PHYTOSOCIOLOGICAL AND ORDINATION ANALYSES OF THE TREE STRATUM OF THE BEECH-MAPLE FOREST TYPE

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ABSTRACT

The tree stratum of the beech-maple forest was sampled using a modified line-strip method in 39 old-growth stands in five Midwestern states. Relative density, frequency, basal area, and importance value measures were used in phytosociological and Bray-Curtis ordination analyses, and in the construction of an "average stand" depicting the beech-maple forest type in general.

The "average stand" showed beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) to be of equal importance.

The ordination of 38 of the stands indicated % sand content of the *A* horizon, and thus soil moisture-holding capacity and cation-exchange capacity, to be major factors in species distribution and stand character.

INTRODUCTION

The beech-maple, or Fagus-Acer saccharum, forest "type" (sensu Whittaker 1962) is an integral part of the vegetation of Midwestern United States. On the whole, it occupies a large portion of the Eastern United States and Canada, reaching from New York and Ontario, west to Indiana, Illinois, and Wisconsin (Braun 1950). In the area of study (Fig. 1), it covers (or had covered prior to clearing) a large area of three states (Ohio, Indiana, and Michigan) and a portion of two others (Wisconsin and Illinois).

Being contiguous to such a diversity of other forest types (eg., oak-hickory, northern hardwoods, and western mesophytic), it is of interest to determine those factors (environmental, historical, etc.) that have resulted in the present areal extent of the beech-maple forest, and that limit the distribution of the individual species associated with the forest type. These evaluations are, of course, best achieved by studying many stands. Further demonstrable by data from a large number of stands is the variation within a so-called "homogeneous" forest type.

The objectives of this study, then, are 1) in general terms, to describe phytosociologically the beech-maple forest of the Upper Midwest; 2) to gather edaphic data for each stand; 3) to relate the edaphic data to the vegetation by means of indirect gradient analysis (ordination); and 4) to attempt a determination of those edaphic factors limiting the extent of the beech-maple forest in the Midwest.

MATERIALS AND METHODS

Data Collection

Thirty-nine old-growth beech-maple stands in five Midwest states were selected for study. The main criteria used in their selection were a freedom from any severe natural or man-induced disturbance for at least 50 years and a size of at least 4 ha. The stands represent not only typical beech-maple areas as mapped by Braun (1950) and Küchler (1964), but also the western, southern, and northern borders of the beech-maple type in eastern Illinois, southern Indiana, and eastern Wisconsin (Fig. 1). Most of the stands represent the best remaining remnants of what was once the original forest cover in the central and western segment of beech-maple type. For individual stand descriptions, locations, stand tables, etc., see Dunn (1978).

