THE GROUNDLAYER OF THE BEECH-MAPLE FOREST: SPECIES COMPOSITION AND COMMUNITY STRUCTURE[1]

James B. Levenson[2] and Marion T. Jackson
Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809

Abstract.--The groundlayer stratum in each of 21 old-growth beech-maple forest stands in Indiana, Michigan and western Ohio was sampled by recording all vascular plants less than 0.5 m tall in each of 40, 1 x 2.5 m rectangular plots in each stand. Density, frequency and importance percentage were calculated for each species of every stand. Regional measures of abundance, constance and importance percentage were compiled in an association-wide summary.

Sugar maple (*Acer saccharum* Marsh.) and woodbine (*Parthenocissus quinquefolia* (L.) Blanch.) were the predominant species of the groundlayer. However, within each stand, specific microsite conditions supported recurring assemblages of subordinate species at locally high densities. Indices of association for the 30 most common herbaceous species were calculated to test the significance of the recurring assemblages.

A community ordination of the 21 stands was constructed. The ordination was linear and determined by the degree of domination by sugar maple and woodbine. A general inverse relationship between the two species suggested available light as a major variable. Actual placement of each stand along the gradient was correlated with moisture requirements of the species.

Additional keywords: Beech-Maple Association, Groundlayer, Indiana-Michigan-Ohio forests, Ordination, Species Association.

INTRODUCTION

Urbanization and agricultural development in the central United States have reduced and fragmented once-regional ecosystems into widely isolated forest remnants. The vegetation of such forest systems has become the focal point of recent research efforts (Forman and Elfstrom 1975; Greller 1975; Suhrweir and Tramer 1976; Levenson 1980). Maintenance, management and preservation of original communities and endangered species becomes more difficult as natural systems become more limited and isolated.

---

[1]A research grant from the Indiana Academy of Science is gratefully acknowledged.

[2]Present address: Energy and Environmental Systems Division, Argonne National Laboratory, Argonne, Illinois 60439.

The initial step in the preservation of regional biotic diversity is to obtain a quantified inventory of the community types remaining. The predominant forest vegetation of the central region of the Midwest was the Beech-Maple Association (Braun 1950). Studies of the tree composition of the Beech-Maple Association were completed by several workers (Braun 1950; Curtis 1959; Escobar 1971; Dunn and Jackson 1978). A review of the literature indicates few quantitative groundlayer studies, most of which were in Wisconsin, the northwest extent of the Beech-Maple Association. Curtis (1959) incorporated the results of previous findings by Whitford (1949), Curtis and McIntosh (1951), Whitford and Salamun (1954), Ward (1956) and Struik (1957) into the most complete regional description of the groundlayer available. Recently, Rogers (1980) analyzed groundlayer vegetation in maple-basswood and beech-maple dominated old-growth forests of Minnesota, Wisconsin and Michigan.

In light of these facts, the objectives of this paper were to: 1) survey the groundlayer of some of the few remaining old-growth beech-maple stands of Indiana, Ohio and Michigan; and 2) present a quantitative description of the groundlayer vegetation for the central region of the Association's range.

STUDY AREA

The Beech-Maple Region, as described by Braun (1950), lies entirely within the area encompassed by Wisconsinan-aged glaciation (Fig. 1). The western border of the Beech-Maple Region represents the prairie-forest margin where the Beech-Maple Association interdigitates with a mosaic of Oak-Hickory and Prairie Associations. The "Prairie-peninsula" extends into Indiana and Michigan with outliers in Ohio and even into Pennsylvania (Transeau 1935). Outliers of the Beech-Maple Association exist along the southeastern edge of Wisconsin. These stands are disjunct from the major Beech-Maple Region and are separated from it by Lake Michigan.

The northern boundary across Michigan is arbitrary and is based on the soil transition zone between the spodosols of the hemlock-northern hardwoods association and the alfisols of the more southern deciduous forests (Veatch 1932). The Beech-Maple Association is not found throughout southern Michigan; instead, it occurs on small isolated tracts of slightly higher ground overlooking swamps and bogs (Bingham 1945). It is probable that the Beech-Maple Association was formerly more widely spread, but the shortage of well-drained sites in this region led to the clearing of the better sites for agriculture.

The Beech-Maple Region extends across southern Ontario to Lake Ontario, and skirts the southern shores of Lakes Erie and Ontario into Pennsylvania and New York. The eastern and southern border of the Region follows the terminus of early Wisconsinan glaciation. Here the boundaries in Ohio and Indiana lie adjacent to the Unglaciated Allegheny and Central Low Plateau physiographic provinces (Fenneman 1938; Thornbury 1965). These areas are forested with the mixed-mesophytic and the western mesophytic forest associations described by Braun (1950, 1961). The Beech-Maple Association reached its maximum development on the tillplains of Ohio and Indiana. The tillplains are highly valued as rich agricultural lands and have been extensively cleared. Küchler (1964), Escobar (1971), and Lindsey *et al.* (1969) describe

