An ecological analysis of central Iowa forests:
An ordination and classification approach

by

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A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
MASTER OF SCIENCE

Department: Botany
Major: Botany (Ecology)

Approved:

Signatures have been redacted for privacy

Iowa State University
Ames, Iowa

1982

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INTRODUCTION

Original land office survey records of the mid-nineteenth century show that, prior to settlement, the native deciduous forests of Iowa occupied 2.7 million hectares, or 16% of the total land area (Dick-Peddie, 1955). These occurred along the major streams, rivers, and drainage systems in the state. In central Iowa, these forests were along the Des Moines and Raccoon Rivers. Today, only .65 million hectares, less than 4% of Iowa's native woodlands, remain (Thomson and Hertel, 1981).

This encroachment on natural vegetation is a result of increased urbanization, croplands, and grazing areas for livestock. Use of trees for rail fences, building, railroad ties, and fuel has also contributed to the diminishment. The preservation of forests is a growing concern. The vegetation is important for preservation of biological diversity, wildlife habitats, erosion control, production of valuable timber, recreation, and aesthetics. Increased knowledge of forest composition and structure is a prerequisite to conservation and management planning.

The purpose of this study is twofold: 1) to obtain information on the species composition of temperate deciduous forests in central Iowa with regard to patterns and factors affecting the distribution of these species, and 2) to compare and contrast ordination and classification techniques used to analyze the data collected.

More specifically, the objectives of this study are:

1) to determine species composition of forested slopes in central Iowa to include sites on and off the Des Moines lobe of the

Wisconsin glacier;

2) to sample slopes of varying inclination, aspect, and position;

3) to ordinate samples and species data by direct and indirect gradient methods;

4) to classify the patterns of species composition within stands using Dominance type and Orloci agglomerative classification techniques;

5) to compare the ordination methods of Weighted Averages, Principal Components Analysis, Polar Ordination, and Reciprocal Averaging to determine which methods effectively describe the vegetation of Iowa's forested slopes;

6) to compare the ordination and classification results and to suggest possible environmental and phytosociological factors relating to these results.

LITERATURE REVIEW

Iowa Studies

The vegetation of central Iowa as described by survey crews and early settlers in the 1830s to the late 1860s consisted of tall-grass prairie with forests primarily restricted to the slopes of the major streams which flow diagonally in a southeastward direction (Hewes, 1950). Though qualitative in nature, these accounts did provide a list of tree species native to forest areas. Estimations of densities were calculated later using distance to witness trees from original survey notes (Dick-Peddie, 1955).

The plant geography and vegetation of Iowa have since been described by Shimek (1948) and Conrad (1952). Transeau (1905, 1935) included Iowa within the prairie peninsula and the western extent of the climax stage of the deciduous forest center. Based on tree dominance, Braun (1947, 1950) considered central Iowa to be in a transitional zone where at least two major climax associations merged: the mesophytic maple-basswood forest from the northeast and the oak-hickory forest extending north from Missouri. Kuchler (1964) mapped central Iowa as oak-hickory forests along the streams and mixed tall-grass prairie and oak-hickory forest areas upland from streams.

Up to the 1900s, accounts continued to be descriptive, particularly addressing the topic of the limited distribution of forests in the state. MacBride (1895, 1919) suggested that soil formation during geologic time and subsequent fires resulted in the restriction of forests. Shimek

(1899) also regarded fire as an important factor. He suggested that drift areas in the state were best adapted to graminous vegetation, while the loess areas which had less fuel for fires were more suited to forest vegetation.

More studies into the 1900s were considering the environmental conditions present in forest communities. Pammel (1907) compared the vegetation of two other states with northeastern and central Iowa by looking at factors such as topography, geology, soil properties, and plant formation. Trenk (1925) was able to interpret the distribution of hickory trees within the state using soil information. A transect study of the forest community in central Iowa dealt with the structure of trees and shrubs in relation to the environmental conditions under which species grow (Aikman and Smelzer, 1938). Results showed that the oak-hickory communities generally had a greater number of dominant species and represented a greater portion of upland forest cover in central Iowa. Their canopy, however, was more open than that of the maple-basswood communities which represented the highest development in central Iowa and were found on the mesic, north-facing slopes. Aikman and Smelzer (1938) observed that *Acer nigrum* exceeded the westward extend of *Acer saccharum*, replacing it in central Iowa.

An investigation of the distribution and structure of forests along the Des Moines and Missouri Rivers at equal latitudes was undertaken by Aikman and Gilly (1948). By comparison of edaphic and climatic factors with forest flora, three woody plant communities were recognized along the lower Des Moines. From mesic to xeric they were the maple-linden community, the oak-hickory community, and the shrub community. Aikman (1941), upon studying the effect of slope aspect on climatic factors, concluded that north slopes in Iowa represented the most mesic conditions with east, south, and west slopes increasingly xeric.

