

Ecological species groups of upland northern hardwood – hemlock forest ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan

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A tabular, field-oriented method of developing ecological species groups was applied in a classification study of upland northern hardwood – hemlock ecosystems in the Sylvania Recreation Area, Upper Peninsula, Michigan. Sixteen species groups were formed, consisting of a total of 76 upland herb, shrub, and moss species. The groups were constituted based on patterns of presence and absence and coverage values of species along gradients of soil fertility and soil moisture. The ecological responses of species within many of the groups were very similar. The environmental tolerances of the species groups in relation to soil fertility, moisture, forest floor conditions, and shade tolerance were described and contrasted. The groups were more differentiated along a fertility gradient than along a moisture gradient. The tabular method was relatively simple, yet effective in determining the species groups. The method is suitable for extensive land-classification activities; its essential element is that physiography, soil, and vegetation are examined simultaneously in the field. Species groups are more reliable in site classification and mapping than a subset of a few key species and the groups also simplify the use of many indicator species for field workers and ecosystem mappers.

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Des écosystèmes de forêt décidue à pruche ont été classifiés dans les hautes terres de la Haute Péninsule de Michigan à l'aide d'une méthode de terrain utilisant des tableaux en vue de définir des groupes écologiques d'espèces. Seize de ces groupes, comprenant des plantes arbustives, herbacées et muscinales, ont été formés. Ils ont été établis sur la base de patrons de présence et absence et de recouvrement, observés le long des gradients de fertilité et d'humidité du sol. La réaction écologique des espèces appartenant au même groupe a été très semblable. La tolérance des groupes d'espèces vis-à-vis de la fertilité, de l'humidité du sol, des conditions du sous-bois et de l'ombre a été mise en évidence et décrite. Les groupes se différençaient plus le long du gradient de fertilité que de celui d'humidité. La détermination des groupes d'espèces au moyen de la méthode des tableaux est relativement simple et efficace. Elle est utile pour la classification de vastes territoires. Son principal avantage est qu'elle permet l'examen simultané, sur le terrain, de la physiographie, du sol et de la végétation. Les groupes d'espèces sont plus fiables pour la classification et la cartographie des stations qu'un ensemble d'espèce-clé. De plus, ils simplifient l'utilisation d'un grand nombre d'espèces indicatrices au cours des travaux de terrain et de la cartographie.

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Introduction

The utility of ground-cover vegetation in assessing the productivity of forest land has been recognized for many years (Cajander 1926; Rowe 1956; Daubenmire 1976). Plants integrate many important environmental factors which are difficult to measure directly and plants can be used relatively easily to estimate site quality and to classify and map forest land. The use of indicator plants in forestry is not without limitations (Coile 1938; Daubenmire 1976). For example, the occurrence of ground-cover plants is often controlled by factors such as understory light conditions or chance factors of herbivory and dispersal that may be poorly related to the site characteristics that determine timber productivity. Given the limitations of using indicator plants, approaches to multifactor land classification have been developed that integrate the occurrence and abundance of ground flora with characteristics of physiography and soil to assess site quality and produce more reliable land classifications (Hills 1952; Schlenker 1964; Jurdant 1968; Barnes et al. 1982).

Although some of the limitations of assessing forest land quality with indicator plants are inherent, a result of the ecological nature of the species, others are a result of the specific

method which is employed. Some approaches identify sites using field keys based upon a few indicator plants, often a small subset of the total ground flora (Coffman and Hall 1976; Coffman and Willis 1977). This approach is very susceptible to what Austin (1971) has called the "zero value" problem. The absence or zero value of a plant on a site may result from factors related to site quality, such as soil acidity, or to factors unrelated to site quality, such as understory light conditions or chance events. The field worker relying upon a few key species may not be able to distinguish between these two cases, particularly when the autecologies of the key species are poorly known. The problem can be mitigated by incorporating many indicator plants into the classification and the classification key, thereby increasing the chances of correct identification of site conditions. The use of many indicator species is facilitated by classifying the species into ecological species groups based on their environmental tolerances.

A key element in the species-group method is a good understanding of the site relationships of many species. For most forested areas in the United States, such information is lacking or not adequate for forest land evaluation and classification. In the upper Great Lakes region, for example, there has been considerable recent interest in forest land classification (Coffman and Willis 1977; Barnes et al. 1982), but knowledge of the indicator values of many species is poor. Close species-site relationships of herbs and shrubs have been documented in

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TABLE 1. Site characteristics of 13 upland ecosystems (site units) of the Sylvania Recreation Area

Site unit	No. of plots	Site characteristic					
		Topographic position ^a	Aspect	% slope	Soil texture (0–150 cm) ^b	Soil drainage ^c	pH (0–10 cm)
1	4	HP	All	4	LS/CS	SE	4.6
2	4	HP	All	1	SL/S	W	4.5
3	4	LS	All	2	FSL	MW	4.4
4	1	HP	All	1	SL	MW	5.1
5	6	LS	All	3	FSL	MW	4.5
6	3	HP	All	2	L	SP	4.4
7	1	HP	All	2	L	SP	4.9
8	1	LS	All	3	SL	SP–P	4.4
9	8	US	S–NW	6	SL	W–MW	4.1
10	12	US	NW–SE	5	FSL–SL	W–MW	4.9
11	17	US–LS	All	9	SL	W	5.3
13	3	LS	NE	20	SL	W	5.3
14	3	US–LS	SW	25	L–LS	SE	4.2

^aHP, high plateau; US, upper slope; LS, lower slope.

^bCS, coarse sand; S, sand; LS, loamy sand; SL, sandy loam; FSL, fine sandy loam; L, loam. Two soil textures separated by a solidus indicates a two-storied soil.

^cSE, somewhat excessive; W, well; MW, moderately well; SP, somewhat poor; P, poor.

studies in this region in pine–oak forests in central Wisconsin (Wilde and Leaf 1955), jack pine plains in upper Michigan (Beaufait and Brown 1962), aspen forests in northern lower Michigan (Benninghoff and Cramer 1963), and northern hardwood forests in northwestern lower Michigan (Overlease and Overlease 1976).

We employed ecological species groups in ecosystem classification and investigation of species–site relationships in two areas in upper Michigan, the Cyrus H. McCormick Experimental Forest (Barnes et al. 1982; Pregitzer and Barnes 1984) and the Sylvania Recreation Area (Spies 1983; Spies and Barnes 1985). Pregitzer and Barnes (1982) and Pregitzer et al. (1983) have found that selected species groups were strongly associated with soil nutrient and moisture conditions in the McCormick Experimental Forest. The objectives of this paper are (i) to describe a useful method of determining ecological species groups, (ii) to describe the indicator values of the species groups of upland, northern hardwood – hemlock ecosystems of the Sylvania Recreation Area, and (iii) to evaluate the within-group similarity in patterns of occurrence of the species. A detailed quantitative analysis of the species–site relationships will be reported elsewhere.

General approach

Ecological species groups have been developed and used most extensively in site classification in West Germany (Schlenker 1950; Ellenberg 1950). In North America, Daubenmire (1952) developed ecological groups, termed unions, for northern Idaho and Klinka and Green (1983) described groups of indicator plants for southwestern British Columbia. The concept of ecological groups is attributed to Duvigneaud (1946) (see Whittaker 1978), but plants ecologists have long recognized the occurrence of plants with similar distributions in relation to environment.