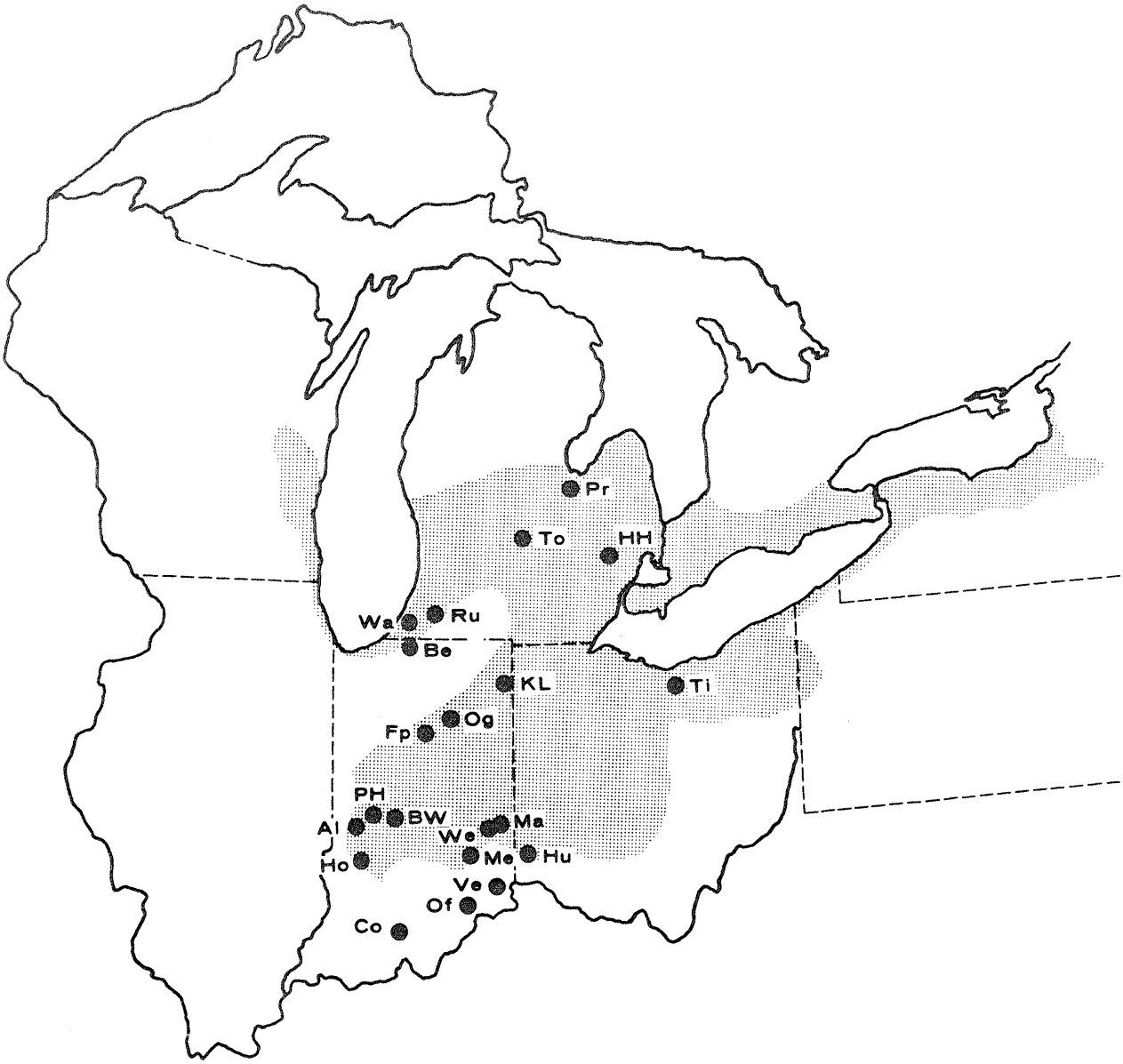

Figure 1. The Beech-Maple Region described by Braun (1950). Stands sampled in this study are indicated. Stand symbols are listed in Table 2.

the presence of the Beech-Maple Association beyond the limits outlined by Braun (1950). For example, several stands exist on favorable sites south of the Wisconsinan glacial boundary in Indiana and Ohio (Jackson and Allen 1969; Vankat et al. 1975). Table 1 summarizes topographic, pedologic and climatic information for the stands sampled. Specific stand locations are found in Levenson (1973).

Table 1. Topographic, edaphic, and mean annual climatic data for each of 21 old-growth beech-maple forests.

Stand	Topography	Soil Texture	Precip. (cm)	Temp. (°C)	Growth Season (Days)
	Northern Moraine and Lake Physiographic Unit (Wisconsinan Glaciation)				
Bendix Gift Park	Moderate east-facing slope	Fine sandy loam	97.8	10	165
Fred Russ Forest	Level outwash plain	Sandy loam	95.0	10	165
Haven Hill	Interlobate moraine	Sandy loam	85.9	8	130
Kado-Lato	River terrace	Fine sandy loam	89.4	10	157
Price Memorial	Lacustrine plain	Fine sandy loam	72.0	8	150
Timberlane Camp	Entrenched terrace	Sandy loam and silt	86.9	10	195
Toumey Woods	Level moraine	Fine sandy loam	78.7	8	180
Warren Woods	Level plain	Silt loam	89.4	10	180
	Wisconsinan-age Glaciation Till Plains				
Allee Woods	Dissected upland	Silt loam	105.9	12	163
Big Walnut Valley	Dissected upland	Silt loam	99.1	12	175
Floodplain	Floodplain	Fine sandy loam	89.9	12	161
Hueston Woods	Dissected east slope	Silt loam	98.6	13	155
Manlove Woods	Level upland w/depressions	Silt loam	101.6	11	163
Meltzer Woods	Level outwash plain	Silt loam & Silty-clay loam	98.8	12	175
Ogden Woods	Level with depressions	Silty-clay loam	86.9	11	155
Pine Hills	North-facing incised terrace	Silt loam	89.2	12	163
Weaver Woods	Gentle west-facing slope	Silt loam	101.6	11	163
	Illinoian-age Glaciation Till Plains				
Hoot Woods	Gentle to moderate east-facing slope	Silt loam	104.6	12	175
Officer's Woods	Dissected north-facing slope	Silt loam	104.6	14	190
Versailles State Park	Gentle northeast-facing slope	Silt loam	102.9	14	178
	Unglaciated Mitchell Plain Physiographic Unit				
Cox Woods	Karst	Silt loam	112.8	13	170

METHODS AND MATERIALS

Stand Selection Criteria

Due to the delicate nature of herbs and their vulnerability to disturbance, the stands were selected carefully. Forests were included in this study only if they met the following criteria: 1) a canopy layer composed of at least 50% American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.); 2) no evidence of disturbance in the form of grazing, or timber harvesting within the past 50 years; and 3) a minimum old-growth sampling area of 10 acres (4 ha).

Stands were also selected to provide broad coverage throughout the Indiana, Michigan, and western Ohio portion of the Beech-Maple Region.

The works of Lindsey *et al*. (1969) and Escobar (1971) were invaluable in locating prospective beech-maple stands in the tri-state area. Field reconnaissance of a number of prospective locations yielded 21 stands which met the pre-defined criteria: 14 in Indiana, 5 in Michigan and 2 in Ohio (Fig. 1). The study sites are among the best remaining examples of the central Beech-Maple Association.

Field Sampling Methods

Each stand was sampled by the stratified-random line-strip method (modified from Lindsey 1955). Disturbed areas such as footpaths, trails, windthrows and stand margins were avoided since such areas do not harbor herbaceous communities typical of the undisturbed forest floor. A series of nested plots was used to sample the canopy, understory, shrub and groundlayers simultaneously within the parallel line strips (Fig. 2). A 100 m tape delimited the midline and length of line-strips. Each strip was partitioned into four 10 x 25 m plots where all individual trees greater than 3 m tall were recorded by species and diameter breast height (dbh) for the canopy and understory strata (Dunn and Jackson 1978). All woody stems between 0.5 and 3 m tall within a 2.5 x 10 m subplot were recorded by species and included in the shrub stratum (Donselman 1973).

Nested within each subplot, a second subplot, 1 x 2.5 m was established to sample the groundlayer. All stems of vascular plants less than 0.5 m tall were recorded by species within the 0.01 ha total area within the 40 plots. Because many of the groundlayer species form a stoloniferous network beneath the leaf litter and reproduce vegetatively, it was often impracitcal to determine the extent of a single plant. Therefore, each stem that originated at ground level was considered an individual (Whitford 1949).

Voucher specimens of unknown individuals were collected and subsequently identified and stored in the Indiana State University herbarium. Nomenclature follows Little (1953) for trees, Gleason (1952) for herbs and Wherry (1961) for Pteridophytes.