More detailed studies have continued since the mid-1900s, facilitated by improved soil and field equipment and the use of statistics and computer analysis. Kucera (1950, 1952) studied the microhabitats of hardwood communities in central Iowa and noted variation in physical and chemical properties of the soil profiles. The per acre yield of the forest floor varied greatly from open wood stands to closed stands. Total nitrogen and organic carbon values were highest in the surface soil profiles. In an analysis of the canopy layer, *Quercus alba* and *Q. borealis* dominated upland xeric areas, whereas in mesic situations, *Tilia americana* and *A. nigrum* were mixed with *Q. borealis*. Sanders (1967) took a closer look at the herbaceous layer in central Iowa forests and found that these species follow certain trends in relation to a continuum-index, as did canopy species. Correlation coefficients were determined for each species-pair and species constellations were produced. A subsequent study (Sanders, 1969) used the ordination techniques of Curtis and McIntosh (1951) and Orloci (1967) on fourteen stands of forest vegetation. The former continuum approach was more favorable as a comparison of selected environmental factors. It was concluded that Iowa slope forests vary in a continuous manner rather than forming discrete vegetational units. Cover values and importance values of tree species showed the same general trends. *Q. alba*, *Carya ovata*, and *Q. borealis* were important tree species on xeric sites, with *Ostrya virginiana* in the understory. Species with high importance values in more mesic sites were *A. nigrum*, *T. americana*, *Q. borealis*, and *Fraxinus nigra*. Regression analysis and an analysis of variance approach were helpful in determining the relationship of soil factors, temperature, moisture, light intensities, and distributional patterns of species on various sites.

Methods of ordination and classification were used to investigate the individualistic behavior of species across an environmental gradient in central and northeast Iowa (Niemann, 1977; Cahayla-Wynne and Glenn-Lewin, 1978). Niemann (1977) denoted at least four community types across an environmental gradient in Woodman Hollow State Preserve: the prairie opening, stream bottom north-facing slope, and the combined uplands and south-facing slopes. The north-facing slopes had mainly *T. americana* and *A. nigrum*. In addition to *O. virginiana*, *Carpinus caroliniana* was dominate in the understory. Near the slope break on south exposures, *Q. alba* and *Q. borealis* became dominant. According to Niemann (1977), diversity index values suggested a successional series from stream bottom to maple-basswood slopes without implying an actual sequence. The bryophyte and pteridophyte flora of this preserve was studied by Peck (1980).

Classification and Ordination

The use of both classification and ordination techniques for vegetation analysis in Iowa has become more common in recent years (Niemann, 1977; Niemann and Landers, 1974; Cahayla-Wynne and Glenn-Lewin, 1978).

The choice of techniques, however, has varied depending largely on the vegetation type, the data set, and the ecologist.

The origin of scientific classification dates back to early European plant geographers. Humbolt presented the concept of growth-forms as major types distinguishing plant communities; Grishbach introduced introduced the concept of the formation (cited in Whittaker, 1973). In the United States, however, the use of classification of vegetation developed mainly from the work of Clements (1916). Clements believed that all succession of a particular region led eventually to one climatically controlled final stage he called the climax association. Subsequent classifications have been based on visual observations of habitats, detailed quadrat analysis, chi-square values, and more complex methods using multivariate analysis (Sanders, 1969; Orloci, 1967). The ecological groups and character species groups used in classification often are decided by similarity relationships and field observations, and are thus subjectively delineated.

Ordination techniques have a number of origins from Russian, Polish, German, and American literature (Whittaker, 1973). Development within the United States came heavily from the opposition of Gleason (1926, 1939) to the community-unit theory of Clements. Gleason proposed that species are individually distributed along continuous gradients by the individual properties of each species and by environmental characteristics. This individualistic concept of vegetation has been supported through research in gradient analysis and other ordination techniques by Whittaker (1967) and the Wisconsin school (Curtis and McIntosh, 1951;

Curtis, 1959).

Literature concerning the principles and use of ordination methods is abundant. Several suggested references are Whittaker (1973), Noy-Mier and Whittaker (1977), Orloci (1975), Gauch (1977), and Maarel (1979). Orloci (1975) suggests five uses of ordination methods: summarization of data sets, trend seeking and prediction, multidimensional scaling, reciprocal ordering of species and stands, and classification of major groups. He also suggests that regression analysis can help to reveal correlations with environmental variables by ordering vegetation stands according to certain environmental criteria.

Another use of ordination study has been to provide evidence for the continuum concept of vegetation structure supported by Gleason (1926, 1939). The results of most ordination studies are presented as point plots in which the position of stands are shown on an axis system. In this way, the continuity of vegetation data can be demonstrated (Dale, 1975). Whittaker (1967) demonstrated this by arranging stands in order from xeric to mesic to hydric, plotting importance values for species along this axis.