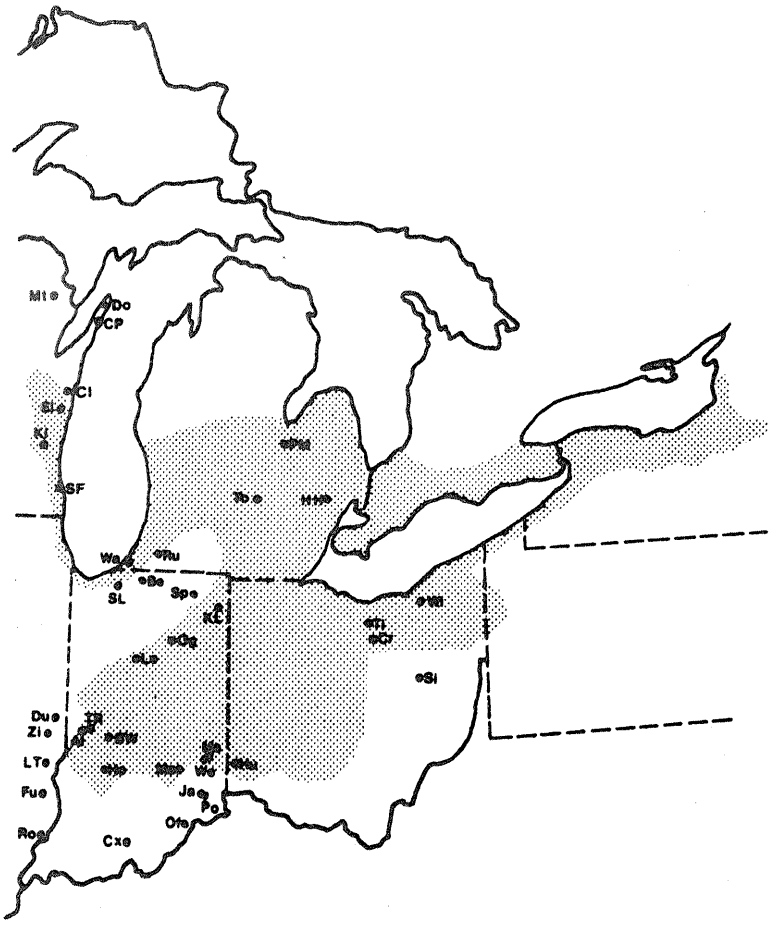

Figure 1. Location of the study sites in relation to the Beech-Maple Region of Braun (1950). Stand symbols are listed in the Description of Study Areas.

Trees greater than 10.0cm dbh were tallied using a metric modification of the line-strip method of Lindsey (1955). This method has been tested in a number of forest types, including a "Maple-beech" woods (Lindsey 1955) included in this study. Its accuracy justifies its use here.

Most stands were large enough to allow for the random sampling of forty 1/40ha plots, yielding a total sample area per stand of 1.0ha For all 39 stands collectively a sample of almost 40ha was taken within the upper midwest portion of the beech-maple forest type.

Five soil samples of approximately 500g each were collected from the A horizon at each study site for texture analysis. It has been shown (McIntosh 1950; see also Brown and Curtis 1952) that the A horizon and vegetation are more closely correlated than is any other horizon, owing to the fact that the A horizon is most greatly affected by organic matter decomposition. Further, it is in (or on) the A horizon that seeds germinate and initiate growth.

Because it was impractical to set and regularly check microclimatic monitoring equipment in each of 39 stands, it was impossible to obtain local climatic data. Rather, the Climates of the States, was the source of standard U.S. Weather Bureau records of monthly annual average temperature and precipitation values, as well as other pertinent information. Although it is well-known that microclimates within a forest stand may be quite different from neighboring urban or open areas Wolfe et al. 1949; Geiger 1965; Lee 1978), the Weather Bureau data were the best available. Weather stations selected were the nearest locations to the study sites; however, in a few cases two stands were proximate to the same station.

Data Analysis

Soils were analyzed for texture by the Bouyoucos, or hydrometer, method (Bouyoucos 1936). The values of % sand, % silt, and % clay for the individual soil samples per stand were averaged to give mean soil texture percentages.

Relative importance values (% I.V.) of each species were calculated by averaging the relative values of density (D), frequency (F), and basal area (BA). Relative importance values were used in a two-dimensional Bray-Curtis ordination analysis (Bray and Curtis 1957). The ordination was computer-generated using ORDIFLEX (Gauch 1977).

Components of several edaphic and climatic factors were superimposed on the ordination to examine what (if any) aspects of the ordination could be explained by these environmental variables.

An "average stand," based on all 39 stands, was constructed typifying the beech-maple type in the Midwest United States.

RESULTS

Phytosociology

Although the beech-maple forest type has been described as floristically uniform (Braun 1950; Lindsey and Schmelz 1970; Vankat *et al.* 1975), the 39 stands manifest a great deal of stand-to stand variation (Dunn 1978). All stands, of course, have a high combined relative importance value of beech (*Fagus grandifolia* Ehrh.) and sugar maple (Acer saccharum Marsh.); however, the associated (in the loose sense of the word) species are very diverse (see Dunn 1978). Including beech and sugar maple, 57 species were tallied, ranging from 6 to 27 species per stand. The average number of species was 16.8.