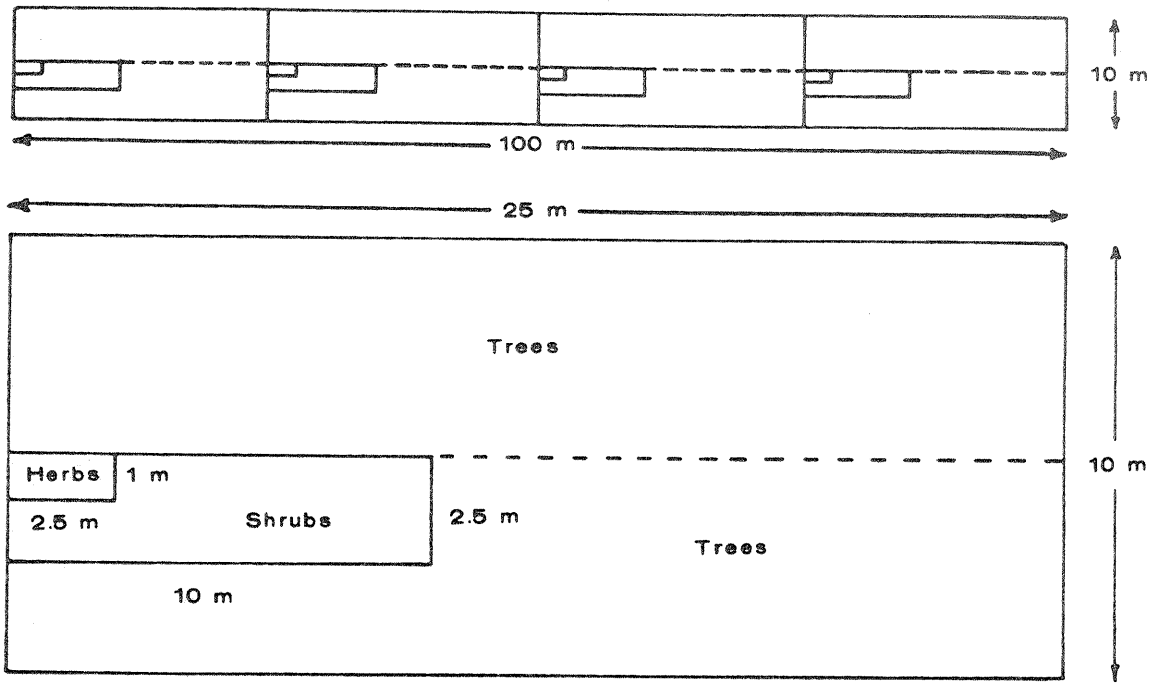

Figure 2. Dimensions and arrangement of the nested plots utilized in sampling the canopy, shrub and groundlayer strata.

Data Analysis

Sample data were organized on two levels: on the stand level and on the regional level. Tables of species attributes, including density, relative density, frequency, relative frequency and importance percentage (Lindsey 1956) were compiled for each stand. Abundance (Whitford 1949) and coefficient of association (Cole 1949) were determined at the stand level (Levenson 1973).

Regional species' attributes were derived for the overall Beech-Maple Association based on the 21 stands sampled. An Association Importance Percentage was derived in a similar manner by averaging the relative density and relative frequency for each species.

Constancy (Braun-Blanquet 1928) is a character which is analogous to frequency, but at the Association level, and expressed also as a percentage.

Abundance gives the average number of individuals of a species per subplot (expressed as a percentage) for the subplots in which it occurs. Abundance indicates the extent of clumping or the distribution of the species, as well as an insight into the efficiency of reproductive dispersion. Abundance lends itself well to both intrastand and interstand comparisons. For the Association-wide comparison, the total density of a species for all stands was divided by the total number of subplots of occurrence for all stands.

$$\text{Abundance} = \frac{\text{number of individuals of a species}}{\text{number of subplots in which species occurred}} \times 100$$

The presence-frequency index (Anderson 1948) represents an index of commonness and is directly related to the probability "of finding that particular species at any given point in any stand of the community" (Curtis 1959). This study did not lend itself to calculating presence, but since constancy is so closely related to presence, it was substituted for presence resulting in the constancy-frequency index (C-F Index). Simpson's Diversity Index (Simpson 1949) was calculated for each stand.

The ecological associations between species were determined by Cole's (1949) Coefficient of Association Index. The significance of each association was tested to the 0.95 level of probability using the Chi-square test and 1 degree of freedom. Because of the large number of species involved, only the top 30 herbaceous species were tested (as based on the Association Importance Percentage). Woody species and spring ephemerals were omitted.

A community ordination (modified from Bray and Curtis 1957) was constructed using the importance percentage as the integrating expression. The resultant model represents a gradient of species composition change, or continuum, for one stand to another.

RESULTS AND DISCUSSION

Species Attributes

A total of 174 species was encountered in the groundlayer, of which 60% (108) were herbaceous (Table 2). The mean percentage of herbaceous species in the groundlayer, calculated for each stand, was 58% with a standard deviation of 7%. Individual stands ranged from a low of 36 species in Toumey Woods to a high of 74 at Allee Woods and Timberlane Camp. Density per 0.01 ha varied from only 1,169 in Toumey Woods to 3,827 in Floodplain Beech-Maple, with a mean value of 2,343. Big Walnut was the most diverse stand at a .055 Simpson's Index Value (Table 2).

Table 3 presents a study-wide summary of all species encountered arranged in order of decreasing Association Importance Percentage. The list closely parallels that of Williams (1936) and Curtis (1959), with the same species having similar quantitative attributes.

The lower the abundance value, the more randomly the species is distributed. In general, an abundance value greater than 10 indicates a strong tendency for the species to clump due to one of several reasons: 1) the species has a narrow range of site preference and a high density at the site, e.g., *Asarum canadense* and *Impatiens pallida*; 2) the species is stoloniferous, creating an apparent density that is higher than actually exists, e.g., *Parthenocissus quinquefolia* and *Rhus radicans*; or 3) the species has multiple stems emanating from the same rootstock, e.g., *Cystopteris fragilis* and *Galium* spp. For perennial plants, distribution patterns are related primarily to vegetative reproduction (Struik and Curtis 1962).

Table 2. Stand density, herbaceous composition and species diversity for each of 21 old-growth beech-maple forests. (Subsections of the table represent the major physiographic units of Table 1.)

