sandstone of the basal Pottsville (Beatley 1959). This formation is very porous, resulting in abundant seepage waters into the ravine sides and bottoms. Almost all of the forests in Jackson County are second growth (Beatley 1959). No special notes were made of the successional status of plots included in this study.

Plots were taken in two main locations within the Lake Katharine Preserve. Plots 3-10 were taken near a ravine flowing into the northwest corner of Lake Katharine. Plots 1-2 and 11-17 were taken east of Lake Katharine, near Little Salt Creek. Plot 18 was taken on a cliff immediately northeast of Lake Katharine.

MATERIALS AND METHODS

Eighteen circular 1000-m^2 plots were sampled on 15-17 September 1983. The plots were placed subjectively in areas with relatively homogeneous vegetation and topography to represent as full a range of vegetation and site types as possible within the short time available. The species and diameters at breast height (dbh) of all woody stems greater than or equal to 5 cm dbh were recorded. The total percentage of the plot covered by the leaves of woody stems less than 5 cm dbh (including seedlings and small shrubs) was estimated visually for each species, according to the following scale: 1 = less than 5% coverage; 2 = 5-25%; 3 = 25-50%; 4 = 50-75%; and 5 = 75-100%. Topographic variables recorded for each site were slope, aspect, and surface configuration (i.e., ridge top, edge, upper slope, lower slope, cove, flood plain of a small creek, or terrace of a large creek). Edge, here, refers to a relatively flat upland site adjacent to a cliff.

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Soil samples were taken by removing leaves (Oi, Oe, Oa layers) and collecting soil from the top 15 cm for several locations per plot with a soil corer. Standard soil chemical analyses for available phosphorus (P), exchangeable potassium (K), magnesium (Mg), and calcium (Ca), cation exchange capacity (CEC), pH, and percent base saturation (disregarding sodium) (North Dakota Agricultural Experiment Station 1980) were done by the Ohio Agricultural Research and Development Center in Wooster. The percentages of sand, silt, and clay were determined by the Bouyoucos hydrometer method (Brewer and McCann 1982). Species nomenclature follows Braun (1961) for shrubs and Little (1979) for trees.

Species importance values, expressed as relative basal areas in each plot, were converted to the Domin scale (usually used for percent coverage values) to give extra weight to rare species. Species present but with no stems greater than or equal to 5 cm dbh were automatically given a value of 1.0 in this transformation. The resulting values were ordinated with a detrended correspondence analysis technique (DECORANA; Hill 1979a), which Gauch (1982) found most successful in applications to community analysis. Vegetation data also were classified with a two-way indicator species analysis (TWINSPAN; Hill 1979b). A stepwise regression procedure (Helwig and Council 1979) was used to relate the ordination axis scores to soil and topographic variables. This procedure was run with and without a topographic variable having values of 1 for convex upper slopes, 2 for midslopes, 3 for coves, 4 for floodplains by small creeks, and 5 for floodplains by Little Salt Creek, the major drainage stream of the Lake Katharine Preserve. Variables were added until the coefficient of the last variable included was not significantly ($P \leq 0.05$) different from zero.

RESULTS

The first axis of the ordination separated the oak and pine sites of the edges, upper slopes, and ridges from lower, more mesic sites (Fig. 1). The second axis distinguished mesic sites occurring in narrow, rock-rimmed coves and shaded ravines from the gently sloping terrain of the lower slopes and flat terraces near Little Salt Creek. The classification of the plots by TWINSPAN produced similar results (Table 1). Following that classification, seven groups of plots, or site-types, were recognized: edges (plots 9, 18); upper slopes (5, 8, 10, 17); ridge-tops (1, 2); coves on slopes (3, 4, 16); floodplains along minor streams (6, 7); lower slopes (13, 14, 15); and terraces by Little Salt Creek (11, 12).

