The forest vegetation of the driftless area, northeast Iowa

by

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INTRODUCTION

Iowa is generally pictured as a rolling prairie wooded only along the water courses. The driftless area of northeast Iowa is uniquely contrasted to this image; northeast Iowa is generally forested throughout, often with rugged local relief. The landscape is so well dissected that the region is easily delimited by its deviation from the usual rectilinear road pattern on the state highway maps.

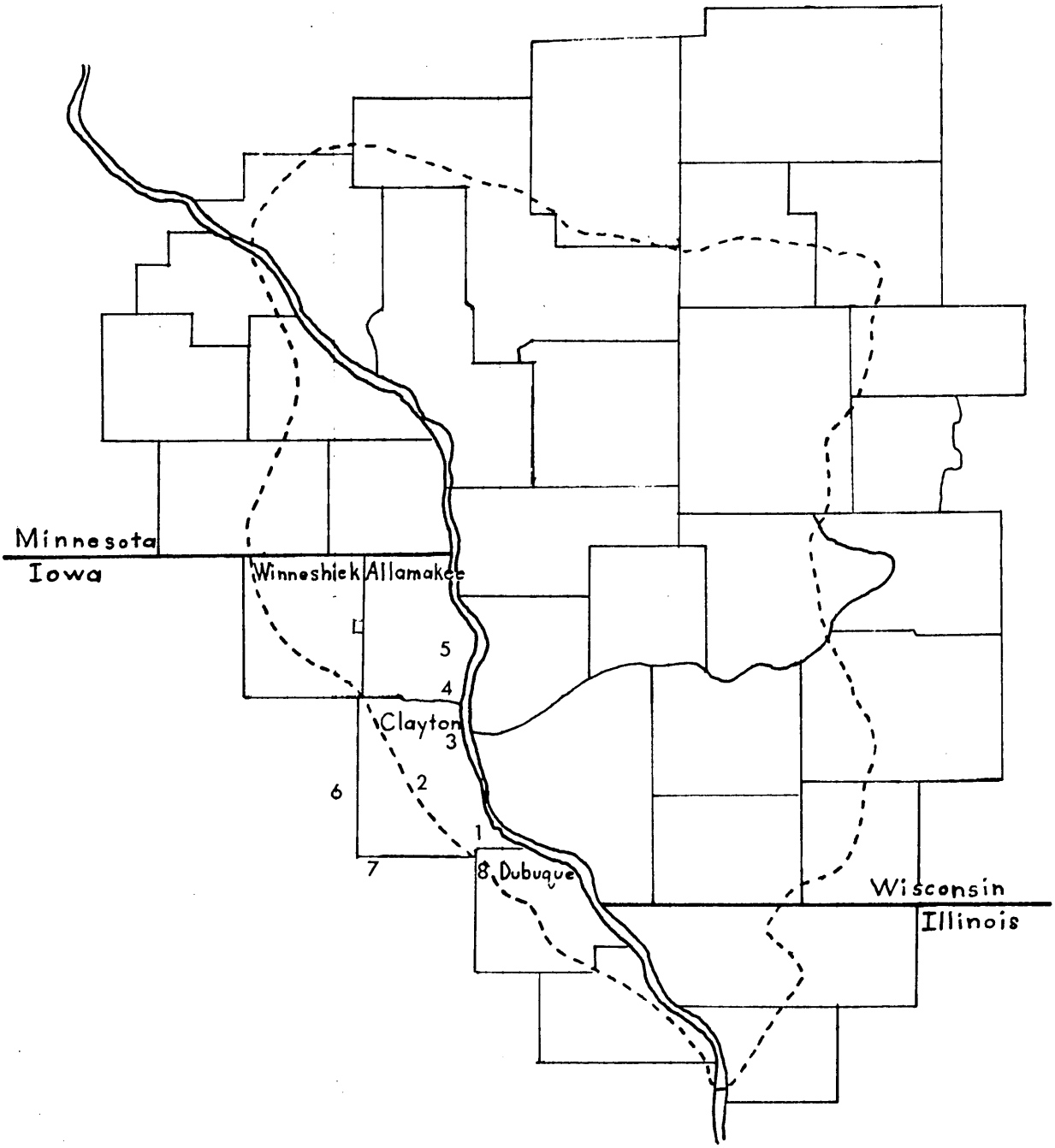
The driftless area is a region devoid of Pleistocene till, covering an area of 38,850 sq km in four states, including northeast Iowa, northwest Illinois, southwest Wisconsin, and southeast Minnesota (Figure 1, from Hartley 1966). The northeast Iowa portion was covered by Nebraskan till, but this has eroded away so that the area today is like the true driftless areas of adjacent Wisconsin and Illinois (Shimek 1948, Braun 1950, Hartley 1957, 1966).

The vegetation of northeast Iowa has been described as a prairie-deciduous forest transition zone (Livingston 1921, Curtis and McIntosh 1951). More specifically, Shantz and Zon (1924) classified northeast Iowa as part of the oak-hickory forest of the southern hardwood formation, which is characteristic of drier climates and extends farther west into the prairie than any other hardwood forest. Braun (1950) acknowledged the transitional nature of the region and the wide distribution of oaks and hickories but felt that it should be included in the maple-basswood forest because maple-basswood is the apparent climax vegetation, although restricted to the better sites. The area has also been classified as the western limit of the mixed coniferous-deciduous forest of the Great Lakes region (Shimek

Figure 1. The driftless area:

1. Merritt Forest State Preserve
2. Retz Memorial Woods
3. Pike's Peak State Park
4. Effigy Mounds National Monument
5. Yellow River State Forest
6. Brush Creek Canyon State Preserve
7. Backbone State Park
8. White Pine Hollow State Preserve

Border of driftless area (includes some Kansan and Nebraskan drift)


Minnesota
Iowa
Winneshiek
Allamakee
5
4
Clayton
3
2
6
1
7
8 Dubuque
Wisconsin
Illinois

1948, Tolstead 1938). The variety of classifications has resulted because the area is indeed transitional and does contain elements of all these forest types.

Quantitative methods in the form of gradient analysis have been applied to similar vegetation in southern Wisconsin (Curtis and McIntosh 1951, Curtis 1959), but this is the first study to apply these methods to the upland forests of northeast Iowa in relation to moisture and successional status. The moisture gradient is assumed to be the plant available moisture which is primarily controlled by topographic position (Whittaker 1967) within a region of relatively uniform precipitation. The successional gradient is defined as the change in species composition over time.

Gradient analysis can be divided into two approaches.

> In the first of these approaches vegetation samples are arranged and studied according to known magnitudes of (or indexes of position along) an environmental gradient which is accepted as a basis of study. This approach, to which the term gradient analysis was first applied, may be termed direct gradient analysis. In the other approach vegetation samples are compared with one another in terms of degrees of difference in species composition and on the basis of these degrees of difference are arranged along axes of variation. The axes may or may not correspond to environmental gradients; but if they do correspond, the approach to environmental gradients is indirect or inferential. This approach may consequently be termed indirect gradient analysis (Whittaker 1967).

The premises of these analyses are that species are individually distributed along gradients in response to each plant's physiological characteristics (Gleason 1939) and that these gradients can be identified. This veiw of vegetation distribution is generally contrary to the rigid classification of plant communities known as the 'community-unit theory'

(Whittaker 1956) that was prevalent in the early part of the century.

Gradient analysis has also been used to analyze a wide assortment of vegetation throughout North America (e.g., Whittaker 1956, Bray and Curtis 1957, Ayyad and Dix 1964, Whittaker and Neiring 1965, Lewin 1974). In this paper several direct and indirect gradient analysis techniques are used to analyze the pattern of vegetation distribution in the forests of northeast Iowa in relation to two gradients, moisture and successional status. The use of multiple analytical techniques is desirable because interpretation is facilitated when several techniques yield similar results. The pattern of diversity (species richness) is also considered as is the classification of the upland forest as a regional unit.

STUDY AREA

Northeast Iowa has a continental climate expressed by very cold winters and warm summers (Hartley 1966). Elkader, Clayton County, is centrally located in the study area and is climatically representative of the region. At this station, the average January temperature is -9 C; and for July, it is 23.3 C. The recorded temperature extremes are -38 C and 44 C. The growing season (consecutive days free from killing frost) averages 149 days (7 May to 3 October). The average annual precipitation is 83.3 cm with the majority coming in spring and summer (U.S.D.A. 1941). The Mississippi River has a moderating effect on temperature in the areas directly adjacent to it (Hartley 1966) and may locally lengthen the growing season.

The underlying rocks of the driftless area are for the most part beds of sedimentary rock that dip gently to the southwest (Hartley 1966). In northeast Iowa, the youngest bedrock is a cherty dolomite of Silurian age known as the Niagra formation. Beneath this is a layer of shale followed by a series of dolomites and then St. Peter's sandstone, all of Ordovician age (Hartley 1966). All of these rock formations are exposed by the region's dissected topography, which is due largely to the area's three main river systems--the Yellow, Upper Iowa, and Turkey Rivers.

The driftless area of northeast Iowa lies primarily within the Fayette and Fayette-Dubuque-Stonyland soil associations which formed under forest vegetation (Oschwald _et al_. 1965). Loess caps the uplands while bedrock is exposed on the steeper slopes, resulting in soils formed on weathered bedrock. These soils, although colluvial and residual, are similar to the surrounding drift soils because they are ultimately derived from the same

parent material--limestone, sandstone, and shale (Shimek 1948).

Although northeast Iowa was not covered by the most recent glacial advance (the Wisconsin), Shimek (1948) felt that the present forest vegetation could not have survived so close to the ice, but that it was one of the first areas to be invaded by forest. This is disputed by Braun (1950) and Hansen (1937) who felt that the area was little affected by the ice and was forested throughout the period. This view is supported by a pollen study (Sears 1942) which concluded that the driftless area served as a refugium for several forest species during the glacial period.

Gleason (1923) postulated that a narrow strip of conifers, parallel and adjacent to the ice margin, advanced with the glacier. When the ice retreated, the deciduous trees reinvaded from the south primarily along the river courses (Gleason 1923, Hansen 1937, Sears 1942, Dick-Peddie 1953) leaving only relics of the coniferous forest (Thorne 1964). At this time, the climate became drier and a prairie peninsula advanced as far east as Ohio (Gleason 1923); however, it is likely that the driftless area retained some of the forest in the more protected sites. As rainfall increased, the region was reinvaded by deciduous trees in part from the Ozark center and also from farther east by a route north of the prairie peninsula, resulting in the mixed forest types found in this area (Braun 1950).

The study areas (Figure 1) were public and private parks and preserves where the vegetation is protected in its natural state. Two general criteria were used to select these areas--1) location in the driftless area or directly adjacent to it and 2) degree of protection from disturbance. Eight areas were ultimately selected for study:

White Pine Hollow State Preserve This 264 hectare area was purchased by the state in 1937. It is located in the extreme northwestern corner of Dubuque County about 3.5 km northwest of Luxemberg. It lies on the east edge of the Kansan drift sheet, but, because the area is deeply dissected exposing dolomitic limestone and Ordovician shale, little drift remains and the topography and vegetation are characteristic of the immediately adjacent driftless area. Thorne (1964) considers the vegetation to be an outlier of the mixed coniferous-deciduous forest of the Great Lakes Region. Extremely varied topography permits a variety of habitats and plant associations including: a small boreal community on north facing talus slopes, maple-basswood (See Appendix B for scientific names.) communities on other mesic sites, and a mixed oak-white pine community on the uplands and ridges.

Yellow River State Forest-Paint Creek Unit This unit is located 3 km west of Waukon Junction, Allamakee County. It lies well within the borders of the driftless area. Its total area of 1470 hectares was gradually acquired by purchase between 1936 and 1939. The area suffered a devastating forest fire in the early 1930's (exact date unknown), and the vegetation today is a young mixed oak community of striking uniformity.