For the purpose of this study, four ordination techniques were chosen: Weighted Averages (WA), Principal Components Analysis (PCA), Polar Ordination (PO), and Reciprocal Averaging (RA). These and the classification types used to describe the forest vegetation of central Iowa are described in more detail in the Methods section of this paper. Reviews of the ordination techniques have been addressed by Whittaker and Gauch (1978), Noy-Mier and Whittaker (1977), Orloci (1978a, 1978b), Dale

(1975), and Gauch, Whittaker, and Wentworth (1977).

Gauch et al. (1977) compared the results of RA, PCA, and PO using simulated and actual field data. Results were evaluated for these techniques in response to sample error, outliers, and beta diversity. PO and RA gave good ordination results with beta diversities up to five or more half changes. Beta diversity or between stand diversity is the degree of change in species composition of communities along a gradient. It is commonly measured as the number of half change units, which represent a 50% change in percentage similarity (Pielou, 1974, 1977; Whittaker, 1970). Nonstandardized PCA was the most vulnerable to beta diversity. Standardized PCA displaced samples more strongly than RA. At low beta diversities, PO was the most successful.

Varying levels of sample error resulted in very deteriorated PCA ordinations. RA had the least distortion and PO was just slightly greater. When the sampling design included clumps or duplication of samples, PO and RA results were affected only slightly or not at all. PCA, however, showed great sensitivity. In general, clusters tended to attract the axes of eigenanalysis ordinations, thus appearing as endpoints in RA and PCA.

Stands or samples that have unusual floristic composition as compared with all other stands or samples are called outliers. Gauch et al. (1977) reported that such stands were chosen as endpoints in PO or ordinated near the midpoint of the ordination axis without affecting the position of the other samples. PCA and RA results varied according to the properties of the outlier. For a species that was strongly dominant, i.e., where half of the remaining species have random but modest importance and the other half have negligible importance, the outlier ordinating around the periphery of the ordination field strongly affected the position of other samples. PCA ordinated this outlier centrally to other samples, with little effect to other samples.

Particular problems with PCA have been addressed. Dale (1975) discussed the difficulty in delineating the number of axes or eigenvalues and vectors required for adequate description of the data. Unless a statistical test of significance is performed, the most common choice is to select the first three dimensions that can be graphically displayed. In choosing centered-PCA or noncentered-PCA, Feoli (1977) has suggested that the former is more appropriate in ordinations of plant communities while the latter is more appropriate in cluster seeking.

No single ordination method solves all problems of describing and explaining patterns in natural vegetation. Gauch (1977) recommends that the first analysis of data be RA since this gives the most objective and accurate overall picture of trends in the sample set. Where cost permits, the use of all four ordinations is recommended (Gauch, Whittaker, and Wentworth, 1977; Gauch, 1977). In this way, RA and PCA can be compared with PO, direct ordination, and classification results.

METHODS

Central Iowa has a continental climate expressed by hot, humid summers and long, cold, rather dry winters (Waite, 1967; Peck, 1980). This results from moist, southerly prevailing winds from the Gulf of Mexico during the six warm months of the year and the flow of dry northeast Canadian air during the winter months. Data from official weather stations at Fort Dodge (Webster County), Guthrie Center (Guthrie County), Ames (Story County), Boone (Boone County), Des Moines (Polk County), and Indianola (Warren County) indicate a mean annual precipitation of 76-81 cm (Baldwin, 1973; Collins, 1974). At least 70% of this occurs as rainfall during the months of April through September when thunderstorms are most severe. Seasonal snowfall averages 76-102 cm/year, accounting for 10% of the total precipitation in Guthrie County, 13% in Webster County, and as much as 20% in other sections of central Iowa (Bryant and Worster, 1978; Koppen, 1975; Russel, Dideriksin, and Fisher, 1974).

Normal daily maximum temperatures reach 27-32^{o}C in July, with an average of 23 days/year of 32^{o}C or higher temperatures in Webster County and up to 39 days/year of such weather reported in Warren County. Normal minimum July temperatures are at 58^{o}C. In January, normal daily maximum temperatures range from 7 to -1^{o}C north of Des Moines to -1 to 4^{o}C south of the city. Normal daily minimums are -18 to -12^{o}C and -12 to -7^{o}C, respectively. The average growing season ranges from 152 days in Webster County, to 155 days in Story County, to 166 days in Warren County (Bryant and Worster, 1978; Koppen, 1975).

The state of Iowa was subjected to three major glaciers during the Pleistocene: the Nebraskan, Kansan, and Wisconsin glaciation. The earlier episodes, the Nebraskan and Kansan, covered the entire state. Figure 1 outlines the furthest extent of the Wisconsin glacier. This, called the Des Moines drift lobe, extended 217 kilometers from the Minnesota state line, southward to the city of Des Moines.

Covering 22% of the state (31,857 sq. kilometers) the lobe is positioned just west of the longitudinal center line of the state. The Des Moines River flows southward close to the axis (Ruhe, 1969). There are four major end moraines located on the Des Moines lobe. From north to south, they are the Algona, Humboldt, Altamont, and Bemis. Upon its retreat, the Wisconsin age left two major deposits: loess, or wind-deposited sediment, covering 66% of the state, and glacial drift on the lobe.