Much of the compositional dissimilarity among the stands is owing not only to wide geographic separation, but also to the fact that many of the stands are located along the southern and western extremities of the beech-maple type (Fig. 1). For instance, the western stands contain a higher proportion of oak (*Quercus*) and hickory (*Carya*) species, reflecting a proximity to (and the floristic influence of) the oak-hickory type. They nevertheless retain the essential beech-maple character: high beech and sugar maple dominance.

Similarly, more southern stands contain such species as blackgum (*Nyssa sylvatica* Marsh.), sweetgum (*Liquidambar styraciflua* L.), and buckeye (*Aesculus glabra* Willd.) more commonly encountered in the mixed mesophytic and western mesophytic forests (Braun 1950).

Further, the northern stands manifest obvious influence of the hemlock-northern hardwoods forest (see Braun 1950) by the presence of yellow birch (*Betula alleghaniensis* Brit.), paper birch (*B. papyrifera* Marsh.), hemlock (*Tsuga canadensis* (L.) Carr.), and white pine (*Pinus strobus* L.). Again, the beech-maple character is retained, as clearly demonstrated by the high combined % I.V. of beech and sugar maple and the complement of co-occuring species (see stand tables in Dunn 1978).

To put the species compositions and species attributes of the stands in perspective, an "average" stand table was constructed (Table 1), based on all 39 stands. This is the "measured climax" of Whittaker (1953). Being an ethereal conception, the "climax" is difficult to define; therefore, it ". . . may thus be defined . . . by the counting (and averaging) of populations . . ." (Whittaker 1953). Beech and sugar maple are shown to be equally important with respective % I.V.'s of approximately 30%. Although dominated by beech and sugar maple, the forests have a wide variety of associated species, none of which (except beech and sugar maple are found in all stands and many of which are found in only a few stands.

The equivalent importance values of beech and sugar maple, as expressed in the average stand, are interesting in light of their contrasting reproductive strategies. Beech produces heavy seed crops approximately every 5 years, at least in Wisconsin. Seedling success, however, is very low and reproduction is more common by root sprouts (Curtis 1959). On the other hand, sugar maple produces a very large number of seedlings each year (Curtis 1959; Hett and Loucks 1970; Mulcahy 1975); however, there is a very heavy mortality rate among the youngest seedlings (Mulcahy 1975). Whatever the evolutionary significance of these two strategies may be, the final result, combined with the high shade tolerance of both species, is co-dominance. Forcier (1975) believes the reproductive strategies of each species to be "essential for their coexistence" and to be responsible, in part, "for the stability of the near-climax ecosystem."

Beech and sugar maple are not the largest trees encountered. The mean BA per tree of white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.), tulip tree, and black walnut (*Juglans nigra* L.) exceed either of the two dominant species.

These two aspects (species numbers and size) permit a great deal of variety in beech-maple stands. A similar variety in shrub (Donselman 1973) and groundlayer species (Levenson 1973) makes each stand even more unique. Nevertheless, Braun (1950) and others have commented on the unformity of the beech-maple forest type and the futility in attempting to subdivide it into sections. To resolve this ambiguity, the beech-maple forest may be said to ehibit "parahomogeneity."

Climate

Climatic data for all stands are presented in Dunn (1978). In summary, the mean annual temperature ranges from 14.0°C (57.2°F) to

Table 1. Composite species attributes table for 39 individual old-growth beech-maple forest stands