Pike's Peak State Park Pike's Peak, located directly south of McGregor, Clayton County, contains 240 hectares of the highest bluffs overlooking the Mississippi River. It affords a magnificent view of the Mississippi and Wisconsin River valleys. This scenic bluff has been so highly valued that the area has remained undisturbed except for a rather extensive fire around the turn of the century. The state sawmill was located

here until 1951, but only standing dead timber was removed. Today, nothing is cut except in a small recreational area. The bluff forests, which are mainly mixed oak communities, are subject to wind throw because of their elevation and exposure, resulting in many areas strewn with fallen trees. The area also contains some very deep gorges cut through Trenton limestone and St. Peter's sandstone producing some very protected habitats not unlike those of White Pine Hollow.

Effigy Mounds National Monument Effigy Mounds National Monument was established in 1949 by presidential edict to protect a series of prehistoric Indian burial mounds. It is located 5 km north of Marquette in the extreme southeastern corner of Allamakee County on the bluffs overlooking the Mississippi River. The monument is divided into a north and south unit with a total area of 540 hectares. Quaking aspen covers a large area of the bluffs, indicating extensive disturbance prior to 1949. However, scattered on the steeper slopes are small stands of relatively mature mixed oak communities, grading into maple-basswood on the most protected sites.

Brush Creek Canyon State Preserve Brush Creek Canyon was purchased as a state park in 1936 and dedicated as a nature preserve in 1971. It is situated 2 km north of Arlington in Fayette County and contains approximately 87 hectares. The canyon is located on the northern edge of the Kansan glaciation, but Brush Creek has eroded most of the till away so that the preserve resembles the driftless area adjacent to the east. Brush Creek is a rapid stream that has cut steep ravines through more than 30 meters of dolometic limestone (Eilers 1974), giving rise to several mesic

habitats. The vegetation is mostly dominated by a mixed oak community with maple-basswood becoming important in the most sheltered sites.

Retz Memorial Woods The Retz Memorial Woods is a small tract of 19.6 hectares, located 10 km southwest of Elkader, Clayton County, on the north side of the Turkey River. It was purchased in 1966 by The Nature Conservancy. It is primarily a mixed oak upland that had been selectively logged about 50 years ago. There is a steep north-south ravine through dolomitic limestone where maple-basswood becomes dominant. This ravine also contains other mesophytic species such as yew (*Taxus canadensis*).

Merritt Forest State Preserve This 8 hectare area was dedicated as a nature preserve in 1969. It is located 7 km east of Osterdock in southeastern Clayton County. Although small, this tract is significant because it is probably the only intact remnant of virgin mesophytic forest in the state; the maple-basswood forest reaches its maximal development here, and red oak is also well represented.

METHODS

Field techniques

In each study area, the following criteria were used for sample site selection: 1) no evidence of recent human disturbance, 2) apparent homogeneity of vegetation and topography within the site, and 3) sufficient size to accomodate the sample quadrat.

Within a site, a 0.1 hectare quadrat was erected by arbitrarily selecting a starting point at one end of the site. A 50 meter tape was run in a straight line from that point along the contour of the slope. A 50 x 20 meter rectangle was then defined by measuring a distance of 10 meters upslope and downslope from each end of the tape. The herb layer was sampled by 1 m^2 quadrats every other meter along the 50 meter tape and estimating percent cover by species for each of these smaller quadrats. The herb stratum included vascular herbaceous plants and woody plants under 0.5 meters in height.

Shrub, understory tree, and canopy tree cover were estimated simultaneously by line intercept along the 50 meter tape. Cover for each individual was recorded by stratum and species. The shrub stratum included young trees less than 1.5 meters in height. It was often necessary to estimate the intercept of canopy trees when they were obscured by lower strata.

Diameter at breast height was recorded by species for each individual tree stem over 5 centimeters diameter. Stems sprouting from the same root crown were recorded separately but noted as such. Last, the quadrat was searched for any species not recorded by previous sampling, and environ-

mental data (slope, aspect, position) were recorded.

Analytical techniques

The field data were reduced to the following quantities: canopy tree cover (meters), understory tree cover (meters), tree basal area (cm^2/0.1 ha), tree density (stems/0.1 ha), shrub cover (meters), herb cover (%), and herb frequency (%). Tree basal area was chosen as the best measure of tree species importance because it appeared to accurately represent the vegetation.

Dominance types The assignment of a dominance (based on dominant tree species) type to each stand involved three steps. First, dominant species were subjectively evaluated in the field for each sample. This initial classification was then modified based on the total basal area of each species in each quadrat. This modified classification was then further refined by use of an agglomerative classification (Orloci 1967) based on basal area.

Environmental moisture classes Environmental moisture classes were assigned to stands as the product of the aspect and slope position of each stand (Ayyad and Dix 1964). Sample quadrats were then arranged along the moisture axis. Table 1 shows the numerical assignment for aspect. Lower slopes, middle slopes, upper slopes, uplands, and exposed ridges were assigned values of 1 through 5, respectively. Uplands with internal drainage were assigned a value of 2.

Weighted averages A two dimensional direct gradient analysis using weighted averages (Whittaker 1967) for moisture preference and successional status (as defined by shade tolerance) was carried out using the species weights listed in Table 2. The species weights represent a synthesis of silvics information for each species (U.S.D.A. 1965, Forbes 1955).

A weighted average ordination was also done using climax adaptation numbers (Curtis and McIntosh 1951, Curtis 1959). Species were ranked from 1.0 to 10.0 (Table 2) depending upon how well each species coexists with sugar maple in the natural undisturbed forest, assuming that maple is the dominant climax species. The values for witch hazel, eastern red cedar, white pine, and choke cherry were not listed by Curtis (1959) and were estimated from the available silvics information.

Bray-Curtis ordination Bray-Curtis ordination was used to arrange the samples in two dimensions using axes whose endpoints were chosen prior to the ordination (Bray and Curtis 1957). Percent dissimilarity was computed by Sorensen's Index based on tree basal area and used as a measure of phytosociological distance for the ordination.

Three methods were employed for endpoint selection. The first used stands that were obvious endpoints to perceived environmental gradients--in this case, moisture and successional status. The endpoints chosen for the moisture axis were the same ones earlier defined by the product of aspect and slope position. The endpoints for the succession axis were determined subjectively based on species composition and stand appearance. This was necessary because it was not possible to measure the exact successional age of the stand. Weighted averages for succession and Curtis climax numbers did define the most mature stand, but they did not separate the young stands well, and a subjective decision was necessary. The resulting two dimensional ordination is a form of direct gradient analysis (Whittaker 1967).

The second method required that the endpoints for the first axis be the two most dissimilar stands providing that each endpoint stand have a

similarity of 50% or greater with at least three other stands (Newsome and Dix 1968). The endpoints of the second axis were the two most dissimilar stands from the middle 10% of the first axis. These stands must also have a similarity of at least 50% to three or more other stands. This method did not yield a clear vegetation pattern and, therefore, is not discussed further.

For the third method, the stand with the lowest average similarity to all other stands was chosen as one endpoint for the first axis, and the stand with the lowest similarity to the first endpoint became the second (Beals 1960). Both stands must have a similarity of 50% or more with three other stands. The second axis was chosen the same way as in the second method. Both method two and method three are indirect ordinations (Whittaker 1967).

Reciprocal averaging Reciprocal averaging (Hill 1973) does not require the selection of endpoints prior to the ordination. The axes are, therefore, independent of assumptions about environmental gradients, and the resulting ordination is both indirect and objective (Gauch *et al.*)[1]. This ordination was computed for three axes but only the first axis gave a clear vegetation pattern. A computer generated coenocline was also manufactured using this technique. (This program, CEP-20, was written by Hugh Gauch, Jr. of Ecology and Systematics, Cornell University.)

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[1]Gauch, H. G., R. H. Whittaker, and T. H. Wentworth, Ecology and Systematics, Cornell University, Ithaca, N.Y. Comparative Study of Reciprocal Averaging and Other Ordinations. To be published ca. 1976.

The methods used here to analyze the data are ordination techniques; they rank (order) the quadrats on axes. The exact ecological function of these axes can only be inferred because all environmental variables are not evaluated. (The axes are shown as linear for graphical presentation.) Therefore, standard regression techniques are not applicable, and, instead, the Spearman rank correlation (Steel and Torrie 1960) is used to evaluate the concordance of the analytical techniques.

Table 1. Assignment of moisture numbers by aspect

Aspect	Moisture numbers
N, NNE, NE	1
ENE, NNW	1.5
E, NW	2
WNW	2.5
ESE, W	3
SE	4
SSE, WSW	4.5
S	5
SSW	5.5
SW	6

Table 2. Weights for moisture preference, successional status, and climax adaptation numbers

Species[a]	Weights		Climax adaptation numbers[d]
	Moisture[b]	Succession[c]	
Maple	1	1	10.0
Blue beech	1	1	8.0
Yellowbud hickory	2	1	8.5
Shagbark hickory	3	1	4.5
Hackberry	1	2	8.0
White ash	2	2	6.5
Witch hazel	3	2	4.0
Black walnut	1	2	6.5
Eastern red cedar	4	3	2.0
Ironwood	2	1	8.5
White pine	4	2	3.0
Bigtooth aspen	3	3	4.5
Black cherry	3	2	3.5
Choke cherry	3	2	4.0
White oak	4	2	3.5
Red oak	2	2	5.5
Basswood	1	1	7.5
Red elm	2	2	8.0

[a]See Appendix B for scientific names.

[b]1 = mesic, 2 = sub-mesic, 3 = sub-xeric, 4 = xeric.

[c]1 = climax, 2 = sub-climax, 3 = pioneer.

[d]After Curtis (1959).

RESULTS

A summary of the recorded and computed information for each stand is presented in Table 3. The dominance type classifications shown in Table 3 are the result of dominance expressed by seven tree species--maple, basswood, red oak, white oak, white pine, bigtooth aspen, and shagbark hickory. No clear dominance was expressed in Stand 31, therefore, it is labeled mixed. Bigtooth aspen was important only in one stand where it was co-dominant with white oak, therefore, it is grouped with that type. Shagbark hickory dominated a single stand and is not considered further because it was distributed like the white oak type except in Figures 4A and 4B.

The three criteria used to evaluate dominance (subjective field evaluation, basal area, and the agglomerative dendrogram in Figure 2) generally agreed except that the dendrogram did not recognize the co-dominant situations which comprise 34% of the samples. Co-dominance is defined as the situation where the most important tree species in a stand have similar basal areas, usually within 15%. In these cases, the computer forced the samples into a single classification type sometimes based on the basal area contributed by less important species (i.e., not one of the seven listed above).

Table 4 contains the average basal area (cm^2/0.1 ha) of the tree species found in each of the five dominance types recognized. The co-dominant stands were excluded from the calculations to emphasize their differences; however, it should be noted that the range of basal area values indicates that in reality the forest types of northeast Iowa continuously intergrade.

The five recognized dominance types are described below:

Maple This type is dominated by maple with basswood and white oak of secondary importance. It is usually found in the most mesic and least disturbed sites.

Basswood Basswood dominates this type with yellowbud hickory, maple, and red oak of minor importance. It is found in undisturbed mesic sites.

Red oak Red oak strongly dominates this type with maple as a species of minor importance. This type is found in mesic sites.

White oak This type is dominated by white oak with red oak as a second important species and maple and basswood as minor components. It is usually found in drier sites.

White pine White pine dominates this type with white oak a strong secondary species and red oak and maple as minor components. This type is usually found in the driest sites.

Many of the tree species (Table 4) showed ubiquitous distribution, although most reached a maximum in one type. Ironwood and blue beech, which showed slight peaks in the maple and basswood types, respectively, were generally distributed uniformly throughout the understory of all types. Ironwood was much more common than blue beech. Red elm was found in all except the white pine type, but was most abundant in the basswood stands. Yellowbud hickory and black walnut were also most abundant in the basswood type but were absent from the maple type. White ash was found most often in the red oak type and shagbark hickory in the white oak type. Black cherry and hackberry were found only in the white oak type, giving the white oak type the greatest tree species richness. The maple type had

the fewest number of species. Bigtooth aspen, a disturbance species, was present only in the red oak, white oak, and pine stands. The total basal area of the white pine forest is considerably larger than any of the other types because of a white oak forest developing underneath it.