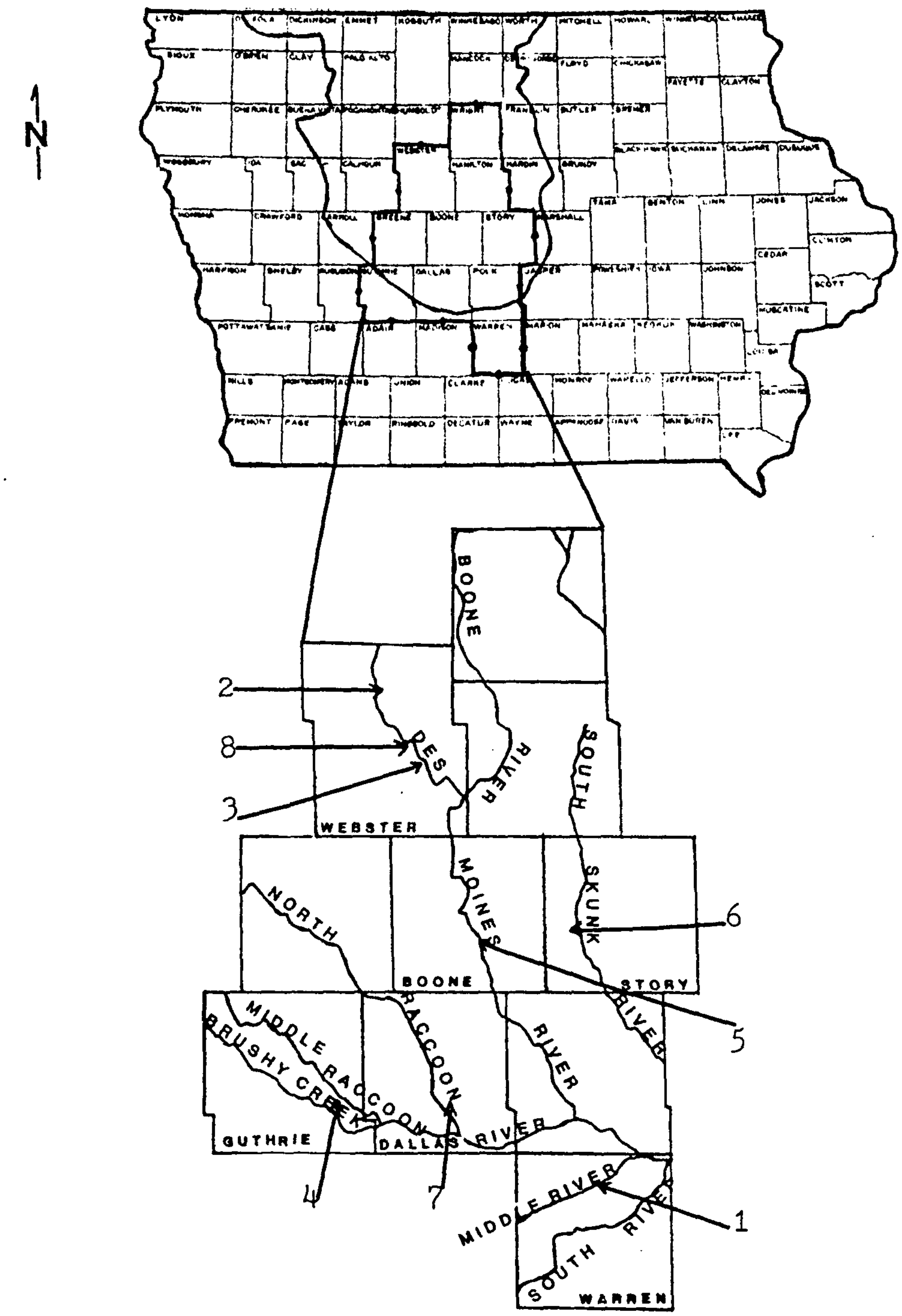
Shimek (1948, p. 20) provided a description of the area:

> The Wisconsin Drift Plain . . . occupies the northern and central part of the state, and it is the highest and most level part of Iowa. Its surface is varied chiefly by the narrow and deep valleys of the Des Moines River and its tributaries, which drain it. . . . The valley of the Des Moines River within this area is a narrow canyon, whose lower half reaches a depth of a hundred feet or more, and which has been carved out of the general level plain by erosion. Its sides are steep bluffs, often cut by short lateral ravines, and with occasional rock-exposures forming ledges and cliffs. This valley is largely wooded, both on the narrow alluvial flats and on its rugged sides, and in the rougher parts, as below Fort Dodge and Boone, it provides for the inland "islands" which contain a number of plants belonging to the forest and rock-ledge flora of northeastern Iowa. . . .
>
> The border of the Wisconsin drift area is occupied by moranicic ridges, which are mostly rather low in the

Figure 1. Central Iowa forest area

1. Berry Woods
2. The Diggings
3. Dolliver State Park
4. Guthrie County Woods
5. Ledges State Park
6. Pammel Woods
7. Silver-Smith Woods
8. Woodman Hollow State Preserve

—— border of Des Moines lobe


N
BOONE
DES
RIVER
SOUTH
WEBSTER
NORTH
MOINES
SKUNK
BOONE
STORY
MIDDLE
RACCOON
BRUSHY CREEK
RIVER
GUTHRIE
DALLAS RIVER
MIDDLE RIVER
SOUTH RIVER
WARREN
1
2
3
4
5
6
7
8

> southern part, but northward the moraine on both sides becomes more rugged.