Ecological species groups have been determined through a number of approaches (Ellenberg 1978). The approach used in this study is based on the methods which have been developed and used in forest site classification in the state of Baden–Württemberg, West Germany (Sebald 1964; Dieterich 1970; Spurr and Barnes 1980) for over 35 years. In the German method, species groups are determined from sample plot data which are arranged and analyzed in tabular form. The method is similar to the tabular method of Braun–Blanquet (see Ellenberg 1956), with an important difference. The columns are not

grouped solely by their floristic similarity, but by their environmental or site similarity as judged by field observations of physiography, soil, and vegetation. A key element in the method is a good understanding of the relationships of the species of an area to important soil and site factors. The indicator values of the species groups in Baden–Württemberg were evaluated in relation to form and quantity of soil nitrogen through pot culture tests (Bücking 1983). However, the development and use of the groups does not require detailed laboratory analyses.

We used the Baden–Württemberg method because of its simplicity and reliability and the fact that a first approximation of the species groups could be developed during fieldwork without the need for soil laboratory data and computer analyses.

Methods

The study was conducted in the Sylvania Recreation Area, an 8500-ha tract of old-growth northern hardwoods and hemlock forests, located at 46°12' N, 89°18' W, about 5 km west of Watersmeet, MI. The uplands are dominated by a mosaic of eastern hemlock (*Tsuga canadensis* (L.) Carriere) and sugar maple (*Acer saccharum* Marshall) forests; yellow birch (*Betula alleghaniensis* Britton), basswood (*Tilia americana* L.), and red maple (*Acer rubrum* L.) are occasional co-dominants. The study area has been classified into 15 upland and 10 wetland ecosystems, also termed site units, using an iterative procedure described by Barnes et al. (1982) and Spies and Barnes (1985). Detailed descriptions of the ecosystems are presented in Spies (1983).

Rectangular sample plots 15 × 30 m (450 m²) were established in a restricted, random design within the upland and wetland ecosystems (Spies and Barnes 1985). In each plot all ground-cover species were enumerated and their areal coverages estimated for a 150-m² subplot by percent cover classes using a modified octave scale (1, trace–0.1%; 2, 0.1–0.5%; 3, 0.5–1.0%; 4, 1–2%; 5, 2–4%; 6, 4–8%; 7, 8–16%; 8, 16–32%; 9, 32–64%; 10, 64–100%). The number and DBH of all overstory and understory species was recorded. Physiographic data were collected, a soil pit was excavated to at least 150 cm, and soil samples were collected by horizon for lab analyses that are described by Spies and Barnes (1985).

Ecological species groups were developed from the species that occurred in 13 upland ecosystems and 4 wetland ecosystems. Important site characteristics of these ecosystems are briefly summarized in Tables 1 and 2.

During the fieldwork phase the cover-class values of the species were recorded in a table in which the rows were species and the columns were plots. After the first approximation of the ecosystem

TABLE 2. Site characteristics of four wetland ecosystems (site units) of the Sylvania Recreation Area

Site unit	No. of plots	Site characteristic			pH of surface soil
		Soil material (surface/subsurface)	Depth to water, cm	Relative rate of water flow	
19	8	Fibric/hemic-sapric	30	Very slow	4.1
20	1	Fibric/sapric	20	Slow	4.9
22	4	Sapric/sandy clay loam	0–50, seasonal	Slow	4.8
25	2	Sapric	20	Moderate	5.1

classification, the columns (sample plots) were grouped by site unit and the site units were ordered along subjectively determined environmental gradients of soil moisture and fertility based on field observations and soil laboratory data. A first approximation of the species groups was determined by arranging the rows (species) into groups of plants with similar patterns of presence, absence, and coverage across the sequence of site units. As refinements in the ecosystem classification were made and as the relationships of the species to the environment were better understood from field observations, new versions of the species – site unit table were prepared. A FORTRAN program was used in arranging successive versions of the tables. The final groups were arranged in a table in which the site units were subjectively ordered along a soil fertility gradient, based primarily on soil pH values. Species relationships to soil moisture were also taken into account, by noting how soil texture, depth to mottling, and physiography varied along the fertility gradient.

The classification of species – site unit responses into ecological species groups was based on two measures of vegetation, qualitative (presence or absence) and quantitative (coverage). Species were grouped together initially based on their patterns of presence and absence in site units. Groups of species restricted to one or a few site units were relatively easily discovered. However, most species occurred in many of the site units and these were then formed into groups based on the quantitative pattern of their coverage values in the site units. For these species, the arrangement of the site units along fertility and moisture gradients was helpful in discerning ecological response patterns which formed a basis for grouping the species. For example, one type of pattern was positive response to soil moisture and little or no response to soil fertility. Other response patterns or ecological group categories were determined by taking into account simultaneously gradients of moisture and fertility and also light, disturbance, and microsite variability based on knowledge of plot conditions. A critical element in the whole process was a thorough familiarity with the vegetation data (including, besides coverage, abundance, vigor, and microsite occurrence) and the range of environmental conditions. This familiarity was gained during reconnaissance, sampling of vegetation and soils, mapping, and comparison of site units by inspection of the sample data.

Rare species, occurring only once or a few times in the entire sample, are particularly difficult to characterize ecologically. Observations recorded during reconnaissance and mapping were used to assign rare species to ecological groups. Species not occurring in sample plots but observed several times during reconnaissance and mapping were assigned to species groups based on estimates of their indicator values.

A quantitative analysis of the pattern of the species responses in the site units was undertaken to help verify within-group similarity and to study the responses of common species. The rank mean based on cover class of each species was determined for every site unit. The deviation of the site unit rank mean from the pooled rank mean ($n/2 + 1/2$, where n is the total number of plots in all site units) was then determined (Strahler 1977). The deviations were graphed along the sequence of site units, to generate "ecological profiles" similar to those of Guillermin (1971) and Bottlikova et al. (1976). The profiles

reveal which ecosystems are "preferred" (positive deviations) or "avoided" (negative deviations) by the species. The profiles of the species of an ecological group were graphed together and the homogeneity of the groups were evaluated by inspection of the concordance of the graphs. The rank mean was used to generate profiles because it enabled nonparametric tests of differences among site units; however, profiles could also have been developed by plotting the site unit deviations of the species as positive or negative percentages of the overall cover class mean or frequency of occurrence.

The Kruskal–Wallis test (Conover 1980) was applied to the data to test the null hypothesis that the distribution of the species is the same in all of the site units. However, because the data contains many zeros and thus many ties, the power of this test is reduced, i.e., the test will recognize only the more obvious differences as significant.

Results

Sixteen ecological species groups were formed, consisting of a total of 76 species. Fifty-eight percent of the 130 moss, herb, and shrub species that were observed in the upland ecosystems were used in forming the groups. Most of the species not included in the groups were observed only once or twice, so their indicator values could not be assessed. The remaining species occurred in disturbed areas and may have some indicator value, but no sampling and analysis of disturbed areas were conducted.