In the herb stratum, Parthenocissus spp. (constancy = 100%), Osmorhiza spp. (100%), Geranium maculatum (86%), and Circaea canadensis (80%) were ubiquitous. Carex spp. (74%), Uvularia grandiflora (72%), Amphicarpa bracteata (66%), Smilacina racemosa (66%), Sanicula gregaria (60%), Podophyllum peltatum (60%), and Smilax herbacea (57%) were also common. Parthenocissus spp. were by far the most important herb species, covering an average of 12% of the forest floor and often exceeding 25% in a single 0.1 hectare quadrat. Hepatica acutiloba, Sanguinaria canadensis, Asarum canadense, Adiantum pedatum, and Mitella diphylla were characteristic of moist slopes, usually in association with red oak. Hydrophyllum appendiculatum was recorded in the most mesic sites of the mature maple-basswood stands of Merritt Forest where it replaced Parthenocissus spp. as the most important herb; its cover exceeded 20% in these areas.

Tree seedlings, especially maple, were a significant component of the herb layer, and their saplings completely dominated the shrub stratum. Maple (herb constancy = 91%, shrub constancy = 85%) was the most frequently encountered tree species in both lower strata with the following species also important: white ash (86%, 40%), yellowbud hickory (77%, 34%), red elm (71%, 26%), basswood (60%, 46%), ironwood (40%, 49%), red oak (57%, 6%), white oak (26%, 6%), and choke cherry (54%, 3%). The constancy figures show that maple, basswood, and ironwood seedlings were the most successful species in attaining sapling status. Xanthoxylem americana and Ribes spp.

were also found in the shrub stratum but were uncommon.

After the dominance types were assigned to the sample quadrats, the stands were ordinated to examine the relationships among moisture, succession, and species composition (dominance). When the dominance types of Table 4 were assigned to the stands ordinated on the environmental moisture axis (Figure 3A), the maple, basswood, and red oak types were located on the mesic 1/3 of the axis; the white oak type occupied a more intermediate position while the range of the white pine type covered all but the most mesic sites.

The distribution of dominance types on the climax adaptation axis (Figure 3B) indicates that the maple stands were closest to climax vegetation (as defined by Curtis climax numbers, Curtis 1959) followed by the basswood, red oak, white oak, and finally white pine types.

The weighted average moisture ordination (Figure 3C) shows a dominance type distribution essentially similar to the climax adaptation ordination, as shown by a high Spearman rank correlation between the two ordinations (0.95, Table 5).

The two dimensional ordination presented in Figure 4A is an analysis using the weighted average moisture axis (Figure 3C) for the abscissa and a weighted average succession axis for the ordinate. Figure 4B shows that maple and basswood stands were found to occupy the most mesic and mature sites while the red oak type was distributed in the less mature sites, the white oak type in the younger and drier areas, and the white pine type in the most xeric sites. The successional trends in Figure 4B demonstrate that both the red oak and white oak forests converge on a maple-basswood forest, while the white pine type goes first through a white oak type to a maple-

basswood type. The moisture trend parallels the weighted average moisture axis.

Figures 5A and 5B are also a two dimensional analysis using Bray-Curtis ordination techniques. The abscissa is the moisture axis with endpoints chosen to be a canyon bottom red oak stand (No. 34) and an exposed ridge white pine stand (No. 8). The ordinate is the succession axis with one endpoint a mature maple stand (No. 13), and a disturbed white oak-bigtooth aspen stand (No. 21) the other. The distribution pattern of dominance types in this ordination is similar to the weighted averages ordination (Figures 4A and 4B). The maple and basswood types still occupy the most mesic and mature sites while the red oak, white oak, and white pine stands occupy the younger mesic, intermediate, and xeric sites, respectively. The red oak stands will succeed to maple-basswood and the white oak stands to maple. The trend for the white pine type, however, is not clear.

Figure 6A, an indirect Bray-Curtis ordination, used a rule by Beals (1960) to select endpoints for the two axes (See methods.). Abscissa endpoints are a lower slope red oak stand (No. 35) and an exposed ridge white pine stand (No. 8). The ordinate endpoints are an upland mixed oak stand (No. 31) and an upland basswood stand (No. 2). This ordination shows few differences from the direct ordinations in Figures 4A and 4B and Figures 5A and 5B. The basswood type is better separated from the maple type and placed in a more mesic position. The successional pattern remains the same as is shown in Figure 5B.

Figure 3D shows the results of the reciprocal averaging ordination. The distribution of dominance types on this axis is very similar to both the weighted average moisture and the climax adaptation axes in Figures 3B

and 3C (Spearman rank correlation = 0.91 in both cases, Table 5).

A coenocline of the five dominant species generated by the computer on the reciprocal averaging axis (Figure 7) shows that the axis is a complex of moisture and successional gradients with young-xeric on the left and mature-mesic on the right. The bimodal distribution of maple is the result of the two separate successional paths indicated in Figure 7.

In addition to analyzing the interaction of moisture and successional status with dominance type distribution, patterns of diversity were examined by plotting the total species richness of each sample against its climax adaptation number (Figure 8). A regression line was fit by least squares to the deciduous and white pine stands separately. The deciduous stands showed a significant ($r = 0.57$, $p < 0.01$) decrease in species richness with increasing climax adaptation, while the white pine stands showed a significant ($r = 0.89$, $p < 0.01$) increase in total number of species. This trend is due primarily to the herb layer as the number of tree species does not vary widely among samples.

Table 3. Summary of sample information

Quadrat	Location	Aspect	Slope (degrees)	Position	Dominance type[a]
1	Retz	S	3	upland	WO
2	Backbone	E	3	upland	B
3	Backbone	NE	12	lower-slope	RO/B
4	Backbone	S	15-22	mid-slope	WO
5	Backbone	N	14	mid-slope	RO
6	Pine Hollow	W	13	upland	WO/WP
7	Pine Hollow	E	14	mid-slope	RO
8	Pine Hollow	SW	7	ridge	WP
9	Pine Hollow	SSE	20	lower-slope	WP
10	Pine Hollow	E	10	ridge	WP
11	Retz	S	12	lower-slope	WO
12	Merritt	NNW	11	mid-slope	BB
13	Merritt	NNE	9	mid-slope	M
14	Merritt	W	11	mid-slope	RO/B
15	Merritt	SSE	12-15	mid-slope	M
16	Pike's Peak	ENE	8	upper-slope	WO
17	Pike's Peak	SE	20	upper-slope	RO/WO
18	Pike's Peak	WNW	8-13	mid-slope	RO/WO
19	Pike's Peak	E	11	mid-slope	M/WO
20	Pike's Peak	W	23	mid-slope	RO
21	Pike's Peak	SW	12	upper-slope	WO/BA
22	Pike's Peak	ENE	11	upper-slope	RO
23	Effigy Mounds	NW	25-28	lower-slope	RO/M/B
24	Effigy Mounds	SE	12	mid-slope	WO/RO
25	Effigy Mounds	NW	5-8	upper-slope	WO/R
26	Effigy Mounds	NE	15-27	lower-slope	RO
27	Yellow River	W	8	upper-slope	WO
28	Yellow River	N	16-22	upper-slope	WO/RO
29	Yellow River	WNW	6	upper-slope	WO/RO
30	Yellow River	NE	8	mid-slope	WO
31	Yellow River	S	5	mid-slope	mixed
32	Yellow River	SE	8	upper-slope	SH
33	Pike's Peak	E	14	mid-slope	WO
34	Brush Creek	W	25	canyon bottom	RO
35	Brush Creek	ENE	23	lower-slope	RO

[a]WO = white oak; RO = red oak; B = basswood; WP = white pine; M = maple; SH = shagbark hickory; BA = bigtooth aspen.

Quadrat	Environmental moisture class	Weighted average		Climax adaptation number	Species richness
		Moisture	Succession		
1	20	3.17	1.84	4.90	52
2	6	1.53	1.15	7.68	38
3	1	1.86	1.60	6.27	41
4	10	3.23	1.87	4.69	42
5	2	1.98	1.88	6.00	44
6	12	3.07	1.89	4.81	36
7	4	2.16	1.89	5.81	37
8	30	3.71	1.96	3.60	23
9	4.5	3.05	1.79	4.81	47
10	10	3.47	1.92	4.15	28
11	5	2.54	1.88	5.74	43
12	3	1.30	1.33	7.55	32
13	2	1.08	1.02	9.17	28
14	6	1.68	1.56	6.67	30
15	9	2.00	1.38	7.83	31
16	4.5	2.82	1.66	5.52	38
17	12	2.67	1.81	5.45	33
18	5	2.61	1.76	5.42	42
19	4	2.48	1.61	6.40	29
20	6	1.78	1.77	6.51	44
21	18	2.88	2.05	5.47	36
22	4.5	2.04	1.83	5.97	37
23	2	1.44	1.33	7.68	34
24	8	2.45	1.68	5.59	49
25	6	2.71	2.05	4.99	47
26	1	1.98	1.85	5.90	33
27	9	3.30	1.95	4.39	43
28	3	2.42	1.81	6.00	45
29	7.5	3.00	2.01	4.73	45
30	2	3.09	1.86	4.54	41
31	10	2.74	1.92	5.07	49
32	12	3.09	1.53	4.55	47
33	4	2.87	1.73	5.25	33
34	0	1.84	1.67	6.62	46
35	1.5	1.91	1.90	5.91	52

Figure 2. Orloci (1967) agglomerative dendrogram classification of samples from northeast Iowa using tree basal area. The number of clustering passes represents sample or group dissimilarity

WP = white pine

WO = white oak

RO = red oak

MM = mixed mesophytic

B = basswood

M = maple

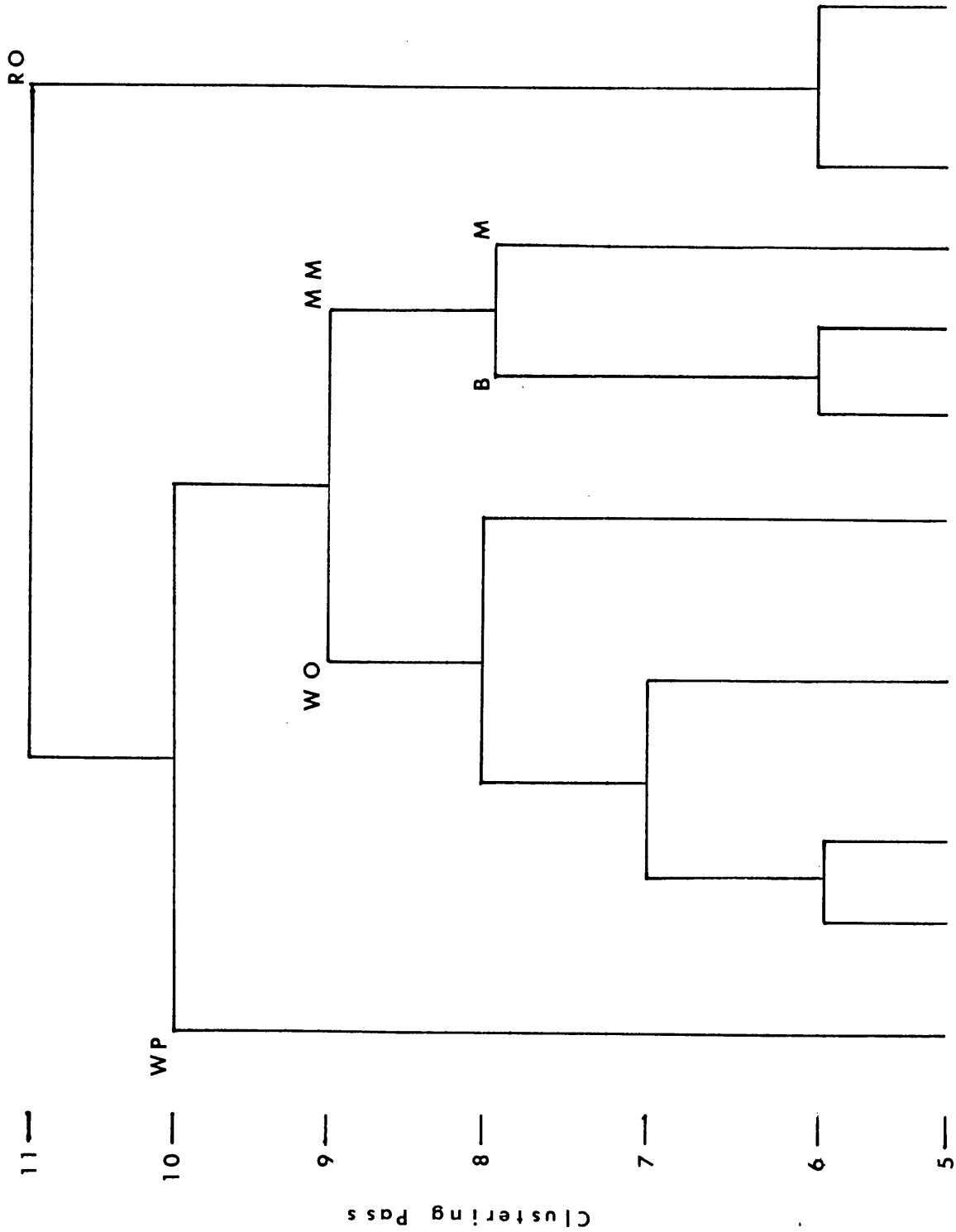

RO
WP
MM
WO
M
B
11
10
9
8
7
6
5
Clustering Pass

Table 4. Average basal area (cm^2/0.1 ha) of tree species in each dominance type in the forests of northeast Iowa