Species	D[1]	%D	F	%F	BA	%BA	%IV	$\bar{x}$BA/tree
Fagus grandifolia	108.09	30.39	82.03	23.15	15.00	38.82	30.79	0.14
Acer saccharum	131.01	36.84	24.27	10.19	26.37	29.16	29.16	0.08
Liriodendron tulipifera	11.55	3.25	17.31	4.89	2.30	5.95	4.70	0.20
Quercus rubra	8.56	2.41	14.73	4.16	1.91	4.94	3.84	0.22
Fraxinus americana	8.21	2.31	12.89	3.64	1.06	2.74	2.90	0.13
Tilia americana	9.28	2.61	12.01	3.39	1.02	2.64	2.88	0.11
Ulmus rubra	8.18	2.30	13.91	3.93	0.60	1.55	2.59	0.07
Ostrya virginiana	9.38	2.64	12.49	3.52	0.18	0.47	2.21	0.02
Acer rubrum	6.43	1.81	9.42	2.66	0.62	1.60	2.02	0.10
Quercus alba	3.86	1.08	7.14	2.01	1.05	2.72	1.94	0.27
Prunus serotina	5.47	1.54	9.27	2.62	0.47	1.22	1.79	0.09
Acer nigrum	3.51	0.99	5.32	1.50	0.51	1.32	1.27	0.15
Juglans nigra	2.90	0.81	5.19	1.47	0.53	1.37	1.22	0.18
Fraxinus pennsylvanica	2.98	0.84	6.17	1.74	0.35	0.91	1.16	0.12
Tsuga canadensis	3.75	1.05	4.71	1.33	0.27	0.70	1.03	0.07
Other[2]	32.48	9.14	55.79	15.71	2.58	6.68	10.51	0.08
Total	355.64	100.01	354.39	99.99	38.64	100.00	100.01	

[1]Attributes are as follows: D = density/hectare; %D = relative density; F = plot frequency; %F = relative frequency; BA = basal area in square meters/hectare; %BA = relative basal area; %IV = relative importance value; and $\bar{x}$BA/tree = average basal area per tree.

[2]In decreasing order of relative importance value: Ulmus americana, Sassafras albidum, Betula alleghaniensis, Carya ovata, Nyssa sylvatica, Carya cordiformis, Celtis occidentalis, Carya glabra, Quercus muehlenbergii, Cornus florida, Betula papyrifera, Quercus velutina, Ulmus thomasii, Carpinus caroliniana, Carya tomentosa, Fraxinus nigra, Liquidambar styraciflua, Platanus occidentalis, Gymnocladus dioica, Fraxinus quadrangulata, Aesculus glabra, Quercus bicolor, Vitis sp., Cercis canadensis, Juglans cinerea, Quercus shumardii, Quercus macrocarpa, Acer saccharinum, Asimina triloba, Carya ovalis, Pinus strobus, Amelanchier arborea, Magnolia accuminata, Robinia pseudoacacia, Carya laciniosa, Crataegus sp., Populus tremuloides, Prunus pensylvanica, Fraxinus tomentosa, Lindera benzoin.

6.4°C (43.5°F), the mean annual total precipitation from 127.1cm (50.03in) to 69.1cm (27.22in), and the mean number of frost-free days from 195 to 119.

Temperature (monthly and annual) generally increases from north to south, whereas precipitation exhibits the opposite trend. The extremes are most pronounced in the northern Wisconsin stands, exaggerating the gradient to some extent.

Soils and Glaciation

The soils are perhaps the most variable of the environmental factors associated with the beech-maple stands. For example, sand content varied from 29.3% to 93.7%, texture from silt loam to sand, and pH from 4.4 to 7.0 (for more detail, see Dunn 1978). The pH range was similar to that of European beech woods: 4.5 to 6.5 (Braun-Blanquet 1932).

The average soil texture of all stands was silt loam to loam (approximately 50% sand, 40% silt, 10% clay), with an average pH of about 5.5. Several stands varied widely from each of these values.

Generally, the soils of the beech-maple forest type are gray-brown podzolics (Braun 1950). The loam to silt loam textures typical of many stands is derived from Wisconsinan glacial till (Braun 1950; Lindsey *et al*. 1965; Pell and Mack 1977); however, despite pronouncements to the contrary (Braun 1950), many beech-maple stands are located well outside the area of Wisconsinan glaciation. Lindsey *et al*. (1965) note that a number of sites occur well into the Illinoian glacial region. In fact, nearly 25% of the stands in this study are south or west of the Wisconsinan glacial boundary (Fig. 2), with one stand on the unglaciated Mitchell Plain in Indiana.