Stand	Symbol	Density per 0.01 ha	Species Total	Species Herbs	Species % Herbs	Simpson's Diversity Index
Bendix Gift Park	Be	2199	45	30	60	.217
Fred Russ Forest	Ru	1524	47	27	57	.141
Haven Hill	HH	2237	68	38	55	.094
Kado-Lato Woods	KL	1820	62	35	56	.248
Price Memorial Forest	Pr	1400	49	34	69	.194
Timberlane Camp	Ti	3767	74	53	71	.061
Toumey Woods	To	1169	36	17	47	.223
Warren Woods	Wa	2023	55	32	58	.128
Allee Woods	Al	3414	74	45	60	.101
Big Walnut Valley	BW	2402	67	40	59	.055
Floodplain Beech-Maple	Fp	3827	50	27	54	.203
Hueston Woods	Hu	1663	49	31	63	.160
Manlove Woods	Ma	1919	47	33	70	.127
Meltzer Woods	Me	3690	54	26	48	.219
Ogden Woods	Og	1626	55	31	56	.096
Pine Hills	PH	1626	58	34	58	.084
Weaver Woods	We	2312	52	33	63	.107
Hoot Woods	Ho	1518	52	29	55	.139
Officer's Woods	Of	3609	40	17	42	.192
Versailles State Park	Ve	2544	65	37	57	.066
Cox Woods	Co	2890	69	38	55	.157
Total		--	174	108	60	--
Mean		2343	55	33	58	.143
Standard Deviation		841	11	8	7	--

Only 6 species occurred in all 21 stands, whereas, 38 species occurred in only 1 stand (Table 3). Constancy, because of the manner in which it was derived, naturally increased with sample and plot size. The increase was least with contagious species and greatest for randomly distributed species (Curtis and McIntosh 1950). The constancy-frequency index (C-F Index) expresses the degree of commonness of the species. The upper limit of the expression is 100, in which case a species occurred in all plots of all stands. Only the two leading species had a C-F Index over 50.

Table 3. Species attributes for 174 groundlayer species encountered within the Beech-Maple Association. Species are ordered according to decreasing Association Importance Percentage. The 70 species represented at less than 0.1 Association Importance Percentage are listed collectively.

Species	Density (0.01 ha)	Frequency	Abundance	Constancy	C-F Index	Association Importance Percentage
Parthenocissus quinquefolia (L.) Blanch.	456.6	55.4	21.03	1.00	55.40	13.10
Acer saccharum Marsh.	176.1	74.5	5.91	1.00	74.50	8.01
Viola eriocarpa Schw.	113.5	32.9	8.63	1.00	32.90	4.03
Impatiens pallida Nutt.	111.9	16.1	17.40	.62	9.98	3.31
Osmorhiza claytoni (Michx.) Clarke	48.8	33.0	3.70	.90	29.70	2.93
Euonymus obovatus Nutt.	84.1	15.7	13.39	.86	13.50	2.69
Ulmus rubra Muhl.	44.1	28.3	3.89	1.00	28.30	2.56
Laportea canadensis (L.) Gaud.	89.2	11.3	19.72	.67	7.57	2.55
Galium concinnum T&G.	76.7	9.6	19.89	.48	4.61	2.19
Arisaema triphyllum (L.) Schott.	43.5	20.0	5.44	.95	19.00	2.07
Prunus serotina Ehrh.	26.3	25.6	2.57	1.00	25.60	2.02
Lindera benzoin (L.) Blume.	28.1	24.4	2.88	.76	18.50	1.99
Asarum canadense L.	75.6	4.8	39.67	.48	2.30	1.89
Fagus grandifolia Ehrh.	18.9	25.0	1.89	.86	21.50	1.83
Sanicula canadensis L.	30.8	19.6	3.92	.81	15.88	1.78
Polygonatum pubescens (Willd.) Pursh.	23.2	20.1	2.89	.90	18.09	1.65
Fraxinus americana L.	24.5	18.8	3.26	.76	14.29	1.60
Rhus radicans L.	51.5	8.7	14.81	.71	6.18	1.60
Phlox divaricata L.	46.7	10.4	11.28	.62	6.45	1.59
Maianthemum canadense Desf.	56.2	6.6	21.09	.14	.92	1.58
Mitchella repens L.	56.8	3.8	37.25	.33	1.25	1.43
Acer nigrum Michx. f.	42.2	7.5	14.06	.29	2.18	1.33
Smilacina racemosa (L.) Desf.	20.1	15.1	3.32	.67	10.12	1.29
Pilea pumila (L.) Gray	32.7	9.4	8.70	.48	4.51	1.24
Carya cordiformis (Wang.) K. Koch	9.6	17.0	1.41	1.00	17.00	1.18
Circaea quadrisulcata (Maxim) Franch.	26.3	10.5	6.28	.67	7.04	1.16
Podophyllum peltatum L.	17.3	12.4	3.53	.67	8.31	1.07
Trillium recurvatum Beck.	18.6	10.5	4.44	.43	4.39	1.00
Galium circaezans Michx.	20.9	8.8	6.01	.67	5.90	.94
Asimina triloba (L.) Dunal.	9.7	11.3	2.14	.62	7.01	.85
Sanguinaria canadensis L.	16.0	8.5	4.72	.52	4.42	.82
Viburnum acerifolium L.	17.5	7.6	5.73	.52	3.95	.81
Galium triflorum Michx.	19.9	6.3	7.87	.43	2.71	.78
Hydrophyllum canadense L.	21.8	5.5	9.93	.43	2.37	.78
Quercus rubra L.	5.8	10.8	1.33	.67	7.24	.74
Phryma leptostachya L.	8.6	9.8	2.21	.57	5.59	.74
Acer rubrum L.	11.8	8.1	3.65	.38	3.08	.71
Cornus florida L.	11.4	8.1	3.53	.43	3.48	.71
Fraxinus pennsylvanica Marsh.	8.6	8.7	2.47	.57	4.96	.68
Carex laxiflora Lam.	13.0	6.8	4.77	.48	3.26	.66
Actaea alba (L.) Mill.	6.4	7.9	2.03	.81	6.40	.59
Boehmeria cylindrica (L.) Sw.	10.7	6.2	4.31	.52	3.22	.58
Carex plantaginea Lam.	7.3	7.4	2.48	.62	4.59	.58
Smilax hispida Muhl.	6.4	7.1	2.25	.90	6.39	.55
Sambucus canadensis L.	6.1	7.0	2.17	.81	5.67	.53
Cystopteris fragilis (L.) Bernh.	20.0	1.8	28.07	.38	.68	.53
Ostrya virginiana (Mill.) K. Koch	4.8	7.3	1.63	.71	5.18	.52
Hydrophyllum appendiculatum Michx.	17.4	2.5	17.38	.14	.35	.51
Celtis occidentalis L.	4.8	7.0	1.69	.48	3.36	.50
Viola papilionacea Pursh.	7.7	5.7	3.38	.43	2.45	.49
Trillium gleasoni Fern.	5.1	5.8	2.18	.57	3.31	.44
Ribes cynosbati L.	7.4	4.8	3.88	.71	3.41	.43
Solidago caesia L.	9.2	4.1	5.68	.48	1.97	.43
Smilax rotundifolia L.	7.6	4.5	4.18	.33	1.49	.42
Amphicarpa bracteata (L.) Fern.	7.6	4.0	4.74	.52	2.08	.39
Polygonum virginianum L.	5.7	4.8	3.00	.57	2.74	.39
Geranium maculatum L.	7.9	3.9	5.03	.38	1.48	.39

Table 3 Continued.