Species	Dominance type				
	Maple	Basswood	Red oak	White oak	White pine
Maple	18900	4600	4700	3200	3800
Basswood	4200	18600	1300	700	600
Red oak	25	3700	26600	7000	5300
White oak	4700	1100	2300	17700	9500
White pine	0	0	0	0	25500
Ironwood	1100	700	500	600	700
White ash	0	300	400	300	40
Red elm	1600	2600	200	800	0
Black walnut	0	1800	500	400	0
Shagbark hickory	0	80	200	1200	100
Yellowbud hickory	0	5000	30	100	300
Bigtooth aspen	0	0	400	65	400
Blue beech	35	85	75	30	50
Black cherry	0	0	0	85	0
Hackberry	0	0	0	200	0
TOTAL	30600	38600	37200	32400	46300
Number of samples	2	2	7	7	3

Figure 3. Single axis ordinations: A) environmental moisture class, B) climax adaptation numbers, C) weighted average moisture, D) reciprocal averaging. The length of the line segment represents the range of dominance (including co-dominant stands) of each species. The mean of the dominance type distribution is indicated on each segment

RO = red oak

WO = white oak

M = maple

B = basswood

WP = white pine

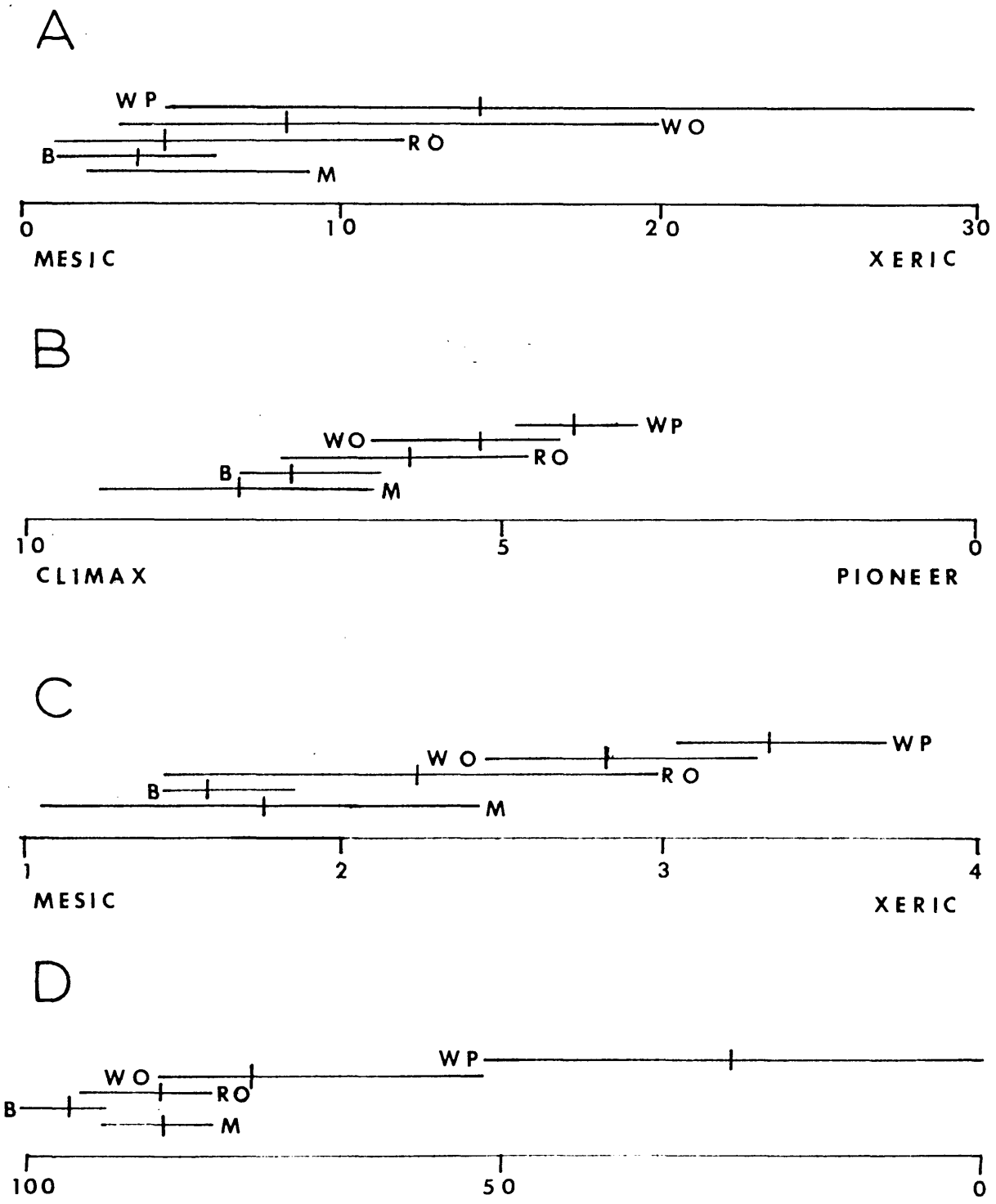

A
WP
WO
RO
B
M
0
10
20
30
MESIC
XERIC
B
WP
WO
RO
B
M
10
5
0
CLIMAX
PIONEER
C
WP
WO
RO
B
M
1
2
3
4
MESIC
XERIC
D
WP
WO
RO
B
M
100
50
0

Table 5. Spearman rank correlations (r_s) of single axis ordinations

	r_s[a]
Environmental moisture class-weighted average moisture	.64
Environmental moisture class-climax adaptation numbers	.50
Environmental moisture class-reciprocal averaging	.58
Weighted average moisture-climax adaptation numbers	.95
Weighted average moisture-reciprocal averaging	.91
Climax adaptation numbers-reciprocal averaging	.91

[a]All values significant at $p < .01$ level.

Figure 4A. Two dimensional weighted average ordination based on tree basal area. Abscissa is moisture averages; ordinate is succession averages. Dominance type delimitations are approximate

RO = red oak

WO = white oak

M = maple

B = basswood

WP = white pine

SH = shagbark hickory

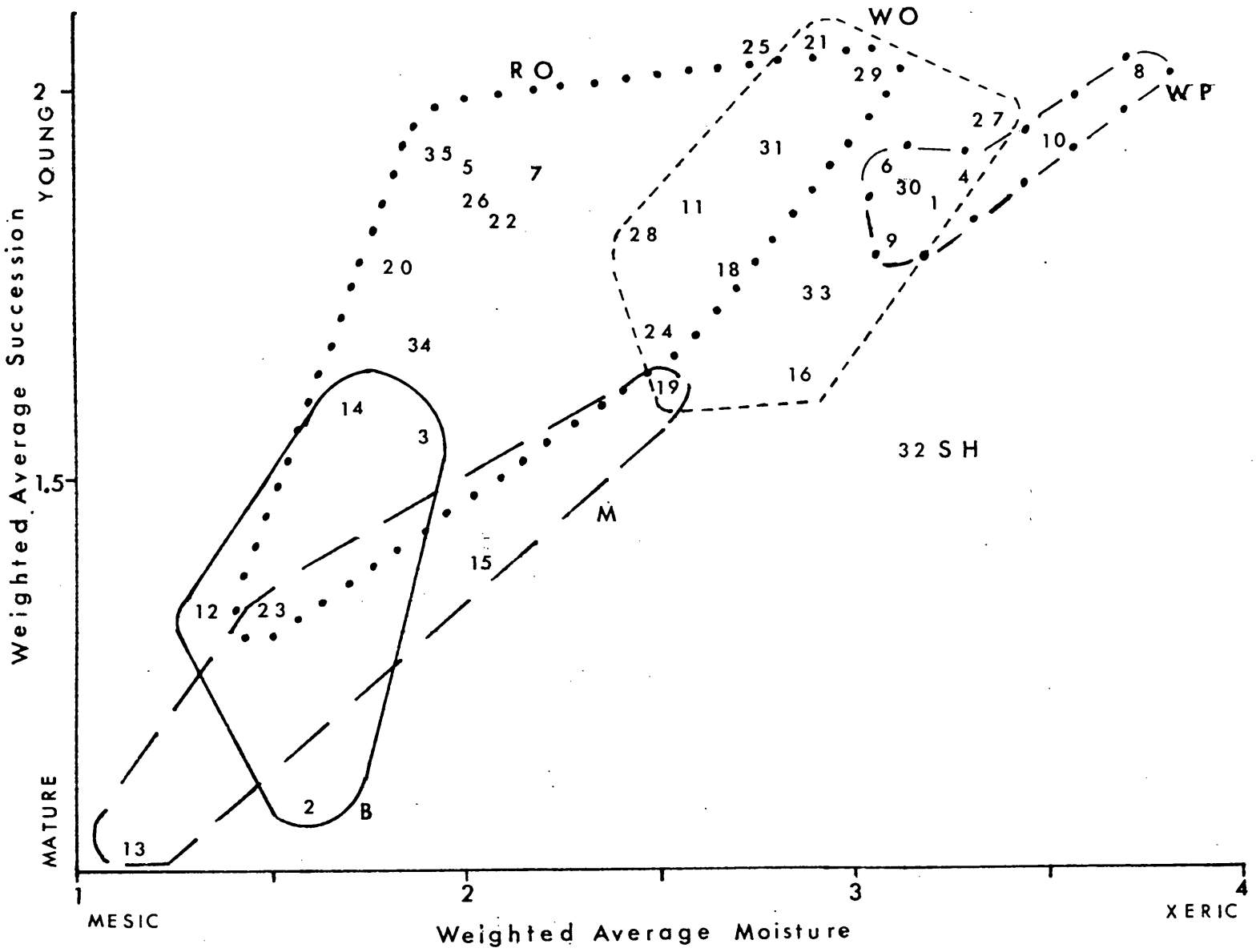

Weighted Average Succession
YOUNG
MATURE
2
1.5
1
2
3
4
MESIC
XERIC
Weighted Average Moisture
RO
WO
WP
B
M
SH
25
21
29
8
27
10
31
35
5
7
6
30
4
1
26
22
11
28
9
20
18
33
24
34
16
19
14
3
32
15
12
23
2
13

Figure 4B. Moisture and successional patterns superimposed on the weighted average ordination (Figure 4A)