Sixty-two of the species forming the groups occurred in the sample plots of 13 upland and 4 wetland ecosystems (Table 3). The upland site units in Table 3 were arranged in approximate order of increasing soil fertility. The wetland site units were arranged in order of decreasing soil fertility.

Only the *Leucobryum* and *Phegopteris* groups occurred exclusively in one site unit. Most groups occurred in three or more units. The differences between the site units in the species groups were both qualitative and quantitative. Many site units could be distinguished quite clearly by the presence or absence of different groups (e.g., the *Clintonia* group for units 9 and 1), whereas some units were not clearly distinguished, differing only in the relative quantities of the groups (e.g., the *Caulophyllum* groups in units 10 and 13) (Table 3). The difficulty in distinguishing some units by a study of vegetation alone demonstrates the need to incorporate physiographic and soil characteristics into a land classification.

Analysis of ecological profiles and description of indicator values

The ecological profiles were useful in examining the ecological amplitude of species in relation to environment and in assessing intra- and inter-group differences. The species of an ecological group should have similar patterns of positive and negative deviations across the sequence of site units. The species groups are discussed here in the order in which they

TABLE 3. Array of coverage class values^a of ground cover species in sample plots of 13 upland

Species group	Upland ^b						
	14	9	8	5	6	1	2
<i>Leucobryum</i>							
<i>Leucobryum glaucum</i>	- 1 1	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -
<i>Cladina rangiferina</i>	- 1 1	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -
<i>Oryzopsis</i>							
<i>Oryzopsis asperifolia</i>	- - -	- - - - -	- - - - -	1 - 1 1 - -	1 - -	2 3 3 3	- - - - -
<i>Carex peckii</i>	- 1 -	- - 1 - + - 2	- - - - -	- - - - 2 -	- - 2	1 2 - 2	- + + - -
<i>Clintonia</i>							
<i>Clintonia borealis</i>	1 - 1	5 4 4 2 2 2 4 2	3	- 1 4 4 3 2	2 - 1	- - - - -	- - - - -
<i>Coptis groenlandica</i>	2 - -	3 5 3 4 1 4 4 2	4	- - 1 - 1 -	1 - 1	- - - - -	- - - - -
<i>Cornus canadensis</i>	2 - -	2 3 2 3 1 1 5 -	3	- 1 2 - 2 2	- 1	- - - - -	- - - - -
<i>Oxalis montana</i>	- - -	2 1 1 2 1 1 3 1	3	1 + 4 2 2 4	1 - 6	- - - - -	- - - - -
<i>Goodyera repens</i>	1 1 -	- 1 1 1 1 1 1 1	-	- - - - -	- - 1	- - - - -	- - - - -
<i>Taxus canadensis</i>	- - -	- 1 - - - - - 1	-	- - - - -	- - -	- - - - -	- - - - -
<i>Monotropa uniflora</i>	- 1 -	- - - - -	1	- - - - -	- - -	- - - - -	- - - - -
<i>Lonicera</i>							
<i>Lonicera canadensis</i>	- - -	1 2 1 - 2 2 2 -	2	- - 2 2 2 -	+ + -	- - 1 +	- - - - -
<i>Acer spicatum</i>	2 - -	2 4 2 2 4 2 6 2	6	- 2 2 2 2 2	- - 2	- - - - -	- - - - -
<i>Polygonatum</i>							
<i>Polygonatum pubescens</i>	- - -	- - - - - 1 - - -	-	2 + - 1 1 -	1 1 +	2 2 1 -	1 + 1 1
<i>Viola selkirkii</i>	- - -	- - - - 1 - - - -	-	- 1 - 1 - 1	- 2 1	- 1 + -	2 2 2 -
<i>Dirca palustris</i>	- - -	- - - - -	-	- - - + - -	- - -	- 3 3 4	2 - - -
<i>Smilacina racemosa</i>	1 - -	- - - - - 1 - - -	-	- 1 2 2 1 -	1 - 1	- + 1 1	1 1 1 -
<i>Trillium cernuum</i>	- - -	- - - - -	1	+ - - 1 - -	1 - -	- - - - -	- 1 1 1
<i>Actaea pachypoda</i>	- - -	- - - - -	-	1 1 - 1 - -	- 1	- - - - -	1 1 1 -
<i>Viola incognita</i>	- - -	- - - - -	1	- - 1 3 1 -	- 1 -	- 1 - 1	- - - - -
<i>Ribes cynosbati</i>	- - -	- - - - -	-	- - - 1 - -	- 1 -	- - - - -	- 1 - - -
<i>Sambucus pubens</i>	- - -	- - - - -	-	- - - + - -	- - -	- - - - -	- 1 - - -
<i>Carex deweyana</i>	- - -	- - - - -	-	- - - - -	+ 1 -	- - - - -	- - 1 - -
<i>Millium effusum</i>	- - -	- - - - -	1	- - - - -	- - -	- - - - -	- - - - -
<i>Arisaema</i>							
<i>Arisaema triphyllum</i>	- - -	- - - - -	-	- - - 1 - -	- 1 1	- - - - -	2 3 2 2
<i>Carex intumescens</i>	- - -	- - - - -	-	- - - 1 - -	- 1 -	- + - - -	1 1 1 -
<i>Osmorhiza</i>							
<i>Osmorhiza claytoni</i>	- - -	- - - - -	-	- - - - -	3 1 +	- - 1 -	1 1 - -
<i>Viola pubescens</i>	- - -	- - - - -	-	- - - - -	- 1 -	- - - - -	- - - - -
<i>Uvularia grandiflora</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- 1 1 - -
<i>Botrychium virginianum</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- - + - 1 -
<i>Caulophyllum</i>							
<i>Caulophyllum thalictroides</i>	- - -	- - - - -	-	- - - + - -	- - -	- - - - -	- - - - -
<i>Adiantum pedatum</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- - - - -
<i>Ribes triste</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- - - - 1 -
<i>Allium tricoccum</i>	- - -	- - - - -	-	- - - - -	- 1 -	- - - - -	- - - - 1 -
<i>Cornus alternifolia</i>	- - -	- - - - -	-	- 1 - - - -	- - -	- - - - -	- - - - -
<i>Phegopteris</i>							
<i>Phegopteris hexagonoptera</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- - - - -
<i>Matteuccia struthiopteris</i>	- - -	- - - - -	-	- - - - -	- - -	- - - - -	- - - - -
<i>Streptopus</i>							
<i>Streptopus roseus</i>	- - -	2 2 1 + - - 1 -	1	3 2 3 2 1 2	2 3 2	1 2 1 1	1 1 + +
<i>Lycopodium lucidulum</i>	- - -	1 - 2 + 2 1 1 2	4	5 2 4 1 1 2	2 6 4	- - + 2	- - - - -
<i>Corylus cornuta</i>	1 - -	+ 1 1 - 2 + 2 3	2	2 1 + 1 - 1	- 1 2	- - 1 -	+ - - - -
<i>Corallorhiza maculata</i>	- - -	- - - - -	-	- 1 1 - 1 -	- 1	- - - - -	- - - - -
<i>Viola renifolia</i>	- - -	- - - - 1 - - -	-	- 1 - - - -	- 1	- 1 - -	- - - - -
<i>Athyrium</i>							
<i>Athyrium filix-femina</i>	- - -	- - - - -	-	- - 2 4 2 1	2 3 2	- - 1 -	1 2 1 -
<i>Gymnocarpium dryopteris</i>	- - -	- - - - -	-	- 2 2 - - + 2	2 3 -	- - - - -	+ - - - -
<i>Phegopteris connectilis</i>	- - -	- - - - -	1	- - 1 1 1 1	2 3 2	- - - - -	- - - - -
<i>Brachyelytrum</i>							
<i>Brachyelytrum erectum</i>	- - -	1 - - - - - -	+	- - + 2 - 1	- 2 +	- 1 - -	- - - - -
<i>Osmunda claytoniana</i>	- - -	- - - - -	-	- - - + -	- - +	- - - - -	- - - - -
<i>Trientalis</i>							
<i>Trientalis borealis</i>	+ - 1	1 2 1 1 - 1 1 +	1	2 - 2 2 1 2	1 - 1	2 - 1 1	1 - 2 -
<i>Lycopodium annotinum</i>	- - -	2 1 1 3 - - - -	-	2 1 - - - 1	- 1 -	- - - - -	- - - - -
<i>Dryopteris spinulosa</i>	- - -	- - - - -	-	- - - - -	- + -	- - - - -	- - - 1
<i>Lycopodium</i>							
<i>Lycopodium dendroideum</i>	- - -	- 2 2 2 - 2 - 1	3	3 2 3 2 1 3	1 2 4	5 2 4 3	- - - - -
<i>Carex arctata</i>	- - -	- - 1 - - - - -	1	2 1 - 1 1 -	1 2 -	1 1 1 1	- 1 - - -
<i>Carex pedunculata</i>	- - -	- - 1 - 2 - - 1	1	- 2 1 3 - 4	1 2 -	1 3 3 -	1 - - - -
<i>Mitchella repens</i>	- - -	- - - - -	-	1 1 1 - - -	1 2 -	1 - 1 1	- - - - -
<i>Maianthemum</i>							
<i>Maianthemum canadense</i>	3 + 2	6 6 8 4 5 5 4 3	4	2 4 5 2 4 2	3 2 4	3 2 1 2	3 + - +
<i>Aralia nudicaulis</i>	- - 3	3 3 2 2 - 3 3 +	-	- 2 2 4 2 2	2 - 3	1 - 2 -	4 + 3 -
<i>Dryopteris</i>							
<i>Dryopteris intermedia</i>	1 - +	5 3 3 3 2 3 3 3	-	5 3 4 4 5 5	3 5 6	3 4 5 4	5 5 3 2
<i>Aster macrophyllus</i>	- - -	- - - - -	-	- - - 2 - -	1 1 -	1 - - -	- - - - -
<i>Rubus idaeus</i>	- - -	- - - - -	-	- - - - -	- 1 2	- - - - -	+ 1 - - -
<i>Galium triflorum</i>	1 - -	+ - + - 1 - - -	-	- + 1 1 1 1	- - -	+ 1 - -	- 2 - 1
<i>Schizachne purpurascens</i>	- - -	- - - - -	-	- - - - -	- - -	- 1 1 -	- - - - -
<i>Carex leptonevia</i>	- - -	- - - - -	-	- - - 1 - 1	- - 2	- 1 - -	- - 1 1