Eupatorium rugosum Houtt.	5.9	4.3	3.42	.52	2.24	.37
Carex platyphylla	4.0	4.7	2.13	.71	3.34	.35
Sassafras albidum (Nutt.) Nees.	4.4	4.3	2.58	.33	1.42	.34
Menispermum canadense L.	4.9	3.6	3.43	.43	1.55	.31
Allium tricoccum Ait.	6.9	2.6	6.59	.38	.99	.30
Vitis vulpina L.	3.0	4.1	1.82	.62	2.54	.29
Poa sylvestris Gray	4.2	3.3	3.14	.52	1.72	.28
Botrychium virginianum (L.) Sw.	2.6	3.8	1.72	.71	2.70	.27
Medeola virginiana L.	5.4	2.7	4.91	.14	.38	.27
Geum canadense Jacq.	3.0	3.5	2.14	.52	1.82	.26
Brachyelytrum erectum (Shreb.) Beauv.	4.6	2.7	4.17	.38	1.03	.25
Cryptotaenia canadensis (L.) DC.	3.3	3.2	2.56	.38	1.22	.25
Trillium cernuum L.	3.0	3.3	2.21	.43	1.58	.25
Aster cordifolius L.	5.8	2.3	6.42	.29	.67	.25
Phegopteris hexagonoptera Fee	5.2	1.9	6.81	.38	.72	.22
Sedum ternatum Michx.	7.3	1.1	17.00	.05	.06	.22
Panax quinquefolius L.	1.5	3.2	1.15	.71	2.27	.22
Viola pubescens Ait.	5.6	1.7	8.37	.14	.24	.21
Athyrium pycnocarpon (Spreng.) Tidet.	4.9	1.9	6.44	.24	.46	.21
Caulophyllum thalictroides (L.) Michx.	1.7	3.0	1.44	.38	1.14	.21
Tilia americana L.	2.2	2.7	2.04	.29	.78	.28
Aralia nudicaulis L.	2.5	2.6	2.36	.14	.36	.20
Mitella diphylla L.	4.9	1.7	7.36	.10	.17	.20
Thelypteris noveboracensis Nieuw.	4.0	1.9	5.25	.19	.36	.19
Morus rubra L.	1.4	2.7	1.26	.38	1.03	.19
Polystichum acrostichoides Schott.	2.3	2.4	2.40	.29	.70	.18
Carya glabra (Mill.) Sweet	4.7	1.3	9.00	.10	.13	.18
Hamamelis virginiana L.	1.7	2.4	1.80	.33	.79	.17
Prenanthes altissima L.	1.8	2.3	1.95	.29	.67	.17
Liriodendron tulipifera L.	1.4	2.4	1.45	.52	1.25	.17
Nyssa sylvatica Marsh.	2.4	2.0	2.88	.24	.48	.17
Fraxinus quadrangulata Michx.	2.0	2.0	2.41	.14	.28	.16
Cornus alternifolia L.f.	2.4	1.7	3.57	.33	.56	.15
Stylophorum diphyllum (Michx.) Nutt.	2.9	1.4	5.00	.14	.20	.14
Desmodium cuspidatum (Muhl.) Loud.	1.9	1.7	2.86	.05	.09	.14
Solidago flexicaulis L.	1.9	1.7	2.86	.10	.17	.14
Epifagus virginiana (L.) Bart.	.9	1.8	1.27	.38	.68	.12
Quercus alba L.	.8	1.8	1.13	.33	.59	.12
Jeffersonia diphylla (L.) Pers.	2.9	1.0	7.63	.10	.10	.12
Phytolacca americana L.	1.5	1.7	1.43	.29	.49	.12
Carpinus caroliniana Walt.	1.6	1.4	2.75	.14	.20	.12
Amelanchier arborea (Michx.f.) Fern.	1.7	1.3	3.18	.14	.18	.11
Dirca palustris L.	1.0	1.5	1.62	.14	.21	.11
Lonicera canadensis Bartr.	2.5	1.0	6.75	.10	.10	.11
Hepatica acutiloba DC.	1.9	1.2	3.90	.10	.12	.11
Adiantum pedatum L.	1.5	1.3	2.91	.29	.38	.11
Oxalis europaea Jord.	3.3	.6	14.00	.14	.08	.11
Additional Species[1]	28.9	0.4	2.47	.09	.05	2.31

[1]Density and Importance Percentage values are totals for lower 70 species; other values are means for lower 70 species. The 70 Additional Species listed in decreasing order of Association Importance Percentage follow: Equisetum hyemale L., Athyrium filix-femina Roth., Liquidambar styraciflua L., Aster shortii Lindl., Smilax herbacea L., Impatiens biflora Willd., Aesculus glabra Willd., Fraxinus nigra Marsh., Euonymous atropurpureus Jacq., Panicum dichotomum L., Uvularia perfoliata L., Conopholis americana (L.f.) Wallr., Uvularia grandiflora Sm., Goodyera pubescens (Willd.) R.Br., Agrimonia gryposepala Wallr., Athyrium thelypteroides (Michs.) Desv., Cercis canadensis L., Botrychium dissectum Spreng., Senecio aureus L., Staphylea trifolia L., Monotropa uniflora L., Carya ovata (Mill.) K. Koch, Corallorhiza maculata Raf., Cubelium concolor (Forst.) Raf., Hydrophyllum macrophyllum Nutt., Dryopteris spinulosa Watt., Disporum maculatum (Buckl.) Britt., Quercus muhlenbergii Engelm., Scutellaria lateriflora L., Rubus occidentalis L., Isopyrum biternatum (Raf.) T&G, Equisetum arvense L., Oxalis stricta L., Aristolochia serpentaria L., Viburnum prunifolium L., Galium lanceolatum Torr., Vitis aestivalis Michx., Cimicifuga racemosa (L.) Nutt., Euonymous americana L., Streptopus amplexifolius (L.) DC., Desmodium glutanosum (Muhl.) Wood, Vinca minor L., Acer negundo L., Asplenium platyneuron (L.) Oakes, Festuca obtusa Biehler, Osmunda cinnamomea L., Trillium sessile L., Quercus velutina Lam., Vaccinium stamineum L., Dioscorea villosa L., Hydrangea arborescens L., Juniperus virginiana L., Onoclea sensibilis L., Celastrus scandens L., Osmunda regalis L., Polemonium reptans L., Sambucus pubens Michx., Aralia spinosa L., Betula alleghaniensis Britt., Campsis radicans (L.) Seem., Corylus americana Walt., Dryopteris marginalis (L.) Gray, Arisaema dracontium (L.) Schott., Hepatica americana (DC.) Ker., Hystrix patula Moench., Juglans nigra L., Quercus macrocarpa Michx., Taraxacum officinale Weber, Viola sagittata Ait., and Arabis laevigata (Muhl.) Poir.

The Association Importance Percentage is an attempt to assess the study-wide contribution of each species as based on an average of its relative density and relative frequency. Woodbine (Parthenocissus quinquefolia) and sugar maple (Acer saccharum) were the Association co-dominants with a combined importance value of 21%. They were present in every stand, had the highest total densities and frequencies and contributed high importance percentages to all but three stands. No other species exceeded 4% importance and only 10 others contributed 2% or more.