The stepwise regression procedure produced the following interpretation of the ordination axes. When topographic position was included, it was the variable most strongly correlated with the first axis ordination value ($r^2 = 0.75$; $P < 0.01$). First axis ordination values also were significantly and positively correlated with pH (increasing r^2 to 0.82; $P < 0.05$). When topographic

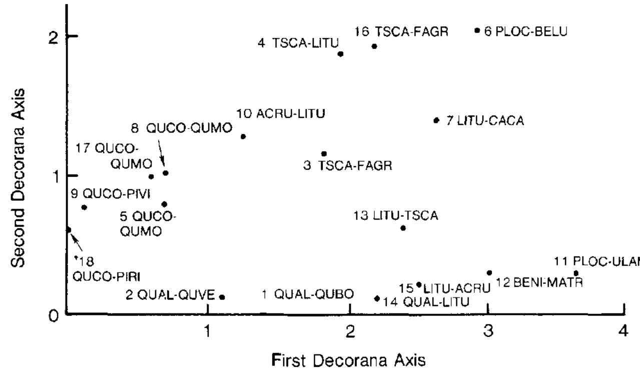

FIGURE 1. DECORANA stand ordination for Lake Katharine State Nature Preserve, Ohio. The two most important species are coded using the first two letters of the genus and species names. Complete names are given in Table 3.

TABLE 1

Dichotomous key to plots and site-types based on a TWINSPAN classification.

1. Plots with *Quercus coccinea*, *Q. velutina*, or *Sassafras albidum*
   2. Plots without *Acer saccharum*
      3. Plots with *Gaylussacia baccata*
         Edge sites: Plots 9, 18
      3. Plots without *G. baccata*
         Upper slope sites: Plots 5, 8, 10, 17
   2. Plots with *A. saccharum*
      Ridetops sites: Plots 1, 2
1. Plots without the three species listed above or with one of those species plus *Lindera benzoin*
   2. Plots without *Carya cordiformis*
      3. Plots without *Carpinus caroliniana*
         Cove sites: Plots 3, 4, 16
      3. Plots with *C. caroliniana*
         Small floodplain sites: Plots 6, 7
   2. Plots with *C. cordiformis*
      3. Plots without *Acer negundo*
         Lower slope sites: Plots 13, 14, 15
      3. Plots with *A. negundo*
         Terrace sites: Plots 11, 12

position was not included, Mg concentration was significantly, positively correlated with the first ordination axis ($r^2 = 0.60$; $P < 0.01$). Although Mg was the variable most strongly correlated with the ordination axis, most indicators of soil fertility (e.g., % base saturation, K, Ca, and Mg levels) increased from edge sites to lower slopes to terraces (Table 2). The second ordination axis was negatively correlated with pH ($r^2 = 0.31$, $P < 0.05$). This effect primarily distinguished the cove and small floodplain sites (lower pH) from the lower slope and terrace sites (Table 2).

The edge and upper slope sites had scarlet oak (*Q. coccinea*) as a dominant (Table 3). Other important species were chestnut (*Q. prinus*), black (*Q. velutina*), and white (*Q. alba*) oaks. Pitch pine (*Pinus rigida*) and Virginia pine (*P. virginiana*) were important; post-oak (*Q. stellata*) was present in the more extreme edge sites. The largest trees on these extreme sites were smaller than the largest trees on any other site. The understory of the edge and upper slope sites was dominated by small stems of most of these species plus sassafras (*Sassafras albidum*), downy serviceberry (*Amelanchier arborea*), sourwood (*Oxydendron arboreum*), black gum (*Nyssa sylvatica*), huckleberry (*Gaylussacia baccata*), mountain laurel (*Kalmia latifolia*), and a number of other ericaceous species. Bigleaf magnolia (*Magnolia macrophylla*) reached its maximum importance (14%) on one of the more protected mid to upper slope sites, which was transitional to the cove sites.

The flat ridge tops contained primarily a mixed oak forest dominated by white oak with black oak and northern red oak (*Q. rubra*) as important secondary species. Species reaching their maximum understory importance values here included hawthorn (*Crataegus* spp.), mapleleaf viburnum (*Viburnum acerifolium*), red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and slippery elm (*Ulmus rubra*).

Common canopy trees of cove sites were hemlock (*Tsuga canadensis*), tuliptree (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*). Sapling and shrub species covered less area here than in any other site-type. The largest median stem sizes also were found in these plots.

TABLE 2

Topographic characteristics, soil nutrient and size-class composition, and stem characteristics (basal area and density) for plots in Lake Katharine State Nature Preserve, Ohio.