^a+ , occurrence within the 450-m² sample plot, but not within the 150-m² subplot where coverage estimates were made. Each column in the table represents one plot.

^bArranged (from left to right) in approximate order of increasing fertility.

^cArranged (from left to right) in approximate order of decreasing fertility.

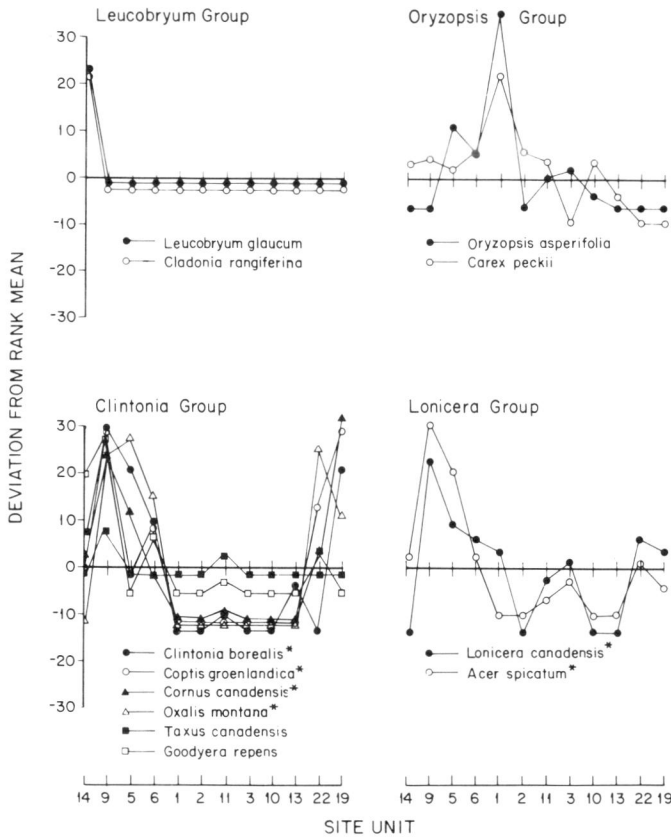


FIG. 1. Deviation from rank mean of coverages of species of *Leucobryum*, *Oryzopsis*, *Clintonia*, and *Lonicera* groups in 10 upland and 2 wetland site units of the Sylvania Recreation Area. The upland units (14–13) are arranged in approximate order of increasing soil fertility. The wetland units (22 and 19) are arranged in order of decreasing soil fertility. Coverages of species with an asterisk (*) are different among site units at the 0.05 level of significance (Kruskal–Wallis test).

appear in Table 3.

Detailed descriptions of the relationships of the groups to soil moisture, soil fertility, and light conditions are also presented. The descriptions of the indicator values are based upon plot data, ecosystem mapping, and reconnaissance. They are intended for use both inside the Sylvania Recreation Area and outside, in nearby areas on the Watersmeet Moraine (see Discussion). The groups are described in an abbreviated format. The first phrase describes the most characteristic occurrence of the group; the following phrases describe the ecological ranges, variability, and specific tolerances of selected species.

The two species of the *Leucobryum* group (Fig. 1) occurred only on the sandy, extremely acid soils of site unit 14, a hemlock-dominated ecosystem on exposed, fire-prone lake and wetland margins. Indicator value: Characteristic of exposed sites with thick, acid humus. Very dry to dry. Very infertile. Moderately tolerant of shade.