Eight study sites (Figure 1) were selected within central Iowa for collection of forest vegetation data. These consisted of state parks and preserves and privately-owned areas where the natural vegetation has been protected and where the following criteria were met: 1) location on or just off the Des Moines lobe, within a 60-mile vicinity of Ames, Iowa; and 2) protection from human disturbance.

Study Sites

Berry Woods - Berry Woods is a 16.8 hectare (42 acre) mixed hardwood forest in Warren County, Iowa. A preserve of The Nature Conservancy, it is situated south of the Middle River just off the Cary drift of the Des Moines lobe at a latitude of 41°25' and a longitude of 93°35'. Legally the property is designated as Warren County: Township, T76N, R42W, S.W. section 2.

The land was a gift of the late newspaper publisher, Don L. Berry, and his wife, Bertha, who were charter members of the Conservancy. The property was preserved in memory of Captain B. C. Berry and William H. Berry and was deeded on September 13, 1961 (DeLisle, 1966). The Berry family protected the area for several years before its donation, using only some of the downed lumber for firewood. Since 1961, the area has been used for scientific study and teaching. Being completely fenced, it is bordered on the west by a dirt road (NW 13th St.), on the south and east by agricultural fields, and on the north by a cut-over woodland rapidly being converted to crop planting (Figure 2).

Berry Woods is in the Ladoga-Gara-Armstrong soil association, which consists of nearly level to strongly sloping soils on loess-covered ridgetops and side slopes with strongly sloping to very steep soils formed in glacial till (Bryant and Worster, 1978). There were five sample plots located in this site representing the Clinton, Color, and Gosport soil series (Appendix B). The plots are labeled 1 through 5 in Figure 2.

The Diggings - The Diggings is a 2.8 hectare (7 acre) upland forest situated in Webster County just north of Fort Dodge, Iowa, latitude 42°32', longitude 94°10'30" (Figure 3). A gift of Susan H. Atwell to The Nature Conservancy, this area exhibits 30 to 40 years of natural healing from an area that had previously been hand-dug for coal earlier in this century. It is an oak-maple-basswood forest on the Des Moines River, with north and west facing slopes in the S.W. ¼ sect. 8, S.E. ¼ sect. 7, T89N, R28W of the Cooper Township, Webster County.

The Diggings is in the Storden-Hayden-Wadena soil association, which is located mainly along the Des Moines River. It consists predominantly of nearly level to very steep, well-drained, loamy soils on bottom lands, benches, and valley sides (Koppen, 1975). There was one sample plot (labeled 6, Figure 3) located in this site; it was in the Hayden-Storden soil series (Appendix B).

Dolliver Memorial State Park - Dolliver Memorial is located in Webster County, roughly 4.8 kilometers (3 miles) northwest of Lehigh, Iowa. Dedicated on June 28, 1925, this park is a memorial to Senator

Figure 2. Berry Woods: Modified from United States Geological Survey Map, Scotch Ridge, Iowa, 1972

Sample No.	Aspect	Elevation ft/m
1	Level	910/277
2	S @ 200°	855/260
3	E @ 80°	830/253
4	NE @ 30°	855/260
5	Level	875/267