RO = red oak

WO = white oak

M = maple

WP = white pine

B = basswood

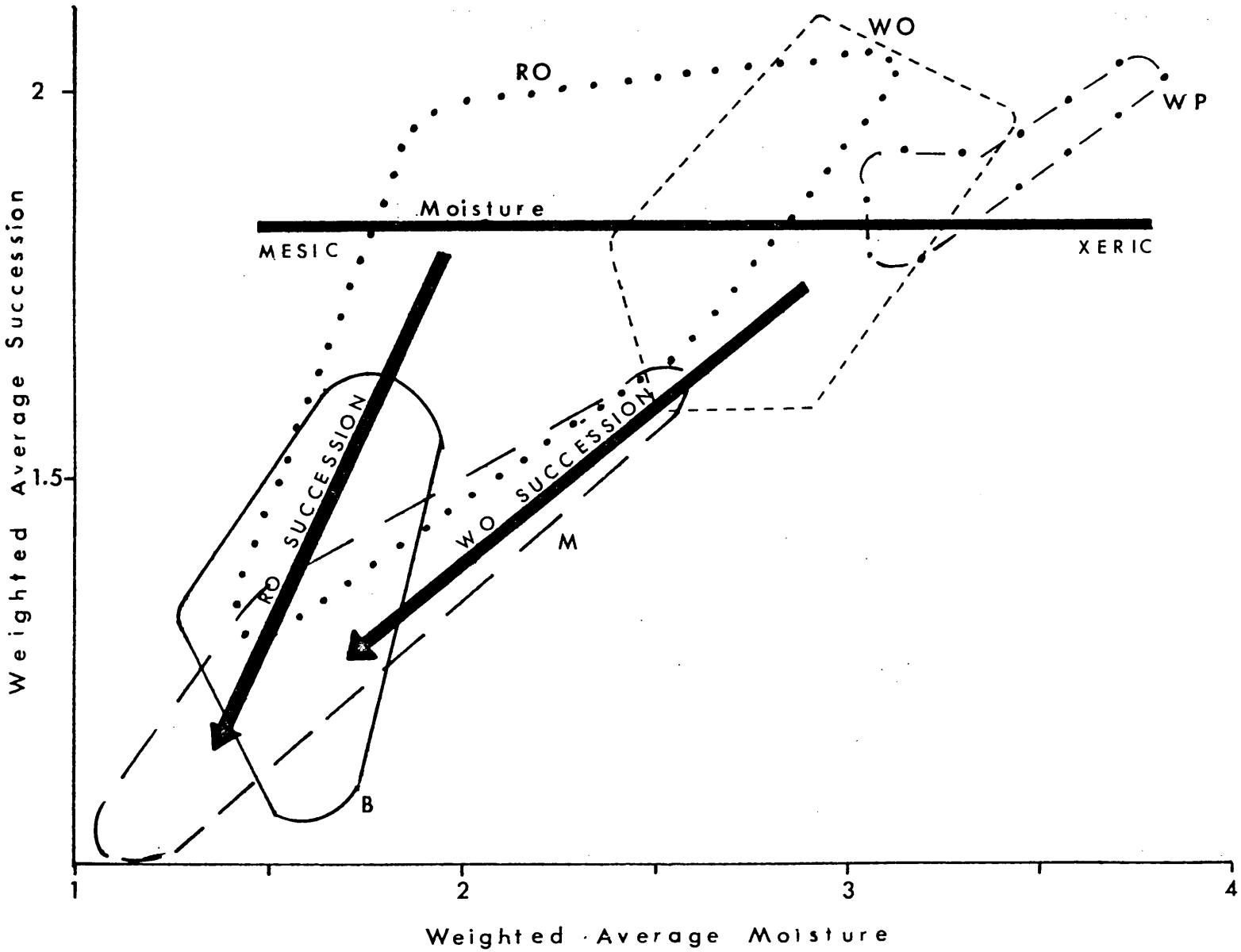

WO
RO
WP
Moisture
MESIC
XERIC
RO SUCCESSION
WO SUCCESSION
M
B
2
1.5
1
2
3
4
Weighted Average Succession
Weighted Average Moisture

Figure 5A. Two dimensional direct gradient analysis using Bray-Curtis ordination based on tree basal area. Abscissa (moisture axis) endpoints were a canyon bottom, red oak stand (No. 34) and an exposed ridge, white pine stand (No. 8). Ordinate (succession axis) endpoints were a climax maple stand (No. 13) and a disturbed white oak-bigtooth aspen stand (No. 21). See methods for endpoint selection criteria. Dominance-type delimitations are approximate

RO = red oak

WO = white oak

M = maple

B = basswood

WP = white pine

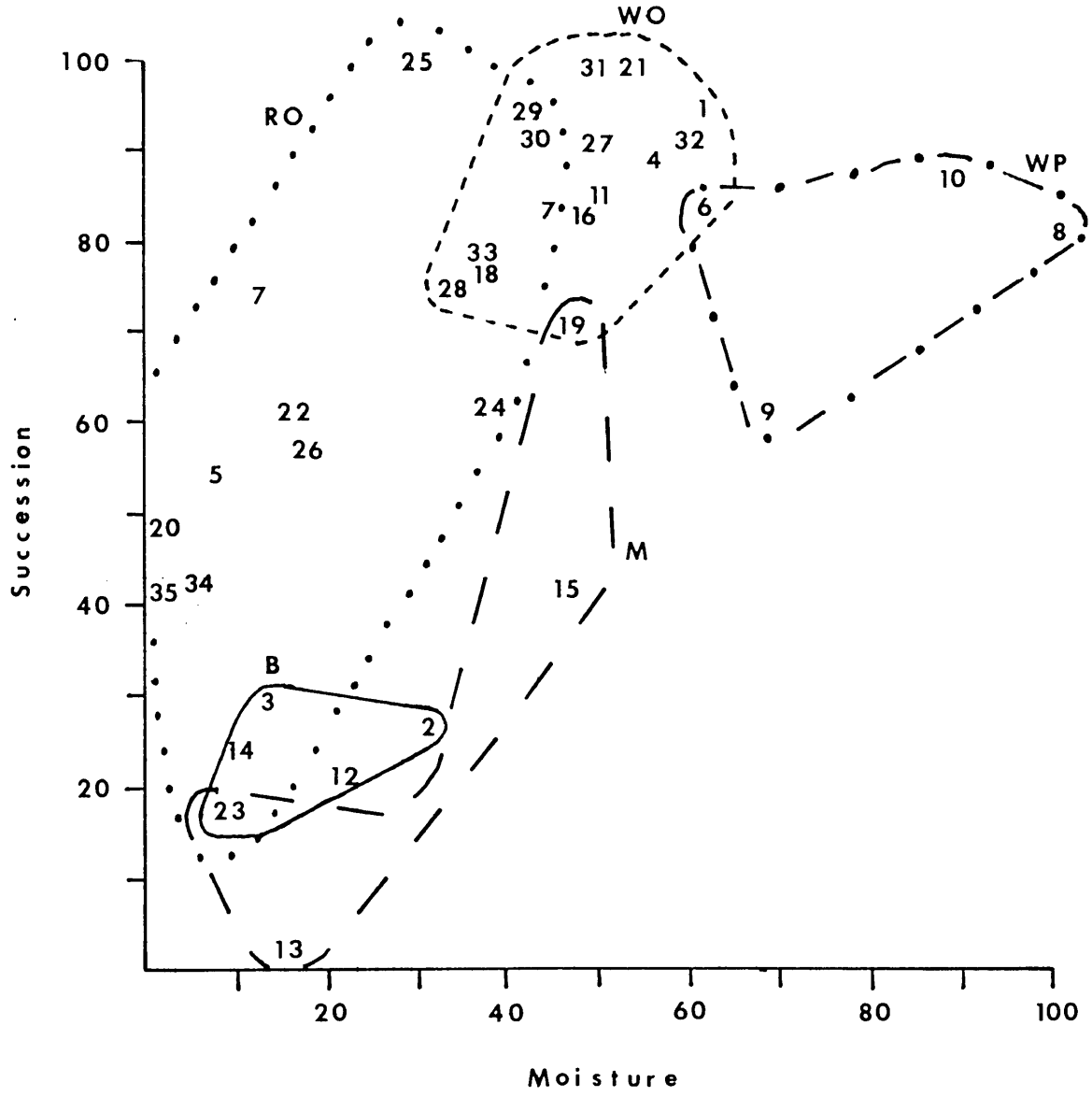

WO
RO
WP
B
M
Succession
Moisture
100
80
60
40
20
20
40
60
80
100
25
31 21
29
30
27
4
32
1
10
11
7
16
6
8
33
18
28
7
19
24
9
22
26
5
20
35
34
15
3
2
14
12
23
13

Figure 5B. Moisture and successional patterns superimposed on direct gradient Bray-Curtis ordination (Figure 5A)

RO = red oak

WO = white oak

M = maple

B = basswood

WP = white pine

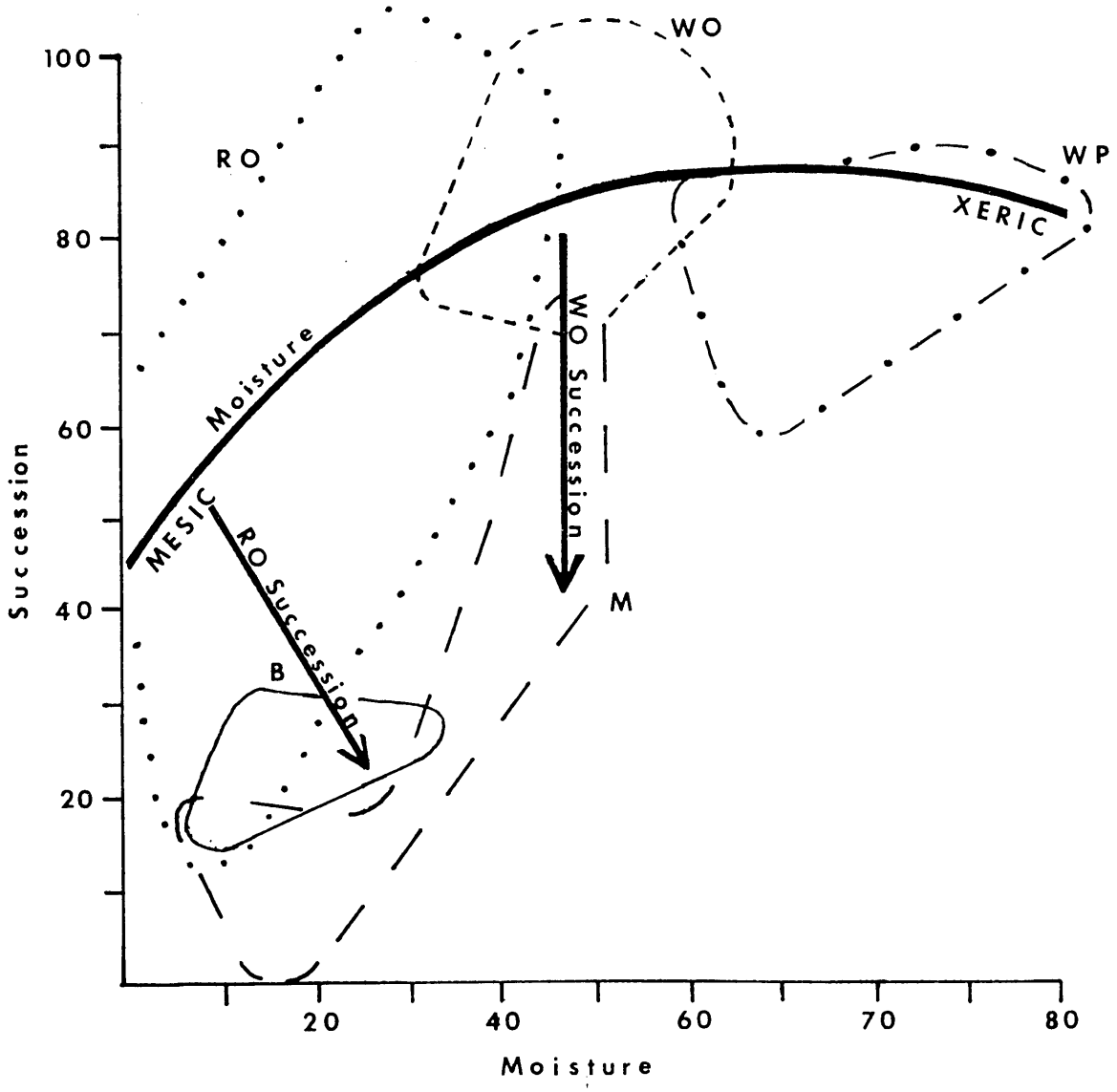

WO
RO
WP
XERIC
Moisture
MESIC
RO Succession
WO Succession
M
B
100
80
60
40
20
Succession
20
40
60
70
80
Moisture