The *Oryzopsis* group (Fig. 1) is characterized by a large positive peak in site unit 1. Both species had low positive values in moister units 5 and 6, but very low or negative values in other more fertile, upland site units and in the wetland site units. Intragroup variability is low. Indicator value: Occurs most abundantly in relatively open stands on dry, infertile soils. Very dry to moist. Very infertile to somewhat fertile. Somewhat tolerant of shade. Has higher cover in open stands, but occurs only infrequently and with low coverage on poorly

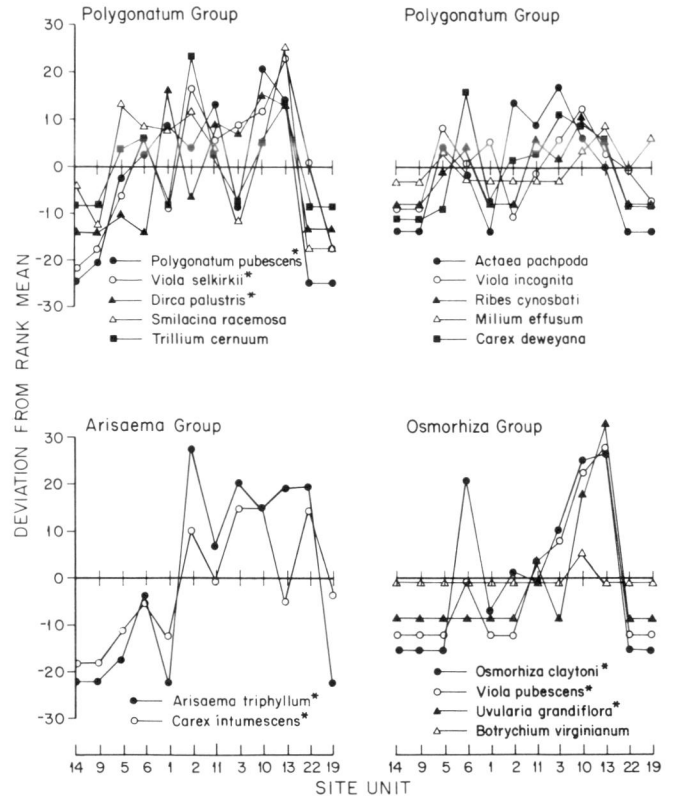


FIG. 2. Deviation from rank mean of coverages of species of *Polygonatum*, *Arisaema*, and *Osmorhiza* groups in 10 upland and 2 wetland site units of the Sylvania Recreation Area. The sequence of the site units and meaning of the asterisks (*) are the same as in Fig. 1.

drained soils even where the stand is open.

The species of the *Clintonia* group had peaks in units 9, 5, 6, 22, and 19 (Fig. 1). All these ecosystems are characterized by raw, acid humus and low soil fertility. Intragroup variability is low. Only *Taxus canadensis* did not exhibit a second peak in any of the wetland units. Indicator value: Most common on moist, very infertile soils supporting stands dominated by hemlock or other conifers. Dry to wet. Very infertile to infertile. Tolerant of shade. Occurs infrequently on dry sites. Very common on hummocks of extremely acid organic material in wetlands. High association with thick, raw, acid humus. *Oxalis montana* is most abundant on very moist to wet soils.

The *Lonicera* group (Fig. 1) is similar to the *Clintonia* group, but is composed of two medium-sized shrubs, which do not increase in cover in the wetlands as sharply as the *Clintonia* group. Intragroup variability is low. Indicator value: Most common on moist to very moist, infertile soils. Dry to wet. Very infertile to somewhat fertile. Tolerant of shade. Small individuals occur on almost any site where stand conditions are relatively open.

The *Polygonatum* group (Fig. 2) is a large, diverse group characterized by species with wide ecological distributions. The species are absent from extremely acid soils of hemlock ecosystems 14 and 9 and the wet, very strongly and extremely acid organic soils of swamp units 22 and 19. However, the species exhibit positive peaks in units 2, 11, 10, and 13, which are dominated by sugar maple. Most characteristic are the positive values of nearly every species of this group in the very strongly acid, well-drained soils of unit 11, an ecosystem characterized by a dense understory of sugar maple saplings and

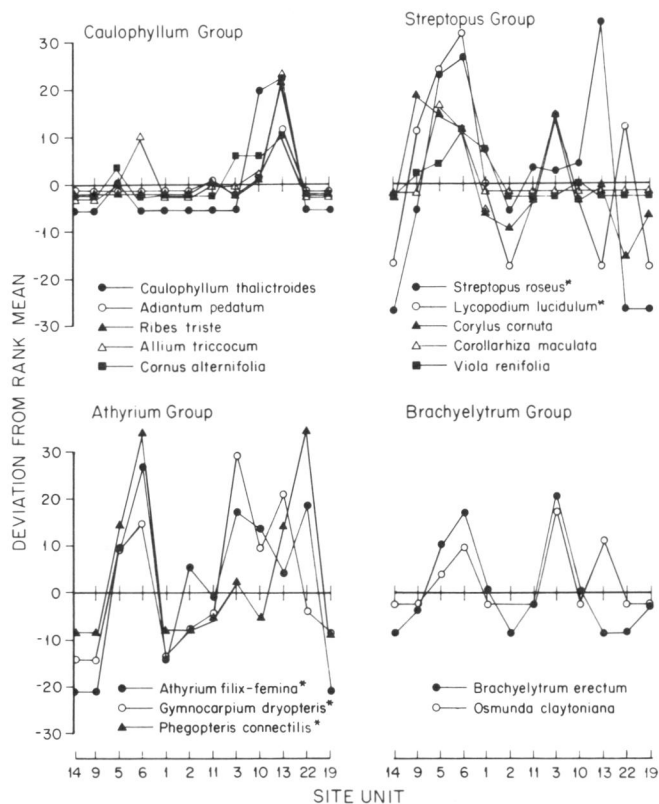


FIG. 3. Deviation from rank mean of coverages of species of *Caulophyllum*, *Streptopus*, *Athyrium*, and *Brachyelytrum* groups in 10 upland and 9 wetland site units of the Sylvania Recreation Area. The sequence of the site units and meaning of the asterisks (*) are the same as in Fig. 1.

seedlings and by relatively low or negative values for most other species groups. Intragroup variability is high within the ecosystems in the central portion of the graph, but all species have negative values in the extreme ecosystems. Indicator value: Most common on moist fertile soils supporting stands dominated by sugar maple, but common wherever sugar maple is dominant. Dry to very moist. Somewhat fertile to very fertile. Very tolerant of shade. Occurs rarely on extremely acid soils.

The *Arisaema* group (Fig. 2) is characterized by positive values in relatively fertile sugar maple ecosystems 2, 11, 3, 10, 13, and negative values in the relatively infertile hemlock or hemlock-hardwoods ecosystems 14, 9, 5, 6, and 1. Both species exhibit a positive response in wetland unit 22, but a negative response in wetland unit 19, which is less fertile. Indicator value: Most abundant on moist to very moist, very fertile soils. Somewhat moist to wet. Somewhat fertile to very fertile. Tolerant of shade. Small individuals may be found anywhere sugar maple is dominant. *Carex intumescens* responds more positively to light and is more tolerant of acidic organic soils and relatively infertile soils of disturbed sites than *Arisaema triphyllum*.