	Edges		Upper slope				Ridge-tops			Coves		Small floodplains		Lower slopes			Terraces	
Soil properties	18	9	17	5	8	10	1	2	4	3	16	7	6	14	13	15	12	11
Aspect	SW	SSW	NW	NNW	SW	WSW	SSE	ESE	NNW	E	SE	flat	flat	NE	NE	flat	E	S
Slope (degrees)	10	30	30	12	25	30	10	12	20	22	45	0	0	25	15	0	2	4
pH	4.2	4.4	3.7	4.6	4.0	4.1	4.4	4.4	3.9	4.6	3.8	4.2	4.4	4.6	4.9	4.4	4.8	5.1
CEC (meq/100g)	16	28	11	9	12	12	13	13	17	10	10	13	14	14	12	16	14	10
% base saturation	2	4	3	5	4	4	6	6	2	5	7	14	8	17	30	18	32	53
K (mg/kg)	31	39	68	40	33	30	40	39	35	28	22	62	48	48	66	56	66	63
Ca (mg/kg)	45	40	65	50	50	50	100	90	45	65	100	285	120	415	575	400	585	775
Mg (mg/kg)	7	8	18	10	12	11	12	13	12	8	12	36	50	32	70	76	114	152
P (mg/kg)	2	2	8	3	3	6	19	59	5	32	8	7	7	154	18	10	8	16
% clay	12	15	8	14	8	8	17	12	7	8	6	16	23	11	14	29	26	21
% salt	23	27	36	29	16	14	35	23	17	13	14	46	50	20	32	42	26	28
% sand	65	58	56	57	76	78	48	65	76	79	80	38	27	69	54	29	48	51
Basal area*	24	31	26	26	20	23	26	29	41	36	27	25	20	33	35	43	24	22
Density**	1080	1120	730	840	1240	880	610	680	610	400	380	600	420	980	990	890	820	770

*Basal area in m^2/ha for stems ≥5 cm dbh.
**Density/ha for stems ≥5 cm dbh.

TABLE 3

Relative basal areas (%) of stems ≥5 cm dbh and cover class values for stems <5 cm dbh in plots in Lake Katharine State Nature Preserve, Ohio. Species are included if they make up >5% of total basal area or, for smaller stems, cover >5% of at least one plot. a, cover at <5%; b, cover at 5-25%; c, cover at 25-50%; d, cover at 50-75%; t, basal area <1%; —, not present.*

	Edges		Upper slopes				Ridge-tops			Coves		Small flood plain		Lower slopes			Terraces	
Species	18	9	17	5	8	10	1	2	4	3	16	7	6	14	13	15	12	11
Pinus rigida	28b	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gaylussacia baccata	c	c	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Quercus prinus	2	10a	29a	21a	16	1	—	—	—	—	—	—	—	—	—	—	—	—
Kalmia latifolia	b	b	c	—	d	b	—	—	—	—	—	—	—	—	—	—	—	—
Quercus coccinea	31b	67a	41a	37a	31	14	—	7	—	—	—	—	—	—	—	—	—	—
Pinus virginiana	12b	13a	—	3a	2	—	—	—	—	—	—	—	—	4	—	—	—	—
Vaccinium vacillans	a	c	a	a	—	a	—	a	—	—	—	—	—	—	—	—	—	—
Sassafras albidum	ta	b	ta	b	a	a	—	a	—	—	a	—	—	—	—	—	—	—
Quercus velutina	3	4	7	—	12	14	13	12	—	—	—	—	—	—	—	—	—	—
Oxydendron arboreum	4b	3a	3a	4b	11b	6a	—	—	7	a	a	—	—	—	—	3	—	—
Quercus alba	16	ta	3	19	7	2	53a	65a	—	—	—	—	—	22	3	2	—	—
Magnolia macrophylla	—	—	a	a	tb	14b	—	—	t	—	a	—	—	—	—	—	—	—
Nyssa sylvatica	tb	2b	4a	ta	3b	—	—	—	7a	4a	—	—	—	—	—	—	1	2
Acer rubrum	tb	ta	11a	6a	10a	17a	2b	tb	9	5a	a	6	19	—	3	11	3	—
Tsuga canadensis	a	a	ta	5b	3a	3	t	a	42a	80b	38a	a	7a	8	16	—	—	—
Prunus serotina	—	—	—	—	—	—	a	4a	—	—	—	—	—	—	—	5a	—	—
Acer saccharum	—	—	—	—	—	—	1a	3b	—	a	—	—	—	9c	tb	tb	—	—
Quercus rubra	—	—	t	—	ta	7	22	6a	—	a	10a	a	a	14	5	11a	2	—
Fagus grandifolia	—	a	a	b	—	7a	—	—	—	8	23a	—	t	ta	t	t	1	—
Cornus florida	—	a	t	1b	—	t	a	a	—	a	—	—	—	—	1	ta	1a	t
Liriodendron tulipifera	a	—	—	a	—	17a	—	—	26	a	15	82	1	19a	67	48	5	—
Fraxinus americana	—	—	—	—	—	—	5a	a	—	t	—	—	—	7a	ta	ta	a	6
Magnolia tripetala	—	—	ta	a	a	1	—	a	ta	a	2a	2a	4a	—	—	ta	21b	6a
Betula lutea	—	—	—	—	—	—	—	—	8	—	13a	t	28	—	—	—	—	—
Carpinus caroliniana	—	—	—	—	t	a	a	—	—	—	—	8b	5c	t	1	5a	4b	5b
Lindera benzoin	—	—	—	—	—	—	—	—	—	a	a	b	b	—	a	a	a	b
Carya cordiformis	—	—	—	—	—	—	—	—	—	—	—	—	—	14a	2a	a	a	2
Staphylea trifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	b	a	—	—	b
Ulmus americana	—	—	—	—	—	—	—	—	—	—	—	—	—	1a	1	5a	ta	15
Betula nigra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	60	11
Platanus occidentalis	—	—	—	—	—	—	—	—	—	—	—	—	35	—	—	—	—	26
Acer negundo	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	a	13b
Gleditsia triacanthos	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10