Figure 6A. Two dimensional Bray-Curtis indirect ordination based on tree basal area. Abscissa endpoints are a lower slope red oak stand (No. 35) and an exposed ridge white pine stand (No. 8). The ordinate endpoints are an upland basswood stand (No. 2) and an upland mixed oak stand (No. 31). See text for endpoint selection criteria. Dominance type delimitations are approximate

RO = red oak

WO = white oak

M = maple

B = basswood

WP = white pine

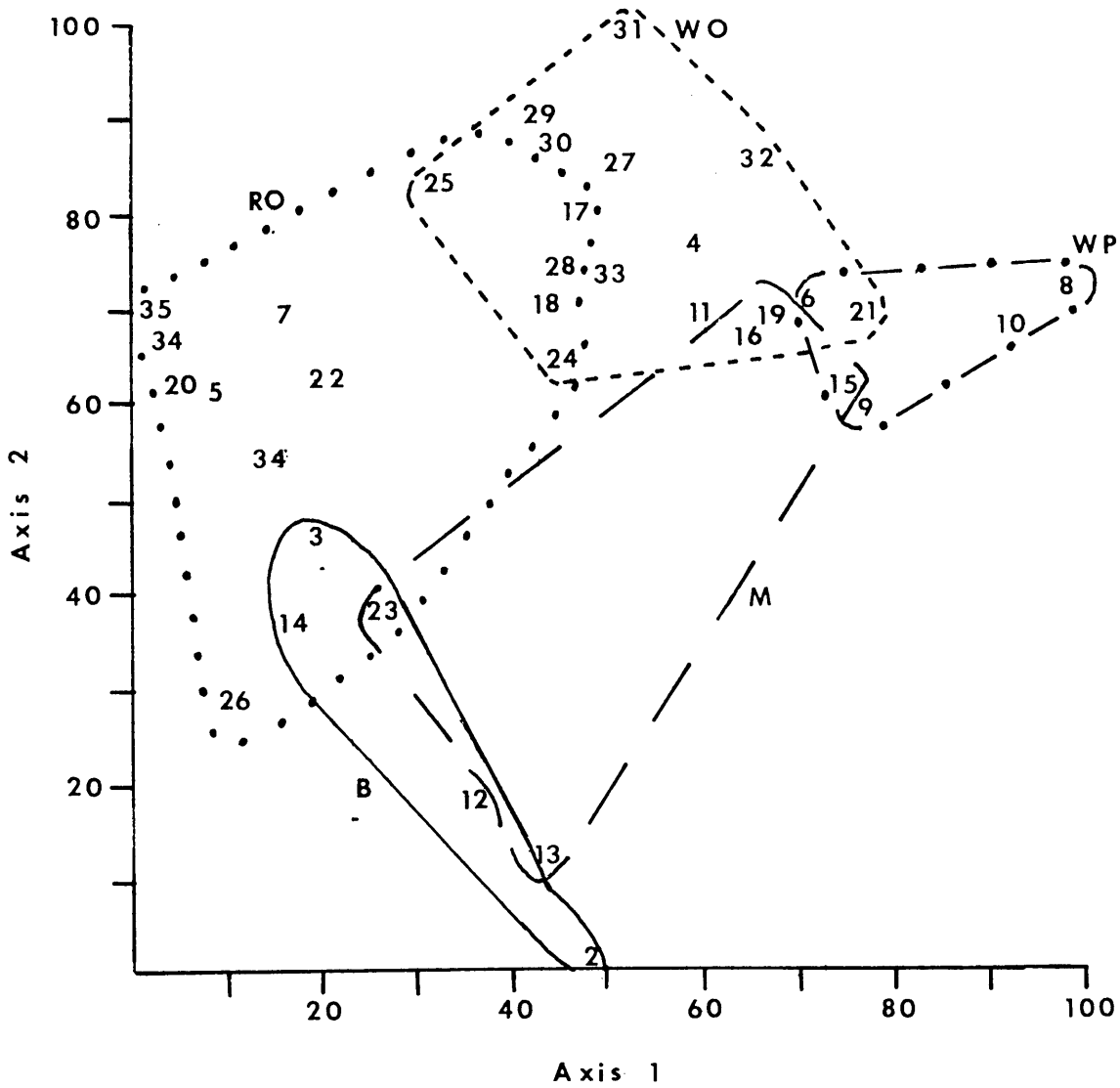

100
80
60
40
20
Axis 2
20
40
60
80
100
Axis 1
31
WO
29
30
27
32
25
RO
17
4
WP
28
33
8
35
7
18
11
19
6
21
10
34
16
24
20
5
22
15
9
34
3
M
14
23
26
B
12
13
2

Figure 6B. Moisture and successional patterns superimposed on the indirect Bray-Curtis ordination (Figure 6A)

RO = red oak

WO = white oak

M = maple

B = basswood

WP - white pine

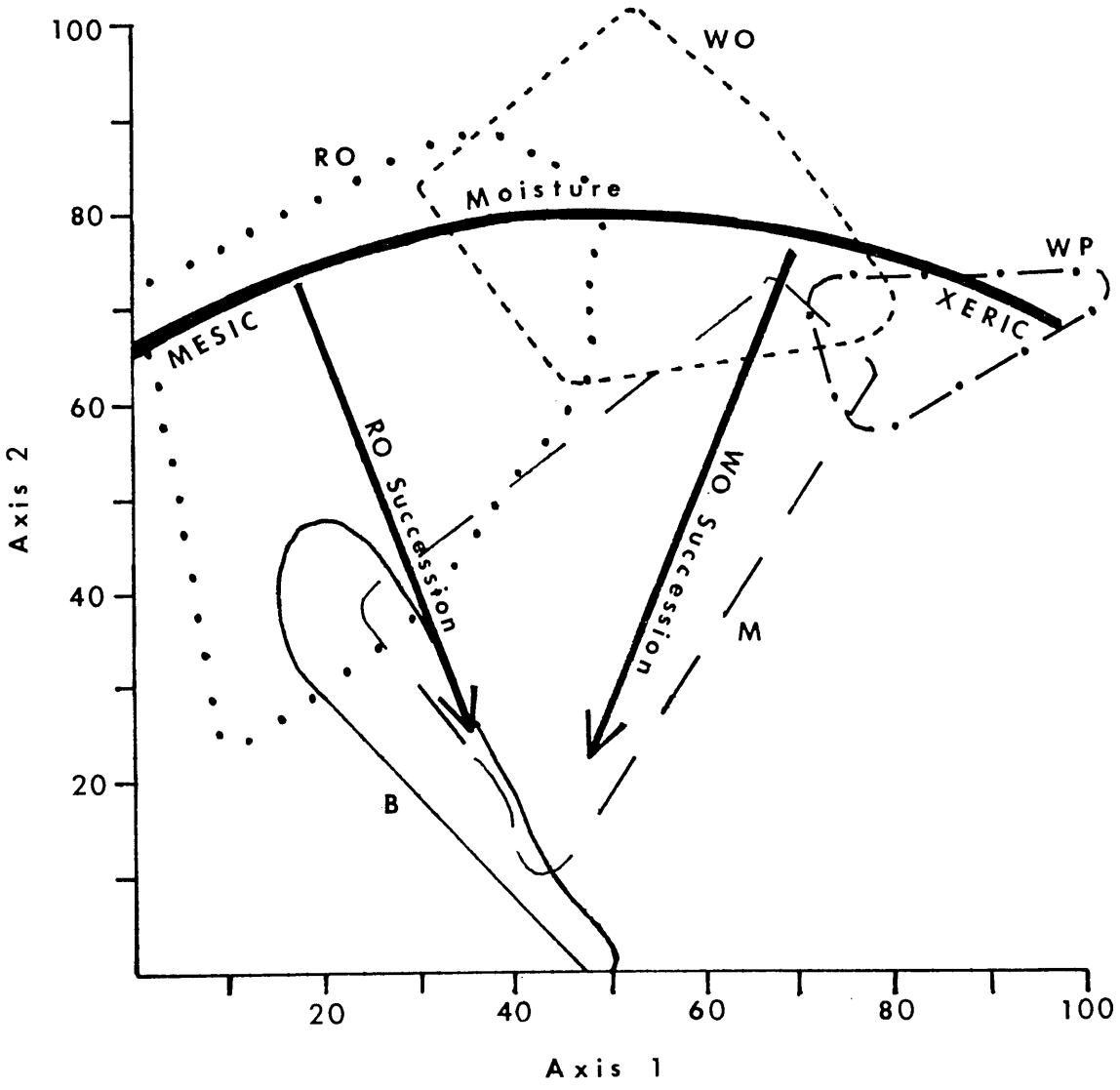

100
80
60
40
20
Axis 2
20
40
60
80
100
Axis 1
WO
RO
Moisture
WP
MESIC
XERIC
RO Succession
WO Succession
M
B

Figure 7. Computer generated coenocline of dominant tree species along the first axis of the reciprocal averaging ordination. The abscissa represents the sample quadrats ranked on the reciprocal averaging axis. The ordinate is the relative basal area of each species in each quadrat. Successional patterns are indicated for the white oak and red oak types