The *Osmorhiza* group (Fig. 2) is similar to the *Arisaema* group, but has much lower values on the sandy soils of unit 2, higher values on the relatively fertile sandy loam soils of units 10 and 13, and is absent from wetland unit 22. Indicator value: Somewhat moist to very moist. Fertile to very fertile. Tolerant of shade. Occurs occasionally on somewhat fertile soils, but is absent from infertile and very fertile soils.

The *Caulophyllum* group (Fig. 3) is characterized by a large

positive peak in unit 13, the most fertile upland unit, lower but positive values in unit 10, and a small positive peak in unit 5. The occurrence of this fertile soil species group in unit 5 is probably due to the relatively large microtopographic and edaphic diversity of units 5 and 6. Indicator value: Characteristic of very fertile, moist to very moist soils. Somewhat moist to very moist. Fertile to very fertile. Tolerant of shade. Species of the most productive sugar maple – basswood stands. Typically occur with low coverage values. *Caulophyllum thalictroides* is most common and more frequent than the other species on less fertile soils.

The *Phegopteris* group is rare and occurred only in ecosystem 4 (Table 3). The species appear to be restricted to very moist, very fertile mineral soils and are shade tolerant.

The *Streptopus* group (Fig. 3) is characterized by strong positive values on the acidic soils of units 9, 5, and 6. It is similar in overall profile to the *Athyrium* group, but has a positive value in unit 9 which is relatively dry and low or negative values (except for *Streptopus roseus* in unit 13) in the fertile units. The species all have positive responses in units 5 and 6 and negative responses in units 14, 2, and 20. Indicator value: Most common on very moist, infertile to somewhat fertile soils. Very common, occurring with low to moderate coverage over a wide range of soil fertility and a narrower range of soil moisture. Somewhat moist to wet. Infertile to very fertile. Tolerant of shade. Abundant in hemlock-dominated stands in protected, humid sites and on somewhat poorly drained soils.

The profile of the *Athyrium* group (Fig. 3) is distinctly bimodal along the fertility gradient and is characterized by positive values in relatively infertile units 5, 6, 3, 10, 13, and 22. These are moist and wet site units. All species have negative values in units 14, 9, 1, and 11, which are very dry to somewhat moist units, and in unit 19, which is characterized by extremely acid, wet peat soils. Indicator value: Most common on very moist to wet, fertile soils or on drier soils in protected, cool, humid sites. Somewhat moist to wet. Infertile to very fertile. Tolerant of shade. Often very abundant where stands are semiopen. *Gymnocarpium dryopteris* is less common on wet soils and in wetlands. *Phegopteris connectilis* is more common on very strongly acid soils.

The *Brachyelytrum* group (Fig. 3) is characterized by strong positive peaks in units 3 and 6, which are moist to very moist. Its profile is similar to that of the *Streptopus* and *Athyrium* groups but the group is much more restricted to somewhat poorly drained soils. Indicator value: Characteristic of very moist to wet, somewhat fertile soils. Moist to wet. Infertile to very fertile. Moderately tolerant of shade. Occurs somewhat sporadically, but is most frequent on somewhat poorly drained to poorly drained mineral soils. The occurrence of *Brachyelytrum erectum* increases with light and it can be found on well-drained soils in semiopen stands.

The *Trientalis* group (Fig. 4) is characterized by positive peaks on the very moist to wet, extremely acid soils of units 5 and 19. The strongest positive response is in wetland unit 19, but the group occurs sporadically throughout the uplands (Table 3). Indicator value: Occurs most abundantly on very infertile to infertile, wet organic soils in relatively open stands. Dry to wet. Very infertile to fertile. Moderately tolerant of shade.

The *Lycopodium* group (Fig. 4) is composed of common species characterized by strong positive responses in units 5, 6, 1, and 3. The group is similar to the *Oryzopsis* group (Fig. 1),

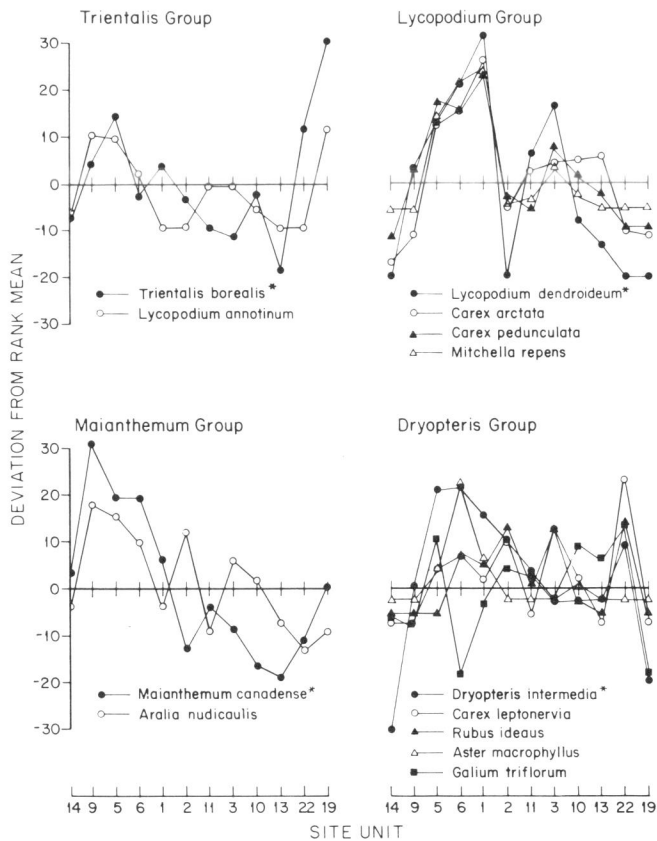


FIG. 4. Deviation from rank mean of coverages of species of *Trientalis*, *Lycopodium*, *Maianthemum*, and *Dryopteris* groups in 10 upland and 2 wetland site units of the Sylvania Recreation Area. The sequence of the site units and meaning of the asterisks (*) are the same as in Fig. 1.

but occurs more commonly and is apparently more tolerant of the very moist soils of units 5, 6, and 3. Indicator value: Very common species group occurring most abundantly on infertile to somewhat fertile soils in relatively open stands. Dry to very moist. Very infertile to very fertile. Moderately tolerant of shade. Common in open stands.

The *Maianthemum* group (Fig. 4) is a very common group characterized by species exhibiting a strong positive response in upland ecosystems (units 9, 5, and 6) with acid, infertile soils. However, as Table 3 demonstrates, these species occur in every upland site unit. Indicator value: Most abundant on extremely acid soils. Very dry to wet. Very infertile to very fertile. Shade tolerant. Least abundant on fertile, moist soils in deeply shaded sugar maple ecosystems. Flowering individuals most common in relatively open stands. *Aralia nudicaulis* is less common on wet, organic soils.

The *Dryopteris* group (Fig. 4) is a collection of species with diverse ecological responses and wide ecological amplitude, occurring in nearly every plot (Table 3). Indicator value: Most abundant on very moist soils, otherwise has little site indicator value. Very dry to wet. Very infertile to very fertile. Somewhat to very tolerant of shade. *Dryopteris intermedia* is very shade tolerant and the most common herbaceous species in Sylvania.