Ordination

To facilitate the interpretation of the edaphic variables and of differences in stand composition, a two-dimensional ordination was constructed. For the ordination analysis, one stand was excluded. The species composition was such (see Dunn 1978) that it tended to throw the ordination into disarray. The stand does exhibit beech-maple characteristics; however, when dealing with a data set of "relative uniformity," a few distinct stands (or even a single one) can readily obfuscate the obvious (Gauch 1977). Had the intent been to study ecological differences *between* community types, exclusion would

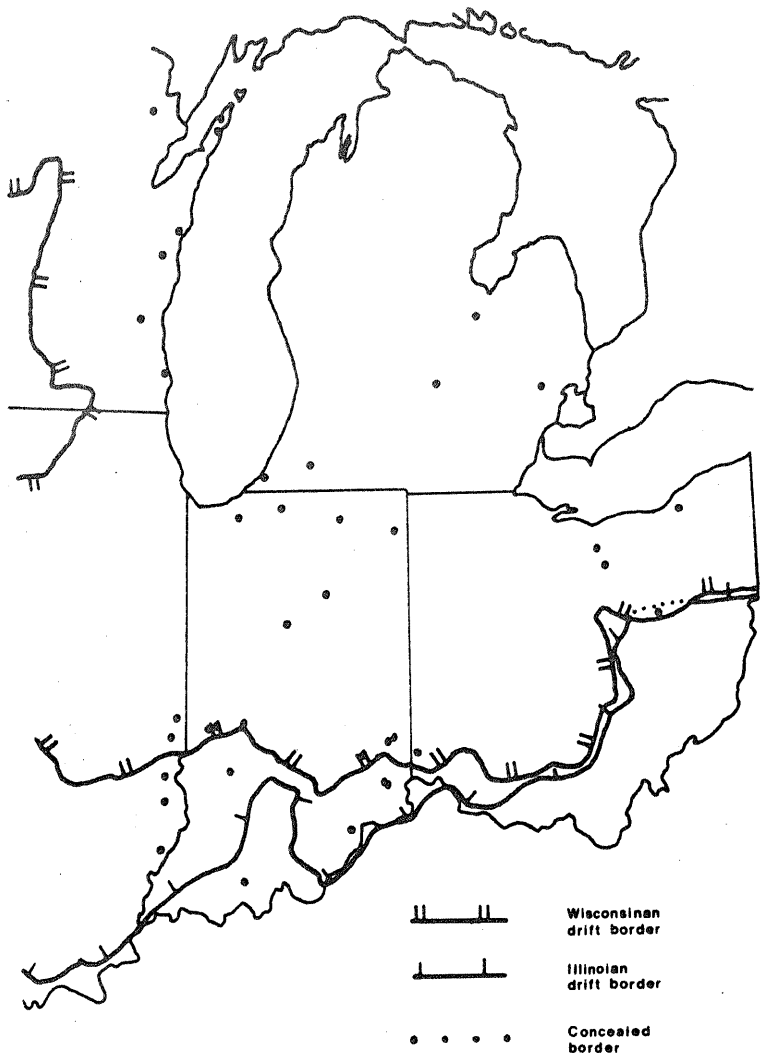

Figure 2. Location of the study sites in relation to the Illinoian and Wisconsinian glacial boundaries.

certainly not be so justified. The positions of the 38 remaining stands are presented in Figures 3 and 4.

The stand positions were superimposed with many environmental factors (mean monthly and annual precipitation and temperatures; mean number of frost-free days; % sand, % silt, and % clay of the soils; soil texture classes; soil pH; etc.) and community structure attributes (diversity indices; importance values of major species; mean BA per tree; etc.). Only the soil texture aspects are discussed here. The other above factors are discussed in Dunn (1978) and will likely be published elsewhere.