WP = white pine

WO = white oak

RO = red oak

M = maple

B = basswood

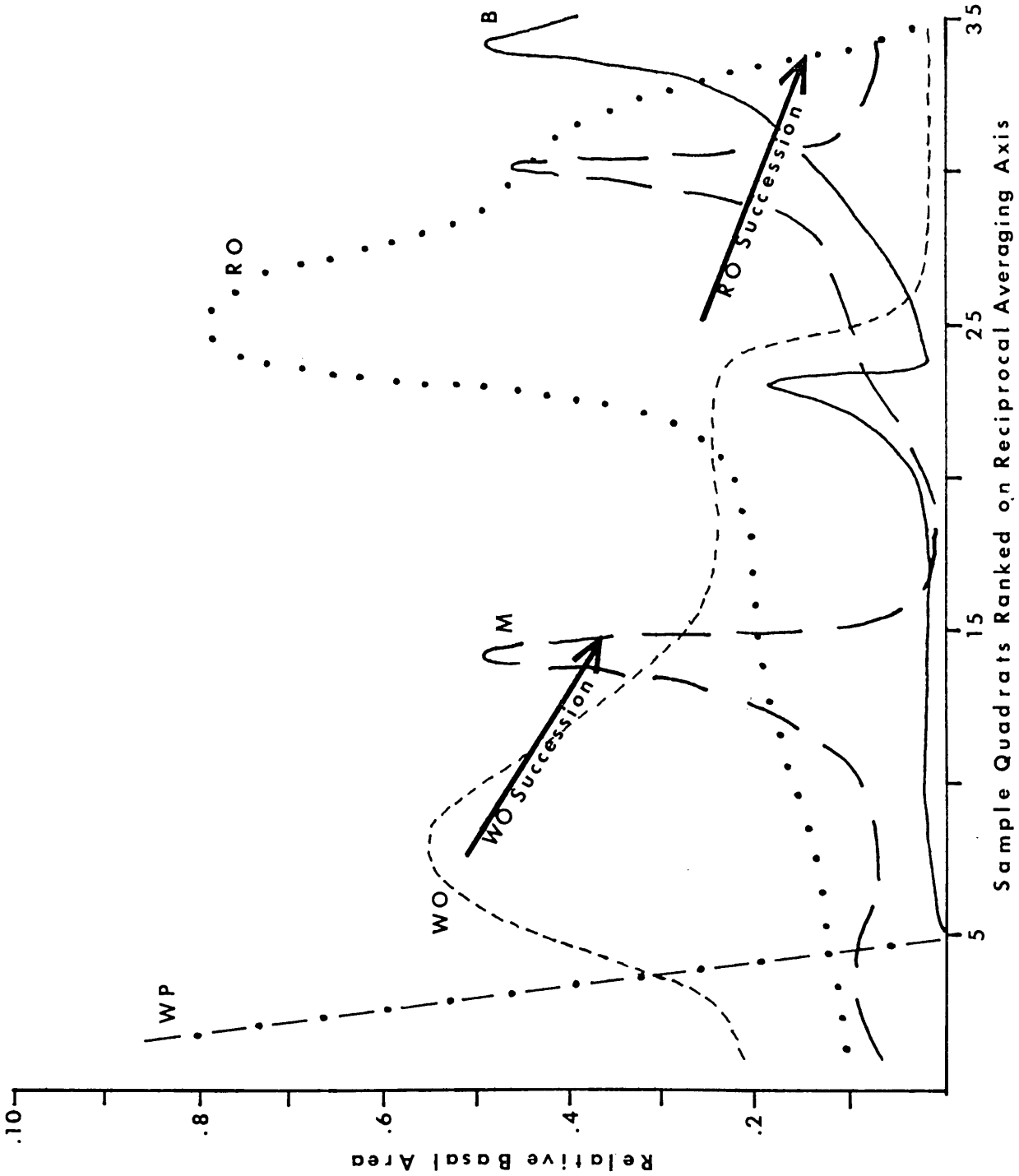
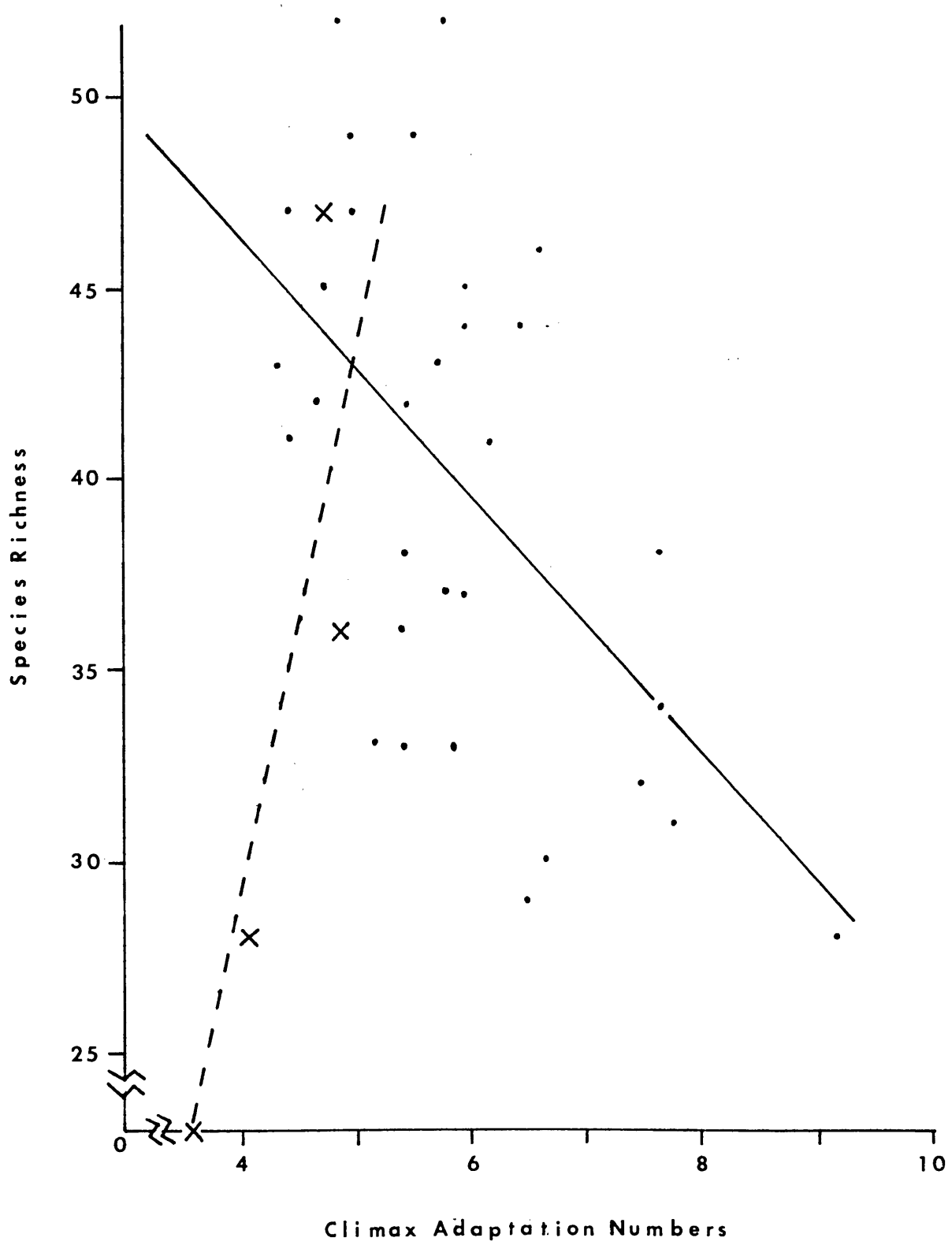

Relative Basal Area
.10
.8
.6
.4
.2
WP
WO
WO Succession
M
RO
B
RO Succession
5
15
25
35
Sample Quadrats Ranked on Reciprocal Averaging Axis

Figure 8. Species richness plotted against climax adaptation numbers. White pine stands are marked with X's. Solid line is least squares fit for deciduous stands. Dashed line is least squares fit for white pine stands


50
45
40
35
30
25
0
4
6
8
10
Species Richness
Climax Adaptation Numbers

DISCUSSION

Dominance types

Prior to the ordination analyses, dominance types were assigned to the sample quadrats by a synthesis of three methods--subjective field evaluation, basal area, and the Orloci (1967) agglomerative dendrogram (Figure 2). The similar results of the three methods justify confidence in the final dominance type classifications. The close agreement between the first two methods is not surprising because the field evaluation was made after the sample measurements were completed; and the raw data, including basal area, were used in the evaluation.

Only the most important tree species were considered in the classifications made by field evaluation and basal area, whereas the agglomerative method groups the stands according to their geometric similarity based on the basal area contributed by all the tree species. This difference in approach means that, with the agglomeration, the grouping of the stands may result from the basal area contributed by the less important species and not solely from the dominance exhibited by one or a few species. Also, the algorithm of the agglomerative method dictates that a stand be assigned to one group or another and not simply described as intermediate. Nevertheless, it is a valuable technique when used in conjunction with other methods and, in this case, proved helpful in placing some problematic stands.

The pattern of vegetation implied by the assignment of dominance types is due mainly to the great potential for dominance possessed by a relatively small number of species (Curtis 1959). The forest varies continuously in

composition from sites where several species are equally distributed and none dominate (e.g., Stands 23 and 31) to sites virtually covered by a single species (e.g., Stand 20), although the dominants rarely grow in pure stands. The data for the five types in Table 4 are averages that give an abstraction of the five forest types that are found in the uplands of northeast Iowa.

When the dominance types are arranged in the order found in Table 4, the basal area distribution in the five average types shows that each of the dominant species is distributed in a manner that approximates the bell-shaped curve of the normal distribution with a peak in its own type. This sequence of dominance types is the same as on the single axis ordinations (Figures 3A, 3B, 3C, and 3D) and supports Gleason's hypothesis (1939) that species are distributed individualistically along gradients according to each species' physiological tolerances. Therefore, the classification of stands by dominance type does not contradict the individualistic distribution of species (Gleason 1939) but is a convenient method to facilitate the manipulation of stands and the interpretation of ordinations (Whittaker 1956).

Only tree species were used for the classification and ordination of samples because they make up the bulk of the biomass and are believed to control the distribution of herbs and shrubs by microclimate modification (Curtis 1959). Herbs and shrubs were found to be distributed in patterns similar to those of the trees in the upland hardwood forests of southern Wisconsin, which forests are of similar composition to those of northeast Iowa (Curtis and McIntosh 1951, Curtis 1959).

Ordinations

As previously stated, the assignment of dominance types facilitates the interpretation of ordinations. The environmental moisture ordination (Figure 3A) is the simplest of the direct ordinations used in this study. It assumes that the moisture available to the plants is a function of aspect and slope position only, and that this is a prime component controlling species distribution. It does not account for other moisture variables such as edaphic factors (Loucks 1962) or for other factors controlling distribution, such as succession. Even with such a simple ordination, a vegetation pattern emerges which agrees with the known silvic characteristics of the species involved; stands dominated by maple, basswood, and red oak occupy the mesic sites, while white oak and white pine stands occupy the drier sites.

A more sophisticated moisture ordination is obtained by using weighted averages (Figure 3C), in which the stands are ordinated by composition of the stands' vegetation (Whittaker 1967). The distribution of dominance types is similar to the environmental moisture ordination (Figure 3A), but there are obvious differences in the range of the dominance types as well as in their mean distribution. The differences are illustrated by the lower rank correlation between the two axes (0.64, $p < 0.01$, Table 5).

In addition to ordinating stands by weighted moisture averages, they were ordinated by averages weighted for successional status. This axis was not done as a single ordination, but as the ordinate for a two dimensional weighted average ordination (Figure 4A). The moisture and successional trends superimposed on this ordination (Figure 4B) are an interpretation of the gradients present. In this ordination, the abscissa accu-

rately represents the moisture gradient, while succession is subdivided into two separate paths for red oak and white oak. Both successional trends converge on the maple-basswood type, showing an increase in mesophytism with succession. The fact that mesophytism increases with succession shows that moisture and succession are not independent; in fact, the rank correlation of the stands on the two axes is very high (Spearman rank correlation = 0.93, $p < 0.01$).

If a line is placed at 45° between the ordinate and the abscissa of this ordination (Figure 4A) and the sample points projected perpendicularly onto the line, the two factors--moisture and succession--can be combined into a single scalar. This new single axis ordination is highly correlated (Spearman rank correlation = 0.94, $p < 0.01$) to the climax adaptation ordination in Figure 3B, demonstrating that climax adaptation, as defined by Curtis (1959), is a function of the interaction of moisture and succession. This is not surprising, but it is difficult to separate quantitatively the effects of moisture and succession on species composition and, therefore, the use of climax adaptation numbers is an acceptable synthesis of the two factors.

The environmental moisture ordination (Figure 3A) is only partly correlated (Table 5) to the weighted average ordinations (Figures 3B and 3C), further illustrating the inadequacy of ascribing vegetation distribution to topographic position only.

The last direct analysis employed a two dimensional Bray-Curtis ordination. The resulting vegetation pattern (Figure 5B) is similar to the weighted average ordination (Figure 4B) even though the methods are different. Both approaches use species composition to ordinate the stands on two

axes, moisture and succession; however, the weighted average ordination uses the silvic characteristics of the component species to ordinate the stands, while the Bray-Curtis method uses the dissimilarity (percentage dissimilarity) between the stands' species composition to ordinate them. The most important feature of this ordination is the curving of the moisture trend (Figure 5B) which causes the successional vectors to change orientation. This ordination does not show white pine type succeeding directly to the white oak type as indicated by the weighted average ordination (Figure 4B) and basal area distributions in Table 4; its fate is unclear.

The Bray-Curtis ordination in Figures 6A and 6B is an indirect ordination because the axes were not chosen to represent known gradients, but to be the main axes of variation in the species composition of the sample stands. The first axis (abscissa, Figures 6A and 6B) corresponded to the moisture axis of the direct analysis and the second axis (ordinate) to succession. The resulting vegetation pattern is, therefore, quite similar to the direct analyses, especially Figure 5B, supporting the contention that moisture and successional status are two important factors controlling species distribution.

Reciprocal averaging, the second indirect analysis, was computed with three axes, but only the first axis is presented (Figure 3D) because the other two did not yield a clear vegetation pattern. A coenocline of the five dominant species generated by the computer on this axis (Figure 7), shows that the distribution of these species is a result of the complex of moisture and successional gradients. The high rank correlation between the reciprocal averaging axis and the climax adaptation axis (0.91, Table 5)

supports this. It is possible that the other two axes do not yield identifiable vegetation patterns because moisture and succession are the most important factors controlling species distribution, and these are accounted for by the first axis.

In summary, the ordinations show that five community types (maple, basswood, red oak, white oak, and white pine) dominate the upland forests of northeast Iowa. These types continuously intergrade with one another along moisture and succession gradients, which may be combined into a single scalar, the climax adaptation numbers (Curtis and McIntosh 1951, Curtis 1959), fully supporting the vegetation continuum hypothesis (Gleason 1939, Curtis and McIntosh 1951, Whittaker 1956, 1967). Moisture and succession are correlated so that an increase in successional status is accompanied by an increase in mesophytism. Both red and white oak communities succeed to the maple-basswood type, while the white pine type succeeds first to the white oak and then to maple-basswood.