Sweet cicely (Osmorhiza claytoni) and yellow violet (Viola eriocarpa) were the most common herbaceous species. Although yellow jewelweed (Impatiens pallida) was represented by higher densities, its importance percentage was restricted by low frequencies. Wild ginger (Asarum canadense), also with high density, was even more restricted by frequency. The abundance value for ginger shows that it has a high tendency to clump and is very site-specific.

Of particular interest is American beech (Fagus grandifolia). Although density was relatively low, it occurred in 25% of the plots and was present in 18 stands. Its C-F Index is high due to its high frequency. Bitternut hickory (Carya cordiformis) also had a low density, frequency and a random distribution. Since it occurred in all stands, it ranked high on the commonness scale. Ginseng (Panax quinquefolius) occurred in 15 stands, with its scattered, often solitary distribution pattern reflected by the exceedingly low 1.15 abundance value.

Maianthemum canadense and Mitchella repens, because of their limited range, show an interesting relationship. Although they have almost exactly the same densities, M. canadense occurred in twice as many plots, but in only half as many stands as M. repens. They both have a tendency to clump and have similar Association Importance Percentages.

Species Association

Initially, species association values were calculated for every species in each stand. As the number of species per stand increased, the number of association comparisons increased by the square of the number of species. The number of significant associations became unmanageable and complicated by the high frequencies of common species. For infrequent species, the data were not suitable due to low densities and, therefore, presumed little interaction.

A total of 10 positive associations and 19 negative associations were significant for the 30 species tested within the 21 stands collectively (Table 4). Sweet cicely (Osmorhiza claytoni) had the most significant associations (3 positive and 6 negative), probably due to its high frequency and commonness as well as its random distribution. It had a significant negative association with the wet-mesic wood nettle (Laportea canadensis), enchanter's nightshade (Circaea quadrisulcata), sedge (Carex laxiflora), false nettle (Boehmeria cylindrica), wood phlox (Phlox divaricata) and white baneberry (Actaea alba). Positive associations occurred with the more mesic bedstraws (Galium spp.) and sanicle (Sanicula canadensis).

Table 4. Significant species associations for the top 30 herbaceous species of the Beech-Maple Association. Cole's Index of Association is significant to at least the 0.95 probability level.

Positive Associations	Compared Species	Negative Associations
Galium circaezans Sanicula canadensis Galium concinnum	⟷ Osmorhiza claytoni ⟷	Laportea canadensis Phlox divaricata Circaea quadrisulcata Carex laxiflora Actaea alba Boehmeria cylindrica
Hydrophyllum canadense Asarum canadense	⟷ Laportea canadensis ⟷	Sanicula canadensis Carex plantaginea
Sanicula canadensis ⟷	Impatiens pallida ⟷	Laportea canadensis Polygonatum pubescens
Galium triflorum ⟷	Smilacina racemosa ⟷	Pilea pumila Carex laxiflora
Phlox divaricata ⟷	Asarum canadense	
Mitchella repens ⟷	Maianthemum canadense	
Viola papilionacea ⟷	Sanicula canadensis ⟷	Circaea quadrisulcata
	Arisaema triphyllum ⟷	Actaea alba
	Carex plantaginea ⟷	Viola papilionacea
	Phlox divaricata ⟷	Smilacina racemosa
	Viola eriocarpa ⟷	Smilacina racemosa
	Polygonatum pubescens ⟷	Phryma leptostachya Polygonum virginianum

In general, the moisture gradients within the beech-maple forest may be separated into the following habitat conditions with "mesic" representing the mean condition:

Xerophytic → Dry-mesic → Mesophytic (mesic) ← Wet-mesic ← Hydrophytic

A species which is described as being "more mesic" implies that the species requires conditions nearer to the mean condition rather than the extremes.

The wood nettle was positively associated with waterleaf (Hydrophyllum canadense) and wild ginger, but negatively associated with the mesic sanicle. By examining positive and negative associates of a given plant and their moisture requirements, it was possible to learn something of the microenvironmental requirements of the species in question. A good example is yellow jewelweed which was negatively associated with wood nettle and Solomon's seal (Polygonatum pubescens). The wood nettle is a wet-mesic species while Solomon's seal is more mesic. From this, it was determined that jewelweed required conditions on the wet side of mesic, similar to sanicle, but not nearly as wet as required by nettle. Other parameters besides moisture must be considered for species site-preference. As Curtis (1959) pointed out, jewelweed is an indicator of past disturbance in the canopy layer. It responds to increased levels of light, as does wood nettle, but to a lesser degree.

Also of interest was the positive association between Maianthemum canadense and Mitchella repens. Daubenmire (1930) and Williams (1936) also noted the association between M. canadense and M. repens. They attributed the association to habitats in which xeric conditions were present and increased soil acidity inhibited the presence of other species. Maianthemum canadense has strong northern affinities while M. repens grows in a wider range of habitats. However, the association of the two species was found only in northern stands or in southern relicts of northern associations. This is not to say that M. repens is a northern species; instead, when M. repens occurs in the Beech-Maple Association, it was usually in northern stands and accompanied by M. canadense.

Ordination

In recent years, several ordination techniques have been developed for use in ecological research. Anderson (1971), Orloci (1966), and Gauch and Whittaker (1972) compared and contrasted the various techniques and their uses. Anderson and Orloci suggested use of principal components analysis and multidimensional scaling. There has been a tendency to favor mathematically complex ordination techniques, but there is no direct relation between the complexity of the technique and its performance in analysis. The technique developed by Bray and Curtis (1957) and Beals (1960) using coefficients of community and a three-axis system was chosen for use in this study.

The importance percentage for each species in each stand was incorporated into the ordination of the 21 forests. A three-dimensional model was constructed which depicted the position of each stand in relation to the remaining stands. Figures 3 and 4 diagram the positions of the stands on the X, Y, and Z axes. Stands in close proximity to each other reflect similar importance percentages for species in common to those stands.