Percentage of sand content of the A horizon is most clearly associated with the ordination (Fig. 3). In fact, it fits the ordination better than any other factor, climatic or edaphic (Dunn 1978). The highest % sand values fall to the right and upper portions of the ordination. The other values, although not exhibiting a linear gradient away from the high values, do cluster in fairly homogeneous groups.

DISCUSSION

Within the "relative uniformity" of the beech-maple forest claimed by Braun (1950) and others, there is room for a great deal of variation and structural and functional complexity. A crude impression of structural complexity is gained simply from studying the tables of species attributes and species richness for each stand (see Dunn 1978).

The quantitative and qualitative similarity of the "average" stand table to stands in north-central Ohio infer that that region of Ohio may be the center of distribution of the beech-maple forest type. This conjecture is not testable; however, the proximity of that area to the mixed mesophytic and Appalachian forests (those forest regions presumed to have been progenitors of the beech-maple forest: Braun 1950) makes such a speculation floristically valid. More southern stands also have some similarity to the average stand. These relationships may be illustrative of the northward post-glacial (Wisconsinan) progression of species from unglaciated refugia.

Ordination

The beech-maple region has been "evolving" (and species of plants and animals co-evolving) for many hundreds of years. The original

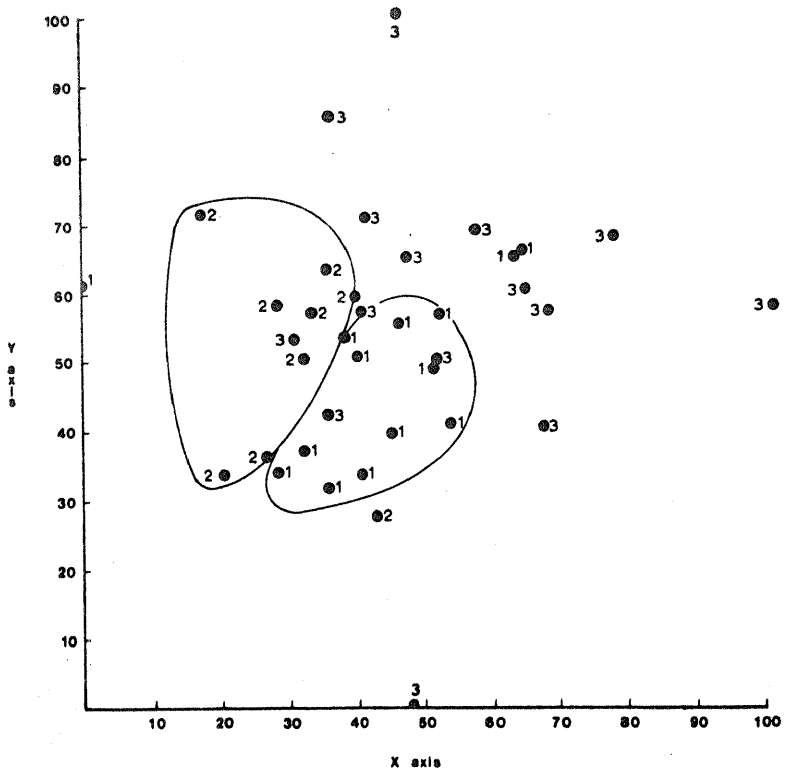

Figure 3. Ordination position of stands in relation to percentage of soil sand content of the A horizon. Code: 1 = less than 40.0%; 2 = 40.1-55.0%; 3 - greater than 55.0%.

(i.e., immediately post-glacial) environment and ecological factors conducive to the present species distributions are difficult to assess. A study of present environmental conditions and their correlation with forest composition perhaps can be conclusive. The ordination procedure used was intended to clarify such relationships, specifically edaphic.