Field observations suggest that in more mesic sites white pine would succeed first to red oak and then to maple-basswood or in very mesic sites directly to maple, although there is no direct evidence to support this. However, Curtis and McIntosh (1951) show that, in northern Wisconsin, white pine succeeds directly to maple, bypassing the oak stage which is present in southern Wisconsin. This presumably could be due to climatic differences.

The interaction of moisture and succession appears to have two components--mesophytism is promoted by microclimatic changes induced by succession, and succession is accelerated by greater available moisture. This is supported by the ordinations and by field observations which show the greatest successional advance (maple-basswood forests) on the moist pro-

tected slopes and the youngest successional stages (white pine forests) in the most xeric sites. In these extreme xeric sites, succession may be restricted to the oak stage by a lack of available moisture.

The forest as a regional unit

The intergradation of the five upland forest types in northeast Iowa supports the observed transitional nature of the area (Livingston 1921, Curtis and McIntosh 1951) and creates a problem when one attempts to classify the forest as a regional unit. White pine is restricted to relic communities on the driest sites where it has been preserved by the slow progress of succession. In the absence of disturbance, however, these stands will eventually be replaced by oak forests. Therefore, it does not seem logical to classify the area as a mixed deciduous-coniferous forest, as done by Tolstead (1938) and Shimek (1948). Braun (1950) classifies the region as maple-basswood because it is apparently the "climax" vegetation of the area, although it is restricted in its distribution to the more mesic sites. The present analysis shows that maple-basswood is the forest type toward which the other types progress, but only a small percentage of the forest is actually dominated by this type (Table 3). Red oak and white oak are the most widely distributed forest types in the area (Table 3), and on this basis the upland forests of northeast Iowa should be classified as a mixed oak forest as was done by Shantz and Zon (1924). Despite topographical differences, this agrees well with the mixed oak classification of central Iowa (Aikman and Smelzer 1938).

Diversity

As shown above, climax adaptation numbers represent a synthesis of moisture and succession, and, therefore, they should provide a suitable axis to measure changes in diversity (species richness). Figure 8 shows that, as the stand climax adaptation numbers increase, species richness decreases, except for the white pine stands for which the reverse is true. (There were only four white pine samples so interpretation of diversity is very tenuous.) This trend is due primarily to changes in the herb layer, although the trees show the same tendency as the maple type was poorest in species and the white oak type the richest (Table 4).

Curtis (1959) found the greatest species richness in areas of intermediate position along the moisture gradient and Odum (1971) found the greatest numbers of species in areas of intermediate successional age. The following proposed sequence supports these observations. The white pine stands occupy the most xeric and successionally youngest sites (lowest climax adaptation numbers) and have the fewest species. The number of species increases with replacement by oak communities (increasing the climax adaptation number), and, finally, the number of species decreases as the oak communities are replaced by the maple-basswood type (highest climax adaptation number).

SUMMARY

The upland forest vegetation of the driftless area, northeast Iowa, is shown to be composed of five dominance types--maple, basswood, red oak, white oak, and white pine. The interaction of two gradients, moisture and succession, primarily determine the distribution of the dominance types. The maple and basswood types are found in the most mesic and least disturbed sites. The red and white oak types occupy the successionally young, mesic and drier sites, respectively. White pine stands occupy the driest sites. Moisture and succession are shown to be highly correlated to climax adaptation numbers (Curtis 1959).

Diversity is shown to initially increase with increasing climax adaptation numbers and then to decrease at the highest climax adaptation values.

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APPENDIX A: SPECIES LIST

Nomenclature follows Gleason (1952).

Pteridophyta
- Ophioglossaceae
  - Botrychium virginianum
- Osmundaceae
  - Osmunda claytoniana
- Polypodiaceae
  - Adiantum pedatum
  - Athyrium filex-femina
  - Camptosorus rhizophyllus
  - Cystopteris bulbifera
  - Onoclea sensibilis
  - Pteridium aquilinum

Spermatophyta
- Gymnospermae
  - Cupressaceae
    - Juniperus virginiana
  - Pinaceae
    - Pinus strobus
  - Taxaceae
    - Taxus canadensis
- Angiospermae
  - Monocotyledonae
    - Araceae
      - Arisaema triphyllum
    - Cyperaceae
      - Carex spp.
    - Gramineae
      - Bromus sp.
      - Elymus sp.
      - Festuca obtusa
      - Hystrix patula
      - Panicum spp.
    - Liliaceae
      - Allium tricoccum
      - Polygonatum canaliculatum
      - Smilacina racemosa
      - Smilax herbacea
      - Smilax hispida
      - Trillium gleasoni
      - Uvularia grandiflora
    - Orchidaceae
      - Goodyera pubescens
      - Orchis spectabilis

Dicotyledonae
- Aceraceae
  - Acer negundo
  - Acer saccharum (includes A. nigrum)
- Anacardiaceae
  - Rhus radicans
- Apocynaceae
  - Apocynum sp.
- Araliaceae
  - Aralia nudicaulis
  - Aralia racemosa
  - Panax quinquefolium
- Aristolochiaceae
  - Asarum canadense
- Asclepiadaceae
  - Asclepias syriaca
- Balsaminaceae
  - Impatiens pallida
- Berberidaceae
  - Podophyllum peltatum
- Betulaceae
  - Betula papyrifera
  - Carpinus caroliniana
  - Ostrya virginiana
- Caprifoliaceae
  - Lonicera spp.
  - Sambucus canadensis
  - Triosteum perfoliatum
  - Viburnum acerifolium
  - Viburnum rafinesquianum
- Celastraceae
  - Euonymus atropurpureus
- Compositae
  - Aster cordifolius
  - Aster shortii
  - Eupatorium maculatum
  - Eupatorium rugosum
  - Heliopsis helianthoides
  - Lactuca spp.
  - Polymnia canadensis
  - Prenanthes alba
  - Rudbeckia laciniata
  - Solidago flexicaulis
  - Solidago ulmifolia
- Cornus
  - Cornus alternifolia
  - Cornus spp.
- Cruciferae
  - Arabis laevigata
- Ericaceae
  - Pyrola elliptica

Fabaceae
- Amphicarpa bracteata
- Desmodium glutinosum
- Desmodium nudiflorum

Fagaceae
- Quercus alba
- Quercus borealis

Geraniaceae
- Geranium maculatum

Hamamelidaceae
- Hamamelis virginiana

Hydrophyllaceae
- Hydrophyllum appendiculatum
- Hydrophyllum virginianum

Juglandaceae
- Carya cordiformis
- Carya ovata
- Juglans nigra

Menispermaceae
- Menispermum canadense

Oleaceae
- Fraxinus americana

Onagraceae
- Circaea canadensis

Oxalidaceae
- Oxalis stricta

Papaveraceae
- Sanguinaria canadensis

Polemoniaceae
- Polemonium reptans

Ranunculaceae
- Actea alba
- Actea rubra
- Anemonella thalictroides
- Aquilegia canadensis
- Hepatica acutiloba
- Ranunculus spp.
- Thalictrum dioicum

Rosaceae
- Agrimonia sp.
- Crataegus sp.
- Fragaria vesca
- Geum canadense
- Potentilla simplex
- Prunus serotina
- Prunus virginiana
- Rubus spp.

Rubiaceae
- Galium aparine
- Galium triflorum

Rutaceae
- Xanthoxylem americanum

Salicaceae
- Populus grandidentata
- Populus tremuloides

Saxifragaceae
- Mitella diphylla
- Ribes spp.

Staphyleaceae
- Staphylea trifolia

Tiliaceae
- Tilia americana

Ulmaceae
- Celtis occidentalis
- Ulmus rubra

Umbelliferae
- Cryptotaenia canadensis
- Osmorhiza claytoni
- Osmorhiza longistylis
- Sanicula spp.

Urticaceae
- Laportia canadensis

Violaceae
- Viola spp.

Vitaceae
- Parthenocissus quinquefolia
- Parthenocissus vitacea
- Vitis aestivalis
- Vitis riparia

APPENDIX B: SCIENTIFIC AND COMMON NAMES OF TREES

Scientific name	Common name
Acer sacharrum	Maple
Carpinus caroliniana	Blue beech
Carya cordiformis	Yellowbud hickory
Carya ovata	Shagbark hickory
Celtis occidentalis	Hackberry
Fraxinus americana	White ash
Hamamelis virginiana	Witch hazel
Juglans nigra	Black walnut
Juniperus virginiana	Eastern red cedar
Ostrya virginiana	Ironwood
Pinus strobus	White pine
Populus grandidentata	Bigtooth aspen
Populus tremuloides	Quaking aspen
Prunus serotina	Black cherry
Prunus virginiana	Choke cherry
Quercus alba	White oak
Quercus borealis	Red oak
Tilia americana	Basswood
Ulmus rubra	Red elm

APPENDIX C: TREE BASAL AREA

	Stand 1	Stand 2	Stand 3	Stand 4	Stand 5	Stand 6	Stand 7
Acer saccharum	2544[a]	3096	2188	1829	4141	5397	4260
Carpinus caroliniana	176						
Carya cordiformis	227	9870		90		20	
Carya ovata		161	543	95	176		452
Celtis occidentalis							
Fraxinus americana	20						254
Hamamelis virginiana							
Juglans nigra	78	1942				102	
Juniperus virginiana							
Ostrya virginiana	938	874	875	1810	2013	380	134
Pinus strobus						10526	
Populus grandidentata	459				1256	2641	1412
Prunus serotina	379						
Prunus virginiana							
Quercus alba	13551	2221	2701	18614	1024	14860	3830
Quercus borealis	3120	1423	14843	6378	33669	7425	22624
Tilia americana		15721	7954			1735	38
Ulmus rubra						28	

[a] cm^2/0.1 ha.

Stand 8	Stand 9	Stand 10	Stand 11	Stand 12	Stand 13	Stand 14	Stand 15	Stand 16	Stand 17	Stand 18
2035	4931	4393	3578	5309	19479	2138	18337	6256	2187	2871
	148		20	172			70			
50	706			154				706		
	133	173						2742		334
			1480							
114			128	615		1017		1362		
										750
			2557	1734				78		
			305							
188	1630	233	368	546	1418	715	690	108	2006	1249
34979	19922	21476								
		1143								
9555	6457	12455	13342			1671	9331	15832	8564	11495
3935	7774	4055	6747	6033		16540	50	3354	9347	10583
	1805		227	21431	8438	13579	20	1668	120	2808
			4744	5126	897	3879	2260			

	Stand 19	Stand 20	Stand 21	Stand 22	Stand 23	Stand 24	Stand 25
Acer saccharum	10839	7286	6556	4313	8067	2016	958
Carpinus caroliniana							
Carya cordiformis	1039			60	1037		70
Carya ovata	1954	113	958		201	1647	176
Celtis occidentalis							
Fraxinus americana	1505		803	1956		615	1273
Hamamelis virginiana							
Juglans nigra				3630			
Juniperus virginiana							
Ostrya virginiana	156	88	228		1484	386	657
Pinus strobus							
Populus grandidentata			9320				5013
Prunus serotina	20						
Prunus virginiana	267						
Quercus alba	12652		10842	6322		12648	12814
Quercus borealis	4456	25218	76	24327	8725	10886	18007
Tilia americana	28			2976	7102	7944	1209
Ulmus rubra	64			919	346	1428	

Stand 26	Stand 27	Stand 28	Stand 29	Stand 30	Stand 31	Stand 32	Stand 33	Stand 34	Stand 35
4596	969	7157	50	660	142	322	6303	7476	1046
		416						222	310
				38				133	
766	346			2974	3484	11377	2375		
					20				
	246		711	120	7315	96	279	314	523
38	280	1015	20	20		282	814	687	833
			773		1385	353			
			38				217		
2042	23087	10094	16399	18234	9017	7710	20920	2512	201
36492	8939	10410	11823	10975	8585	4071	9415	20185	23608
1070	161	445	553	1143	70		1483	3098	1708
	810		2510	308	665	500		530	78