The position of each stand on the X and Z axis was determined, to a large degree, by the cumulative importance percentages for woodbine and sugar maple. The sum of the importance percentages for these two species was plotted along each axis. The contribution of woodbine and sugar maple to the arrangement of stands is clearly evident (Fig. 3). The line connecting Toumey Woods and Floodplain re-creates the gradient of the model. In general, the cumulative

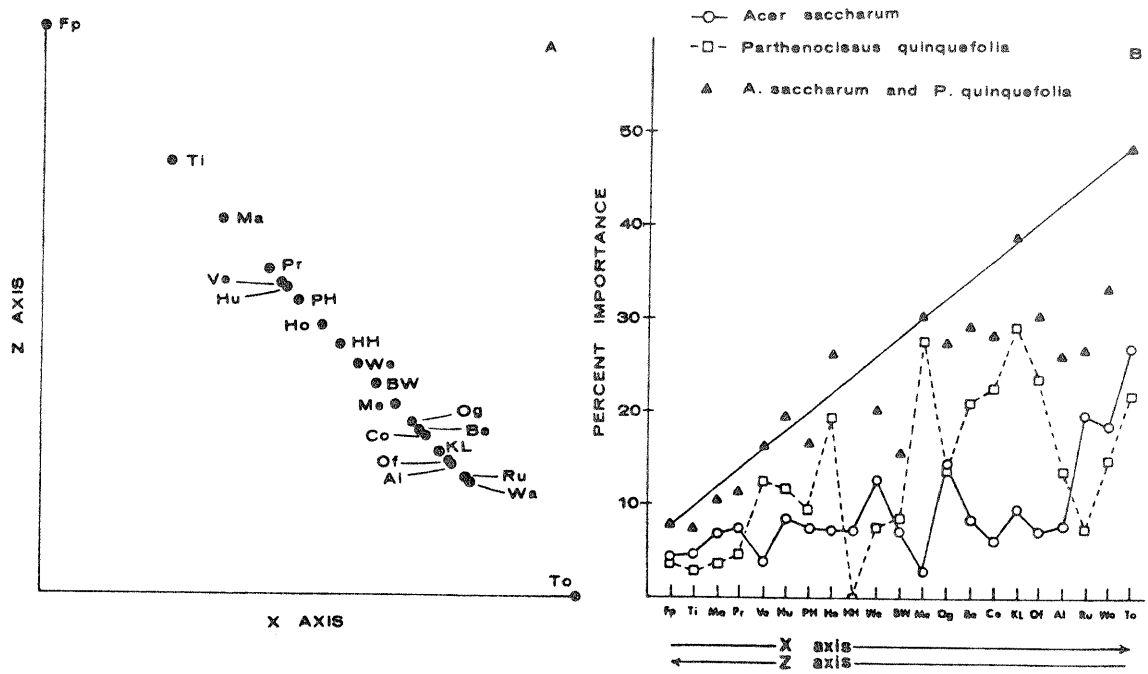

Figure 3. (A) Position of each stand on the X and Z axes of the ordination model based on the species' importance values of the groundlayer. (B) The relative placement of stands on the X and Z axes was largely controlled by the individual and cumulative importance percentages of Acer saccharum and Parthenocissus quinquefolia. Stand abbreviations are found in Table 2.

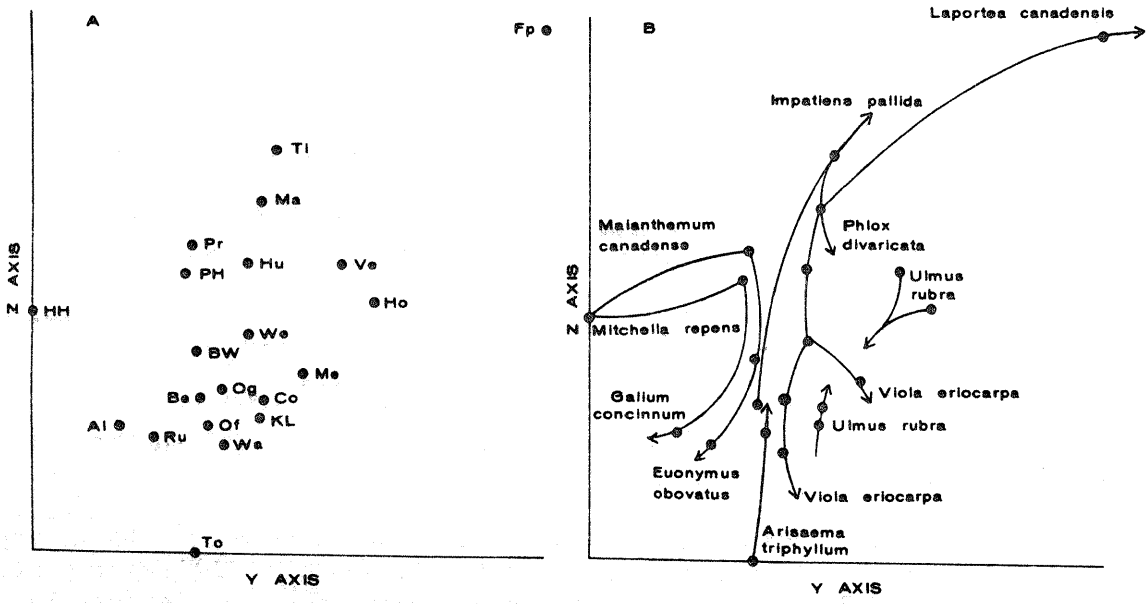

Figure 4. (A) Position of each stand on the Y and Z axes of the ordination model based on the species' importance percentages of the groundlayer. (B) The relative placement of stands on the Y and Z axes was determined by a moisture gradient as evidenced by subordinate species. Stand abbreviations are found in Table 2.

importance percentage of woodbine and sugar maple was proportional to the distance away from the origin on the X axis and inversely proportional to the position of the stand on the Z axis. The apparent inverse relationship between sugar maple (Acer saccharum) and woodbine (Parthenocissus quinquefolia) suggested control by available light.

Most stands fell below the gradient line when only sugar maple and woodbine were considered (Fig. 3). However, every species in each stand contributes to the position of that stand on the model. Other species with high importance percentages (over 2%) were placed on the Y-Z axial plots (Fig. 4). Species common to clusters of stands were connected by arrows. The species formed distributions with optimum values in restricted sections of the model. No two species showed the same location, but each was interspersed to varying degrees with the other species in a continuously changing pattern (Bray and Curtis 1957). Floodplain, in the upper right, was heavily dominated by Laportea canadensis (wood nettle), a wet-mesic species. Toumey Woods, in the bottom center, was heavily dominated by sugar maple, woodbine and Jack-in-the-pulpit (Arisaema triphyllum), all mesic species. Along the gradient are wet mesic yellow jewelweed (Impatiens pallida) and wood phlox (Phlox divaricata) near the top, with such mesic species as yellow violet (Viola eriocarpa) and running strawberry bush (Euonymus obovatus) near the bottom.

In general, the gradient from top to bottom in Figures 3 and 4 is correlated with moisture. The positions of the stands on the ordination model were correlated with the moisture requirements of the species involved which, in turn, reflected the conditions within the stands. Similar results were described by Ratcliffe (1959) and Curtis (1959). They found a soil moisture gradient to be one of the major controlling factors of vegetation. Davidson and Buell (1967) ascribed the gradient of communities to soil moisture and nutrient relations secondarily, with the geologic substrate (the basic determinant of soil diversity), topography and slope-facing as the primary controlling factors.

The ordination model is an expression of the total environment as measured via the species. Interpretation of the model, in this study, by the domination of woodbine and sugar maple and the apparent moisture gradient, single out only two factors. Just as species vary in kind and number from stand to stand, so do the myriad of environmental parameters. Each parameter may be considered as linear and any combination of these parameters may occur in different plots. As only 0.01 ha was sampled within each stand, the ordination position of the stands reflects similar plot compositions and is assumed to reflect similar stand compositions. The three axes of the ordination are compositional gradients and their structure cannot be interpreted as being caused by environmental factors alone, but as a combination and interaction of organisms and environment (Bray and Curtis 1957).