The edaphic regime is an environmental factor of major importance. The question is which portion of the regime exerts greater control, if any. A number of studies have correlated forest or stand composition with soil texture (e.g., Shanks 1953; Lindsey et al. 1965; Peet and Loucks 1977). In this study also, soil texture of the A horizon is the edaphic factor of greatest ecological significance (Fig. 4). Further, when % sand is superimposed on the ordination (Fig. 3) and compared with Figure 4, it is apparent that % sand is an important aspect of soil texture and is more important than other soil parameters alone in determining the nature of the beech-maple stands. This agrees well with Peet and Loucks' (1977) findings that % sand content of the A1 horizon is a primary determinant of the character of southern Wisconsin forests. From the gradient in sand content can be inferred gradients in soil moisture and nutrients, with increasing sand content implying a lower moisture-holding capacity and a lower cation-exchange capacity (Peet and Loucks 1977). The gradient portrayed in Figure 3, then, may be more than simply a gradient in % sand content. The structural and functional complexity alluded to earlier may well be a product of the wide range in soil texture, especially % sand content of the A horizon, and the resultant assumptions regarding moisture-nutrient relations.

The natural environment impinging upon an individual plant or an assemblage of various species is a complex of factors (Gleason 1926, 1939; Billings 1952). Each factor is important in its own way, yet cannot be totally separated from the whole. In some times and places a particular factor may be of greater significance than others. In the beech-maple region of the upper Midwest, sand content (and the implied moisture-nutrient gradient) appears to be a major factor controlling species distribution and forest composition. Age of the soils also seems to be a major consideration (Dunn 1978). The edaphic phase cannot, however, be completely divorced from the climatic factors concomitantly

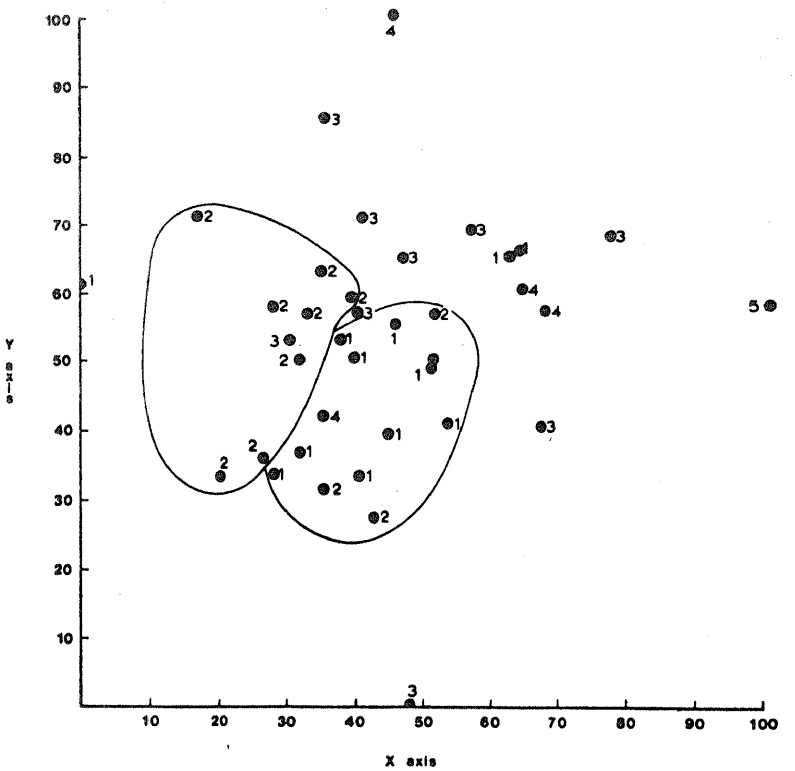

Figure 4. Ordination position of stands in relation to soil texture classes. Code: 1 = silt loam; 2 - loam; 3 = sand loam; 4 = loamy sand; 5 = sand.

tolerances of the individuals (Gleason 1926; Whittaker 1956; McIntosh 1967). Certain species happen to possess similar tolerances to portions of the environment, and therefore by chance are associated within an environmental (and resource) space. It was this train of thought (grossly simplified here) that led Gleason (1926) and subsequent workers to view the "association" (sensu Braun 1950) or "forest type" (sensu Whittaker 1962) as a chance occurrence.