*Other species found at least once were *Amelanchier arborea, Asimina triloba, Carya glabra, C. ovalis, C. tomentosa, Castanea dentata, Corylus americana, Crataegus* sp., *Euonymus americanus, Hamamelis virginica, Hydrangea arborescens, Juglans cinerea, Juniperus virginiana, Quercus bicolor, Q. stellata, Rubus allegheniensis, Sambucus canadensis, Ulmus rubra, Vaccinium arboreum, V. stamineum, Viburnum acerifolium, V. cassinoides, V. dentatum, V. lentago,* and *V. prunifolium.*

Floodplains of the smaller creeks varied in canopy composition: one was composed almost entirely of tuliptrees; the other had yellow birch and sycamore (*Platanus occidentalis*). Both had well developed, lower layers of musclewood (*Carpinus caroliniana*), spicebush (*Lindera benzoin*), and umbrella magnolia (*Magnolia tripetala*). Most stems were small, but a few large ones occurred.

The three lower slope sites showed much variation in the importance values of the dominant species, which were the tuliptree, white oak, northern red oak, hemlock, and bitternut hickory (*Carya cordiformis*). Important shrub and sapling species were sugar maple (*Acer saccharum*), witch hazel (*Hamamelis virginiana*), white ash (*Fraxinus americana*), bladdernut (*Staphylea trifoliata*), and wild hydrangea (*Hydrangea arborescens*).

The terrace sites had the highest average importance values of river birch (*Betula nigra*, 60%), umbrella magnolia (21%), and American elm (*Ulmus americana*, 15%). Other important tree species were tuliptree and sycamore. Many shrub and sapling species reached their maximum importance here, including umbrella magnolia, musclewood, hazel (*Corylus americana*), spicebush, pawpaw (*Asimina triloba*), and box-elder (*Acer negundo*).

DISCUSSION

These data suggest that topographic position is related to many of the observed species distributions. There are several possible mechanisms which might be responsible for this relationship.

One mechanism by which topographic position can affect the distribution of species is its effect on the relative availability of soil nutrients. For the Lake Katharine plots, Ca, Mg, and clay levels were highest in the lower slopes and terraces. Franzmeier et al. (1969) attributed the high base status of lower topographic positions to seepage and the concentration of leaves on lower slopes prior to decay and loss of bases such as K, Ca, and Mg. The high base status of the lower slopes and terraces may also reflect the internal nutrient cycling characteristics of the dominant tree species (Muller and Martin 1983, Boerner 1984).