Patterns along moisture and fertility gradients

The ecological species groups were ordered by their general relationships to site moisture and soil fertility (Table 4). Fifteen species not occurring in sample plots were included in Table 4.

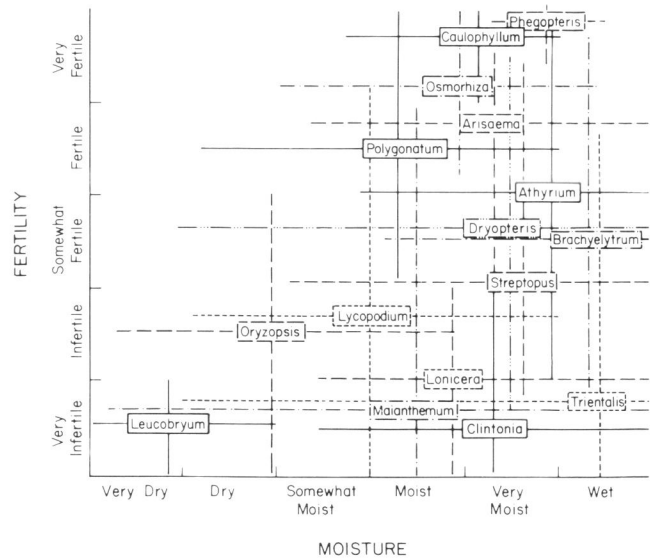


FIG. 5. Occurrence of upland species groups of the Sylvania Recreation Area in relation to gradients of soil moisture and fertility. "Very dry" on the moisture gradient corresponds to a soil with more than 80% sand on a steep, exposed, south- or west-facing aspect. "Wet" corresponds to a poorly drained, silty clay loam soil on gently sloping terrain with mottling present within 25 cm of the soil surface. "Very infertile" on the fertility gradient corresponds to a soil with a deep, acidic O2 layer and a well-developed A2 horizon of pH 4.2 or less. "Very fertile" corresponds to a soil with a thin O2 layer and a distinct but thin A1 horizon with a pH of 5.0–5.8.

Most groups (Nos. 3–12) were characteristic of moist to very moist sites and the majority were most common on soils of moderate to high fertility. Few groups (Nos. 1–4) were characteristic of either dry or very infertile soils and only the *Leucobryum* could be considered to be characteristic of both dry and very infertile conditions. Several groups (Nos. 13–16) occurred on almost any site, although even these were most abundant on moist sites.

The modes and ranges of the groups, which were determined subjectively based on field observation and data analyses, were graphed along moisture and fertility gradients (Fig. 5). Most of the groups occur with their highest coverage in moist to very moist soils. Few of the groups have high coverage where soils are dry to very dry or wet. No sites were both dry and fertile so no groups occur in this part of Fig. 5. A continuous sequence of groups occurs from the very infertile soils (pH 4.2) to the very fertile soils (pH 5.0–5.8). Several of the groups, e.g., *Athyrium*, *Streptopus*, and *Trientalis*, extend into the organic soils of the wetland ecosystems. In the wetlands these groups occurred primarily on mounds, logs, and tree bases above the water table.

The species groups are more differentiated along the fertility gradient in Fig. 5 than along the moisture gradient, although much overlap still exists among the groups. The high degree of overlap results from the relatively narrow range of site conditions (all soils were acidic and light textured) and also from the wide distribution of a few species groups such as *Polygonatum*, *Streptopus*, and *Dryopteris*. The overlap notwithstanding, Fig. 5 demonstrates that the species groups are differentiated with respect to site conditions and indicates that site conditions can be most reliably estimated by examining the presence, absence, and coverage of all the species groups, rather than just a few species.

TABLE 4. Ecological species of group of dryland ecosystems of Sylvania Recreation Area

Groups characteristic of very dry to dry sites	Groups characteristic of moist to very moist sites ^a			Groups occurring over a broad range of site moisture and soil fertility (in order of increasing ecological amplitude)
	A	B	C	
1. <i>Leucobryum</i> <i>Leucobryum glaucum</i> <i>Cladina rangiferina</i> <i>Carex deflexa</i> <i>Polypodium virginianum</i>	3. <i>Clintonia</i> <i>Clintonia borealis</i> <i>Coptis groenlandica</i> <i>Cornus canadensis</i> <i>Oxalis montana</i> <i>Goodyera repens</i> <i>Taxus canadensis</i> <i>Monotropa uniflora</i>	5. <i>Polygonatum</i> <i>Polygonatum pubescens</i> <i>Viola selkirkii</i> <i>Dirca palustris</i> <i>Smilacina racemosa</i> <i>Trillium cernuum</i> <i>Actaea pachypoda</i> <i>Viola incognita</i> <i>Ribes cynosbati</i> <i>Sambucus pubens</i> <i>Carex deweyana</i> <i>Milium effusum</i> <i>Claytonia caroliniana</i> <i>Erythronium americanum</i>	10. <i>Streptopus</i> <i>Streptopus roseus</i> <i>Lycopodium lucidulum</i> <i>Corylus cornuta</i> <i>Corallorhiza maculata</i> <i>Viola renifolia</i> <i>Aplectrum hymale</i>	13. <i>Trientalis</i> <i>Trientalis borealis</i> <i>Lycopodium annotinum</i> <i>Dryopteris spinulosa</i>
2. <i>Oryzopsis</i> <i>Oryzopsis asperifolia</i> <i>Carex peckii</i> <i>Lycopodium clavatum</i> <i>Lycopodium flabelliforme</i>	4. <i>Lonicera</i> <i>Lonicera canadensis</i> <i>Acer spicatum</i>	6. <i>Arisaema</i> <i>Arisaema triphyllum</i> <i>Carex intumescens</i>	11. <i>Athyrium</i> <i>Athyrium filix-femina</i> <i>Gymnocarpium dryopteris</i> <i>Phegopteris connectilis</i>	14. <i>Lycopodium</i> <i>Lycopodium dendroideum</i> <i>Carex arctata</i> <i>Carex pedunculata</i> <i>Mitchella repens</i> <i>Chimaphila umbellata</i> <i>Goodyera spp.</i> <i>Pyrola spp.</i> <i>Moneses uniflora</i>
		7. <i>Osmorhiza</i> <i>Osmorhiza claytoni</i> <i>Viola pubescens</i> <i>Uvularia grandiflora</i> <i>Botrychium virginianum</i> <i>Dicentra cucullaria</i> <i>Dentaria diphylla</i> <i>Panax quinquefolius</i>	12. <i>Brachyelytrum</i> <i>Brachyelytrum erectum</i> <i>Osmunda claytoniana</i>	15. <i>Maianthemum</i> <i>Maianthemum canadense</i> <i>Aralia nudicaulis</i>
		8. <i>Caulophyllum</i> <i>Caulophyllum thalictroides</i> <i>Adiantum pedatum</i> <i>Ribes triste</i> <i>Allium tricoccum</i> <i>Cornus alternifolia</i> <i>Sanguinaria canadensis</i>		16. <i>Dryopteris</i> <i>Dryopteris intermedia</i> <i>Aster macrophyllus</i> <i>Rubus idaeus</i> <i>Galium triflorum</i> <i>Schizachne purpurascens</i>
		9. <i>Phegopteris</i> <i>Phegopteris hexagonoptera</i> <i>Matteuccia struthiopteris</i>		

^aA, groups characteristic of infertile soils; B, groups characteristic of fertile to very fertile soils (in order of increasing soil fertility); C, groups occurring over a broad range of soil fertility, but characteristic of very moist sites (in order of increasing restriction to very moist and wet sites).