Because the structure and function of forest ecosystems are so complex, care must be taken in interpretation of results. Goodall (1970) has warned of the tendency to mingle cause and effect, a point well-taken. Further, it has been pointed out that the interpretation of environmental relations is most effective when dealing with a region of "essentially uniform climate," a condition adequately, although not totally satisfied here.

As with environmental analysis, ordination analysis must likewise be cautious. The purpose of ordination is to give an indication, or some preliminary idea, of the general patterns of interactions between biological (e.g., vegetation) and physical (e.g., environment) phenomena (Bray and Curtis 1957); however, inferring simple cause-and-effect relationships is risky. In fact, ordination may be viewed as a "mapping of complexity" (Bray and Curtis 1957). If the ordination arranges stands in a "meaningful" manner, in such a way that the stand alignments correlate with features of the physical environment, then it can be considered valid (Bray and Curtis 1957). This interpretation should be in terms of "trends of environmental factors across the ordination space" (Austin, 1976; emphasis added). The trends recognizable here include % sand content of the A horizon, and the inferred gradients of soil moisture and nutrients.

The discussion here has been concerned with only a single part of the whole (i.e., the environmental complex). Certainly, % sand content of the A horizon appears to be a significant factor in the ecology of the beech-maple forest type; however, it is by no means the intention to minimize or ignore other factors. The myriad factors determining and peripherally affecting the pattern and process in plant communities are all worthy of investigation. Since all cannot be addressed, the choice of which to concentrate on is determined subjectively by the researcher. It is hoped that future studies will consider additional factors, especially microclimate, soil nutrients, productivity studies, reproductive strategies, interspecific competition, and other functional aspects of the ecology of the beech-maple forest.

APPLICATIONS

The application of the findings in this study, in combination with the previously stated suggestions for future research, include gains in silviculture and forest management (see Loucks 1962). It is a fact that species respond to--and are controlled by--their enviroment (and to a degree vice versa). As such, additional quantitative data on environment and species response will be invaluable in the furtherance of silvicultural and forest management plans. In addition, these data could be helpful in defining management units and in long-range forest yield predictions (Loucks 1962).

A second, and possibly more consequential application, concerns conservation. In light of the the ongoing denudation of the landscape as a result of economic and cultural pressures, the conservation of natural areas is mandatory for a plethora of reasons (Jackson 1971; Bormann 1976; Likens et al. 1977; Slatyer 1977), and there is a growing movement to save "representative" self maintaining ecosystems throughout the world (Ehrenfeld 1976).

Forests are important both as an economic and as an aesthetic resource (Jackson 1971; Bormann 1976). Moreover, forest ecosystems are instrumental in controlling patterns of erosion, hydrology, nutrient cycling, and climate, and in the filtering of air and water (Bormann 1976). Destruction and disturbance to these natural systems will severely restrict their "filtering" efficiency (Likens et al. 1977).

Additionally, undisturbed ecosystems can serve as examples or reference systems both in designing man-dominated ones and in repairing "faulty" ones (Ehrenfeld 1976).

The biogeochemical work carried out in the Hubbard Brook Ecosystem studies (Likens et al. 1977) for many years hence will be the standard against which future research will be measured. The experimental design required undisturbed control as well as experimentally manipulated ecosystems for comparative study. The more such reference ecosystems are preserved, the more comparative studies will be possible, and the better able we will be to judge and predict the effects of disturbance--man-induced and otherwise.

Preservation will be hampered by the fact that many such ecosystems particularly temperage forests, are adjacent to, or within, locales of maximum technical, industrial, and urban development (Bormann 1976). As

such, these natural areas need to be preserved ". . . against the deterioration caused by modern technical production and cultivation methods" (Westhoff 1971). Wright (1974) intimates that the survival of mankind may rest on what has been learned from studying extensive natural ecosystems. Although a rather apocalyptic implication, it is not far from the truth.

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