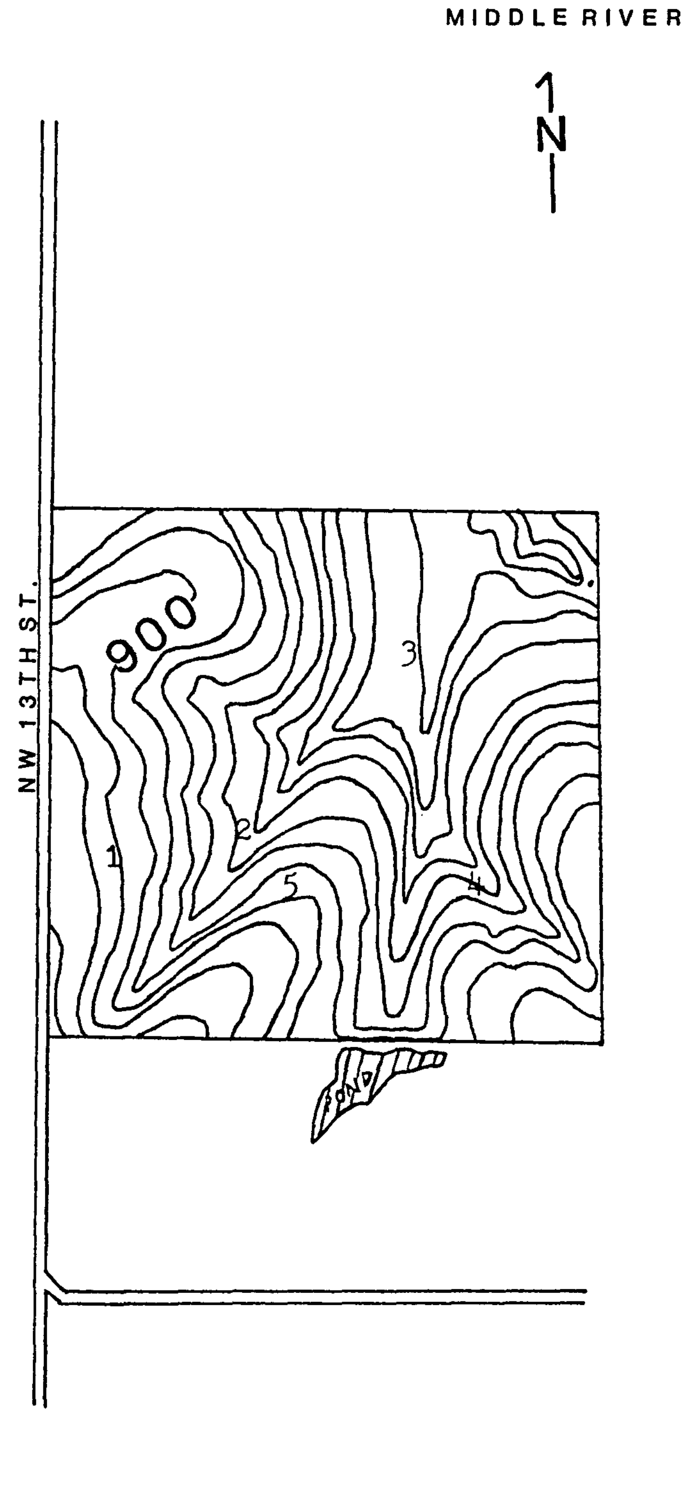
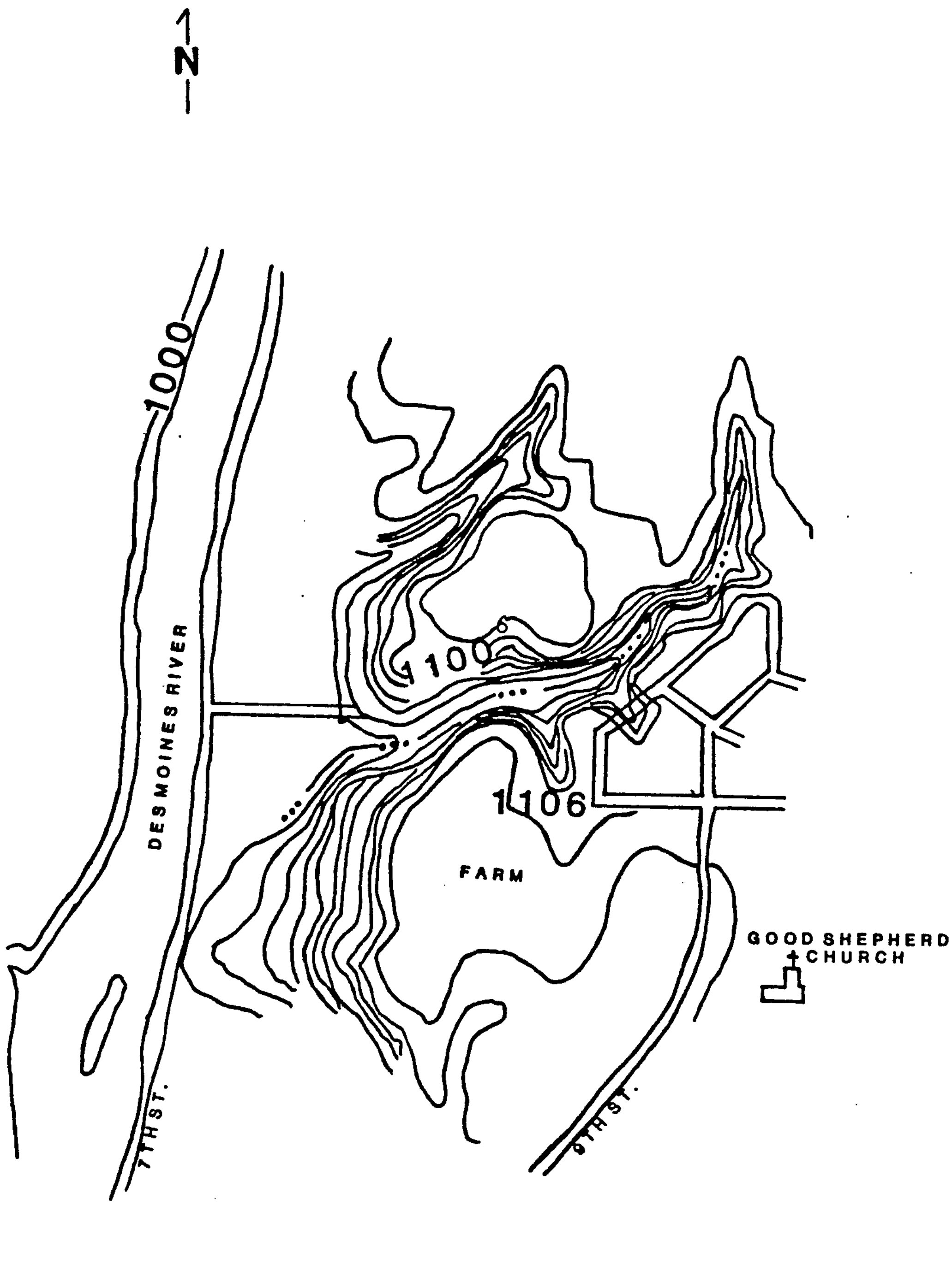