Topographic position can also affect soil moisture availability (e.g., Whittaker 1956, Hack and Goodlet 1960). Beatley (1959) argued that the most important variable influencing the vegetation in Jackson County is soil moisture, which is determined by the movement of water through the bedrock, the physical properties of the soils and parent materials, and the exposure and elevation of the site above base level. In particular, the very porous Pottsville, (i.e., Sharon and Massilon) sandstones of the Lake Katharine area allow for a rapid movement of water from ridges and uplands to slopes and ravine bottoms. Much water is stored in coarser-textured sandstones above their contact with more impervious shales and finer-grained sandstones. Surface runoff and seepage from the sandstone maintain the moisture content of the lower slopes and the valley bottom soils throughout the growing season (Beatley 1959). Several lowland species (e.g., *Liriodendron tulipifera, Betula nigra*, and *Platanus occidentalis*) important in the Lake Katharine area are known to do best on soils that are moist, but well-drained and well-aerated (Auten 1945, Dickson et al. 1965, Wistendahl 1980). The variation in water availability with topographic position may be as important as the variation in nutrient composition. For example, the order of oaks on the first ordination axis was *Q. stellata* < *Q. prinus* < *Q. coccinea* < *Q. velutina* < *Q. alba* < *Q. rubra* (Table 2). If the first axis is interpreted primarily as a moisture gradient, this order becomes compatible with other rankings of different subsets of these species in Crankshaw et al. (1965), Fowells (1965), and McCarthy et al. (1984).

Topography can also influence microclimate. Many of the narrow ravines or coves in the Lake Katharine Preserve support elements of a more northern flora, such as *Betula lutea* and *Viburnum cassinoides*. In southeastern Ohio, hemlock also is almost entirely confined to moist coves and stream gorges (Gordon 1969). Adams and Loucks (1971) attributed the association of hemlock with ravines in southeastern Wisconsin to cold air drainage and a photosynthetic optimum nearer the cooler temperatures of the ravines than the warmer adjacent upland sites. Microclimatic factors may be responsible for the disjunct occurrence of several southern species (e.g., *Magnolia macrophylla* and *Euonymus americanus*) on protected slopes in the Preserve (Wolfe 1951), although historical factors also have been implicated (Wolfe 1942).

The relatively sterile nature of the sandstone-derived soils was evident in the low pH values (3.7-5.1) and low concentration of bases (e.g., Ca^{++} levels of 40-775 mg/kg). These values are similar to those obtained by Boerner (1984) for Neotoma Valley, another site in southern Ohio whose soils are derived from sandstones, and whose species composition is similar to that of the present study. In contrast, Muller (1982) found higher values for pH and for K, Ca, and Mg concentrations in a richer, mixed mesophytic forest in southeastern Kentucky.

Several species (i.e. *Aesculus octandra, Tilia heterophylla*, and *Acer saccharum*), cited by Braun (1950) as indicative of the mixed mesophytic forest region, were either absent or poorly represented in the Lake Katharine Preserve. Although *Aesculus octandra* occurs in Jackson County, it is limited to areas with a more calcareous substrate (Beatley 1959, 1979). The basswoods (*Tilia americana* and *T. heterophylla*), which were noticeably absent, and white ash and sugar maple, species found in low abundance in the Preserve, all grow best on sites having high base status (Crankshaw et al. 1965, Fowells 1965, Muller 1982). The lack of calcareous soil parent materials also may have been responsible for the absence of many of the more nutrient-demanding floodplain species such as *Aesculus glabra* and *Celtis occidentalis* on the terrace soils of Little Salt Creek (Beatley 1959, 1979).

In conclusion, overall patterns in the vegetation of the Preserve seem to have been determined by the relatively resistant nature of the sandstone bedrock that created a strong three-dimensional topographic pattern. Topography, in conjunction with substrate, influences both the external supply of moisture to and the internal drainage of moisture from the sites. Although the Lake Katharine area encompasses a wide array of microclimatic and microedaphic conditions, it still represents a less diverse version of the rich forests of the Cumberlands to the south. We hypothesize that the lower diversity of the flora of this area reflects the low base status of the relatively homogeneous substrate.

An alternative explanation for differences between the vegetation of the Lake Katharine area and the Cumberlands is that climatic differences, particularly winter extremes and length of growing season, may eliminate some species. For example, Beatley (1979) suggested that the distribution of *Aesculus octandra* in southeastern Ohio is controlled by climate more than chemical adaptive variables. Climatic factors undoubtedly do affect the distribution of several species. However, several other typical mixed mesophytic species absent or at low levels in the Lake Katharine area (e.g., *Acer saccharum, Magnolia acuminata, Fraxinus americana, Juglans nigra*) are found further north, implying that soil chemistry and not climate is the primary factor limiting their abundance in the area studied.