CONCLUSIONS

1) Species composition, attributes, distribution and association were obtained for the groundlayer communities in 21 old-growth beech-maple stands in

Indiana, Michigan and western Ohio. A total of 174 species was found. Six species occurred in all 21 stands while 38 occurred in only 1 stand.

2) Parthenocissus quinquefolia and Acer saccharum were the most important groundlayer species for the overall Beech-Maple Association. Osmorhiza claytoni and Viola eriocarpa were the most common herbaceous species.

3) The species association data revealed continually changing species composition within the groundlayer with no one discrete community. Manlove and Weaver Woods, less than 1 mile apart, had little similarity between their groundlayer communities; the same was true for the two stands in Versailles State Park. Species association was a valuable tool in determining moisture preference of species.

4) The ordination was controlled by sugar maple and woodbine with actual placement of the stands correlated to a moisture gradient.

LITERATURE CITED

Anderson, Orlin. 1948. An ecological study of climax vegetation of Taylor County, Wisconsin. Unpublished M.S. Thesis, Univ. of Wisconsin, Madison.

Anderson, A. J. B. 1971. Ordination methods in ecology. J. Ecol. 59:713-726.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156-181.

Bingham, Marjorie T. 1945. The flora of Oakland County, Michigan. Cranbrook Inst. Sci. Bull. 22. Bloomfield Hills, Mich. 155 p.

Braun, E. Lucy. 1950. Deciduous forests of eastern North America. Blakiston Co., New York, N.Y. 596 p.

_____. 1961. The woody plants of Ohio. Ohio State Univ. Press, Columbus. 362 p.

Braun-Blanquet, J. 1928. Pflanzensoziologie. Julius Springer. Berlin, Germany.

Bray, J. Roger and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325-349.

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30:411-424.

Curtis, J. T. 1959. Vegetation of Wisconsin. U. Wisc. Press, Madison. 657 p.

_____, and R. P. McIntosh. 1950. The interrelations of certain phytosociological characters. Ecology 31:434-455.

_____, and _____. 1951. An upland forest continuum in the prairie-forest border of Wisconsin. Ecology 32:476-496.

Daubenmire, R. F. 1930. The relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. Butler Univ. Bot. Stud. 1:61-76.

Davidson, Donald W. and Murray F. Buell. 1967. Shrub and herb continua of upland forests of northern New Jersey. Amer. Midland Natur. 77:371-389.

Donselman, Henry M. 1973. An ecological analysis of the shrub stratum of the beech-maple forest. Unpublished M.A. thesis, Indiana State University, Terre Haute. 127 p.

Dunn, Christopher P., and Marion T. Jackson. 1978. Phytosociological and ordination analyses of the tree stratum of the beech-maple forest type. Proc. Cent. Hardwood Forest Conf. II:2-21.

Escobar, Linda K. 1971. Beech-maple and maple-basswood regions of the deciduous forest formation. Unpublished M.S. thesis, Purdue University, Lafayette, Ind. 536 p.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., N.Y. 714 p.

Forman, R. T. T., and B. A. Elfstrom. 1975. Forest structure comparison of Hutcheson Memorial Forest and eight old woods on the New Jersey piedmont. The William Hutcheson Memorial Bull. 3:44-51.

Gauch, H. G., Jr. and R. H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53:868-875.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

_____. 1952. The new Britton and Brown illustrated flora of the northeastern U.S. and adjacent Canada. Hafner Publ., New York, N.Y. 3 Vols. 1,732 p.

Greller, A. M. 1975. Persisting natural vegetation in northern Queens County, New York, with proposals for its conservation. Environ. Conserv. 2:61-69.

Jackson, M. T. and P. R. Allen. 1969. Detailed studies of old-growth forests in Versailles State Park, Indiana. Proc. Indiana Acad. Sci. 78:210-230.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Publ. 36, New York, N.Y. 166 p.

Levenson, J. B. 1973. The herbaceous stratum of the beech-maple forest: A community structure analysis. M.A. thesis, Indiana State University, Terre Haute. 134 p.

_____. 1980. Woodlots as biogeographic islands in southeastern Wisconsin: A vegetation analysis, In R. L. Burgess and D. M. Sharpe (eds.), Forest habitat islands in man-dominated landscapes, Springer-Verlag, New York, N.Y. (in press).

Lindsey, A. A. 1955. Testing the line-strip method against full tallies in divers forest types. Ecology 36:485-495.

_____. 1956. Sampling methods and community attributes in forest ecology. For. Sci. 2:287-296.

_____, Damian V. Schmelz and Stanley A. Nichols. 1969. Natural areas in Indiana and their preservation. Indiana Natural Areas Survey, Lafayette, Ind. 594 p.

Little, E. L., Jr. 1953. Check list of native and naturalized trees of the United States. Agr. Handbook No. 41, U.S. Forest Service, Washington, D.C. 472 p.

Orloci, L. 1966. Geometric models in ecology I. The theory and application of some ordination methods. J. Ecol. 54:193-215.

Ratcliffe, D. A. 1959. The vegetation of the Carneddau, North Wales. 1. Grasslands, heaths and bogs. J. Ecol. 47:447-481.

Rogers, R. S. 1980. Classification of mesophytic forests at the southern edge of the tension zone: Central Minnesota to southeastern Michigan. Ecology 61: (in press).

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Struik, Gwendolyn J. 1957. The distribution and reproduction of some herbaceous plants in a maple forest. Unpublished M.S. thesis, Univ. Wisconsin, Madison.

_____, and J. T. Curtis. 1962. Herb distribution in an Acer saccharum forest. Amer. Midland Natur. 68:285-296.

Suhrweir, D. and D. J. Tramer. 1976. Tree species richness: farm woodlots as biogeographic islands. Unpublished manuscript.

Thornbury, W. D. 1965. Regional geomorphology of the United States. John Wiley and Sons, Inc., New York. 609 p.

Transeau, E. N. 1935. The prairie peninsula. Ecology 16:423-437.

Vankat, J. L., W. H. Blackwell, Jr., and W. E. Hopkins. 1975. The dynamics of Heuston Woods and a review of the question of the successional status of the southern beech-maple forest. Castanea 40:290-311.

Veatch, J. O. 1932. Soil maps as a basis for mapping original forest cover. Pap. Mich. Acad. Sci., Arts, and Lett. 15:267-273.

Ward, R. T. 1956. The beech forests of Wisconsin -- changes in forest composition and the nature of the beech border. Ecology 37:407-419.

Wheery, E. T. 1961. The fern guide: northeastern and midland United States and adjacent Canada. Doubleday and Company, Inc., New York. 318 p.

Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecology 30:199-208.

_____, and P. J. Salamun. 1954. An upland forest survey of the Milwaukee area. Ecology 35:533-540.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.

Williams, Arthur B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:317-409.