MIDDLE RIVER
N
NW 13TH ST.
900
1
2
3
4
5
POND

Figure 3. The Diggings and vicinity: Modified from United States Geological Survey Map, SW/4 Fort Dodge 15' Quadrangle, Fort Dodge North, Iowa, 1979

Sample No.	Aspect	Elevation ft/m
6	N @ 355°	1080/329


N
1000
DES MOINES RIVER
1100
1106
FARM
GOOD SHEPHERD
CHURCH
7TH ST.
8TH ST.

Jonathan P. Dolliver, who was raised in the area and was highly respected for his conservation practices (Blasky, 1974). The park consists of 240 hectares (600 acres) of hilly and woody areas bordering nearly a kilometer of the west side of the Des Moines River. A small stream flows through the park and many sandstone outcrops exist. A striking feature is the bedding or overlaying sandstone (Gwynne, 1951b). Horizontal layering, as well as slant-wise or cross-bedding layers, are present as a result of the variable currents of the ancient Des Moines River deposits of sand. The stone is over-laid by glacial drift. A unique geological formation known as copperas beds is also found in the park (Blasky, 1974). Vegetated slopes stand as high as 320 m, wandering down to the Des Moines River.

There were three sample plots located in this park, representing the Hayden-Storden, Boone, and Terrill soil series (Figure 4). The soil association is Storden-Hayden-Wadena. The property is located at a latitude of $42^{\circ}23'$ and at a longitude of $94^{\circ}05'$. Dolliver Memorial is in the Otho Township of Webster County, T88N, R28W, S.E. ¼ sect. 34, W. ½ sect. 35, N. ½ sect. 2, N.E. ¼ sect. 3.

Guthrie County Woods - The areas sampled in Guthrie County were located on the east side of the Middle Raccoon River. They represent native forest vegetation located on the terminal glacial moraine, the Bemis, of the Des Moines lobe of the Wisconsin glacier (Ruhe, 1969).

An 83.2 hectare (208 acre) piece of property situated at the corners of sections 9, 10, 15, and 16 of the Jackson Township (T79N, R30W), it had been previously owned by L. Vaux (Rockford Map Publishers, 1971).

Figure 4. Dolliver Memorial State Park: Modified from United States Geological Survey Map, Evanston, Iowa, 1965b

Sample No.	Aspect	Elevation ft/m
7	S @ 200^o	1030/314
8	NW @ 300^o	1025/312
9	SE @ 136^o	1000/305


N
1090
MOINES
RIVER
1100

A 16 hectare (40 acre) piece of land, located in the southeast corner of section 15 bordering road F51, had been owned by A. C. Godwin and Harry and Pauline George. Since the time of the last survey, these areas have been acquired by Central Iowa Power Cooperative.