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LITERATURE CITED

Adams, M. S. and O. L. Loucks 1971 Summer air temperatures as a factor affecting net photosynthesis and distribution of eastern hemlock (*Tsuga canadensis* L. (Carriere)) in southwestern Wisconsin. Amer. Midland Natur. 85: 1-10.

Auten, J. T. 1945 Prediction of site index for yellow poplar from soil and topography. J. For. 43: 662-668.

Beatley, J. C. 1959 The primeval forests of a periglacial area in the Allegheny Plateau (Vinton and Jackson Counties). Bull. Ohio Biol. Surv., N.S. 1(1).

——— 1979 Distribution of buckeyes (*Aesculus*) in Ohio. Castanea 44: 150-163.

Boerner, R. E. J. 1984 Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio. Can. J. For. Res. 14: 794-802.

Braun, E. L. 1950 Deciduous forests of eastern North America. Blakiston Co., Philadelphia. 596 p.

——— 1961 The woody plants of Ohio. Hafner, New York. 362 p.

Brewer, R. and M. T. McCann 1982 Laboratory and field manual of ecology. Saunders, Philadelphia. 269 p.

Brown, D. L., R. Robbins and J. Kerr 1984 U.S. Department of Agriculture, Soil Conservation Service, Soil maps of Jackson County. Unpublished. Soil Conservation Service Office, Jackson, Ohio.

Crankshaw, W. B., S. A. Qadir and A. A. Lindsey 1965 Edaphic controls of tree species in presettlement Indiana. Ecology 46: 688-698.

Critchfield, H. J. 1983 General climatology. 4th Ed. Prentice-Hall, Englewood Cliffs, N.J. 453 p.

Dickson, R. E., J. F. Hosner and N. W. Hosley 1965 The effects of four water regimes upon the growth of four bottomland tree species. Forest Science 11: 299-305.

Fowells, H. A. 1965 Silvics of forest trees of the United States. U.S. Forest Service Handbook 271. 762 p.

Franzmeier, D. P., E. J. Pedersen, T. J. Longwell, J. G. Byrne and C. K. Losche 1969 Properties of some soils in the Cumberland Plateau as related to slope aspect and position. Soil Sci. Soc. Amer. Proc. 33: 755-761.

Gauch, H. G. 1982 Multivariate analysis in community ecology. Cambridge University Press, New York. 298 p.

Gordon, R. B. 1969 The natural vegetation of Ohio in pioneer days. Bull. Ohio Biol. Survey N.S. Vol. 3(2). 109 p.

Hack, J. T. and J. C. Goodlett 1960 Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S. Geol. Surv. Prof. Paper 347. 66 p.

Helwig, J. T. and K. A. Council 1979 The SAS user's guide, 1979 Edition. SAS Institute Inc., Raleigh, N.C. p. 391-396.

Hill, M. O. 1979a DECORANA—A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, N.Y. 52 p.

——— 1979b TWINSPAN—A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York. 90 p.

Kerr, J. W. 1983 An inventory of Ohio's soils: Jackson County. Progress Report Number 69, Ohio Department of Natural Resources.

Little, E. L. 1979 Checklist of United States trees (native and naturalized). U.S. Dept. Agric., Agric. Handb. 541. 375 p.

McCarthy, B. C., T. I. Vierheller and W. A. Wistendahl 1984 Species ordination of upper slope oak-hickory stands of southeastern Ohio. Torrey Bot. Club 111: 56-60.

Miller, M. E. 1969 Climatological summary of Jackson, Ohio. Summary No. 20. National Climatic Data Center, Asheville, North Carolina.

Muller, R. N. 1982 Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. Ecology 63: 1901-1917.

——— and W. H. Martin 1983 Autumn leaf fall and nutrient return in an old-growth and a second-growth forest in eastern Kentucky. Bot. Gaz. 144: 552-558.

North Dakota Agricultural Experiment Station 1980 Recommended chemical soil test procedures for the North Central region. Bull. No. 499 (Revised). North Dakota State University, Fargo. 33 p.

Whittaker, R. H. 1956 Vegetation of the Great Smoky Mountains. Ecol. Monog. 26: 1-80.

Wistendahl, W. A. 1980 River birch-sycamore forest cover type, p. 47. *In* F. H. Eyre (ed.), Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C.

Wolfe, J. N. 1942 Species isolation and a proglacial lake in southern Ohio. Ohio J. Sci. 42: 2-12.

——— 1951 The possible role of microclimate. Ohio. J. Sci. 51: 134-138.