Discussion

Most species occurred in several different ecosystems and the recognition of different groups was based as much on quantitative patterns as on qualitative patterns (i.e., presence or absence within a site unit). Although qualitative differences are most easily seen in the field, quantitative differences can also be used by experienced field workers and mappers. The tabular approach is a simple and effective method of defining ecological species groups. Its success is dependent upon a good understanding of the site conditions. Such an understanding is obviously greatest near the end of the study, but successive approximations of the species groups were developed at the same time as the classification. The tentative groups proved very useful in early site classification and mapping.

The ecological profiles demonstrated that in many of the groups, the responses of the individual species were quite similar (e.g., *Clintonia* group and *Athyrium* group) across the range of site units. In other groups such as *Polygonatum*, the species were very similar only at the extremes of the gradients. In one group, *Oryzopsis*, the species grouped together primarily on their similar strong positive response in only one ecosystem, site unit 1. The ecological profile analysis was conducted when the tabular analysis was nearly completed. However, the profile analysis would be a valuable tool to use in conjunction with the tabular method in the development of the groups. This analysis is especially valuable where species differences among ecosystems are largely quantitative.

It may be possible to develop the groups by a numerical procedure. We did try to determine species groups using a variety of agglomerative clustering procedures, but were not satisfied with the results. Often two species that occurred in plots with very similar soils and physiography were not joined together by clustering algorithms because they happened to occur together in only a few plots. In addition, less common species whose distributions were centered at opposite ends of a gradient were sometimes grouped together if they happened to occur together in one or two plots. The standard agglomerative clustering methods are therefore not suitable for developing species groups because they do not group plots based upon environmental characteristics at the same time as they group species. A technique that we did not try which does group both plots and species was two-way indicator species analysis (TWINSPAN) (Gauch 1982). This is a polythetic divisive technique that ordines samples based upon their vegetative similarity and at the same time classifies both samples and species into groups. TWINSPAN might be useful in determining a first approximation of the groups, but it does not directly use soil and site data and it only recognizes a single gradient in the samples, while most sample sets contain two or more ecologically important gradients. Further research is needed to develop numerical tools to help classify indicator species into ecological groups.

Although the approach used in this study was intensive, the method could be modified for less intensive management. Our experience was that first approximations of the groups were quite helpful in assessing site conditions and mapping ecosystem boundaries. The preliminary species groups were developed from reconnaissance, plot sampling, and tabular analysis during the first field season before soil laboratory analyses were conducted. With our two intensive studies in western upper Michigan as models, we predict that in most cases, a working set of ecological species groups could be developed by a crew after only one or, at most, two field seasons in a climatic—

physiographic district (growth district) of western upper Michigan or northern Wisconsin. The essential element, regardless of intensity of approach, is that vegetation, soil, and physiography should be examined simultaneously in the field during reconnaissance and sampling and that attempts be made as early as possible to develop tentative species groups which are then refined during additional fieldwork and office work. The approach is subjective, but our experience suggests it is reproducible in other regions when applied by personnel who have good training in forest ecology, vegetation, and soils.

Species—site relationships vary regionally with climate and physiography (Walter and Walter 1953; Sebald 1957; Zobel et al. 1976). Thus, the species groups should probably not be extrapolated to other climatic and physiographic regions in western upper Michigan and north central Wisconsin without a test of their validity. Reconnaissance and field studies indicate that the species—site relationships probably hold outside of the Sylvania Recreation Area, over the Watersmeet moraine: a broad end moraine characterized by acidic, light-textured soils, hummocky terrain and ice-stagnation landforms (Dorr and Eschman 1970). The species—site relationships may be different, however, on the nearby ground moraine of southern Iron County, MI, which is characterized by relatively fertile, heavy-textured soils and a gently undulating topography. Although the climate of the two moraines is likely to be similar, landform, edaphic, and floristic differences may result in different or at least new ecological species groups. Differences in species groups are almost certain for the clay soils of the nearby Ontonagon Plain. The ecological groups of the Sylvania Recreation Area and the criteria used in developing them, however, should serve as a useful model that speeds the development of groups in other areas.

The question of the areal validity of species groups is an important one that deserves additional research. A comparison of the species groups of Sylvania with those published for the C. H. McCormick Experimental Forest (Pregitzer and Barnes 1982, 1984) is not strictly valid because those groups were developed using frequency data rather than cover data and used agglomerative clustering techniques rather than the tabular method which was developed subsequently. A superficial examination of the groups from the two study areas reveals differences in both the species list and in the composition of the groups, although there are some similar groups, e.g., the *Clintonia* group is very similar in both areas. Differences in the species lists between the two areas are likely a result of range differences, climatic differences, and differences in the physiographic—soil substrates of the two areas. The McCormick Experimental Forest contains many areas of thin rocky soil, while no thin soils or rock outcrops occur in the Sylvania Recreation Area. Differences in the composition of the groups may also result from shifts in the indicator values of the species. This possibility, which can not be adequately investigated using the published McCormick species groups, is currently being investigated with a new set of McCormick species groups developed using the tabular method.

The use of species groups to identify and map sites was not compared with the use of a smaller set of key species. Such an evaluation would require a different sampling design. However, our field observations and the data presented here indicate that the species-group approach is more reliable for ecosystem identification and mapping than approaches based on a relatively small set of key indicator plants. The species occurrences in some of the groups were often in such close agreement that

whenever one member of a group occurred in a plot, most of the other members occurred. Consequently, almost any single species of many of the groups could distinguish site units as well as the entire group. This speaks strongly for the validity and usefulness of the species-group approach. It should not be assumed, however, that only one key species of a group can be used in identifying and mapping ecosystems. The data result from careful, time-consuming searches of 450-m² plots to find and record every species. With such intensive sampling of a relatively large area, the species groups were often completely represented. A site mapper, relying upon just one or two key species would have to carefully search a large area to confirm the presence or absence of the species. Such an approach is inefficient for ecosystem mapping and ignores the large amount of ecological information present in all the species occupying a site. Under mapping conditions, the patchiness of individual species would be more evident, making the use of many species, combined into groups, more reliable than a few key species.

The species-group approach is probably more easily employed in the identification and mapping of sites than approaches that incorporate many species into the classification, but require the use of both field vegetation keys and detailed plant association descriptions to identify sites (Pfister and Arno 1980). The results of this study indicate that the indicator values of 76 species could be reduced into 16 ecological groups. The species groups greatly simplify the use of many species, yet retain much of the ecological information of the flora. The use of species groups may be most advantageous in regions of diverse flora such as in many parts of eastern North America.

The species groups are really a classification of species based on their site relationships. In developing the groups, the ecologist must use a comparative approach, focusing on differences and similarities of the ecological response of the species. The process itself is quite valuable in determining and understanding species-environment relations.

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