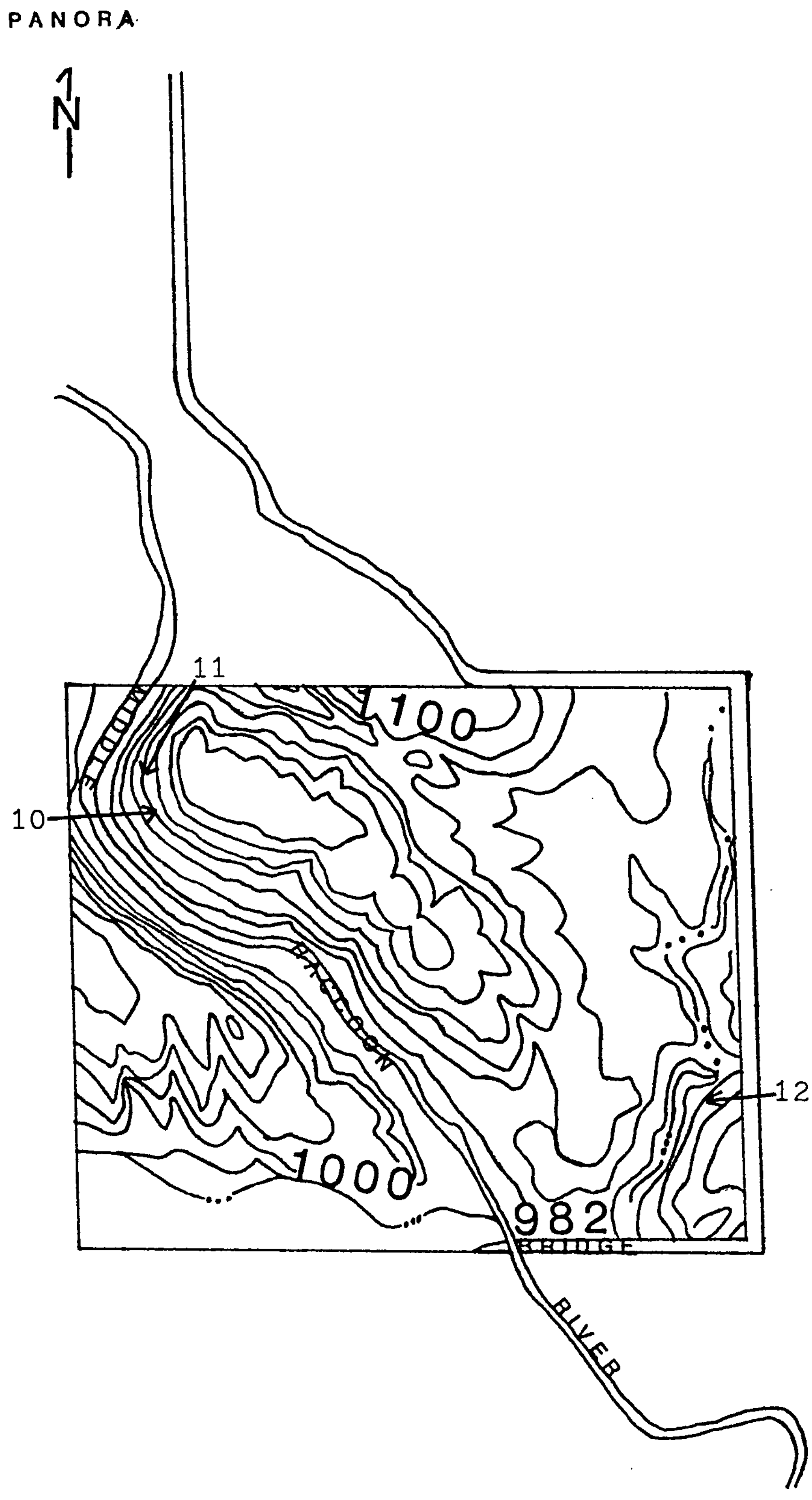
There were three sample plots located in this area on north- and west-facing slopes. These can be located in Figure 5 as samples 10, 11, and 12. The general territory can be located at a latitude of $41^{o}39'$ and a longitude of $94^{o}29'$. The soil association is Gara-Lindley with strongly sloping to very steep, loamy, moderately well-drained soils on an upland glacier (Russel, Dideriksin, and Fisher, 1974).

Ledges State Park - This park represents an area over 518 hectares (1,295 acres) on the east side of the Des Moines River, about 4.8 km (3 miles) south of Boone, Iowa. The name was derived from the buttresses of "Ledges" sandstone which are most evident near the mouth of Peese Creek, a tributary of the Des Moines, entering from the east (Henning, 1919; Diehl, 1919). In some places, the ledges are 23 m (75 ft) high; the sandstone rock consists of rather coarse sand with considerable amounts of lime.

The park itself was formed by erosion around the time of the formation of the coal beds of Iowa. The transgressions of shallow seas over the land deposited sediment, later hardening to limestone and shale (Gwynne, 1951a). Subsequent recession of these waters left swamps in lower depressed areas, in which peat could accumulate. A series of such transgressions and recessions through the ages allowed for the conversion of peat to coal. During the time when the land was raised, a river

Figure 5. Guthrie County Woods: Modified from United States Geological Survey Map, Panora, Iowa, 1952

Sample No.	Aspect	Elevation ft/m
10	W @ 295°	1130/344
11	W @ 290°	1130/344
12	N @ 355°	970/296


PANORA
N
11
10
1100
MIDDLE
RACCOON
12
1000
982
BRIDGE
RIVER

flowing from the north cut a valley through the sediment. As the land lowered, the channel of the stream became choked with sand. Cross-bedding indicates today that the deposits were continuous, much the same as the formations in Dolliver Memorial State Park (Gwynne, 1951a).

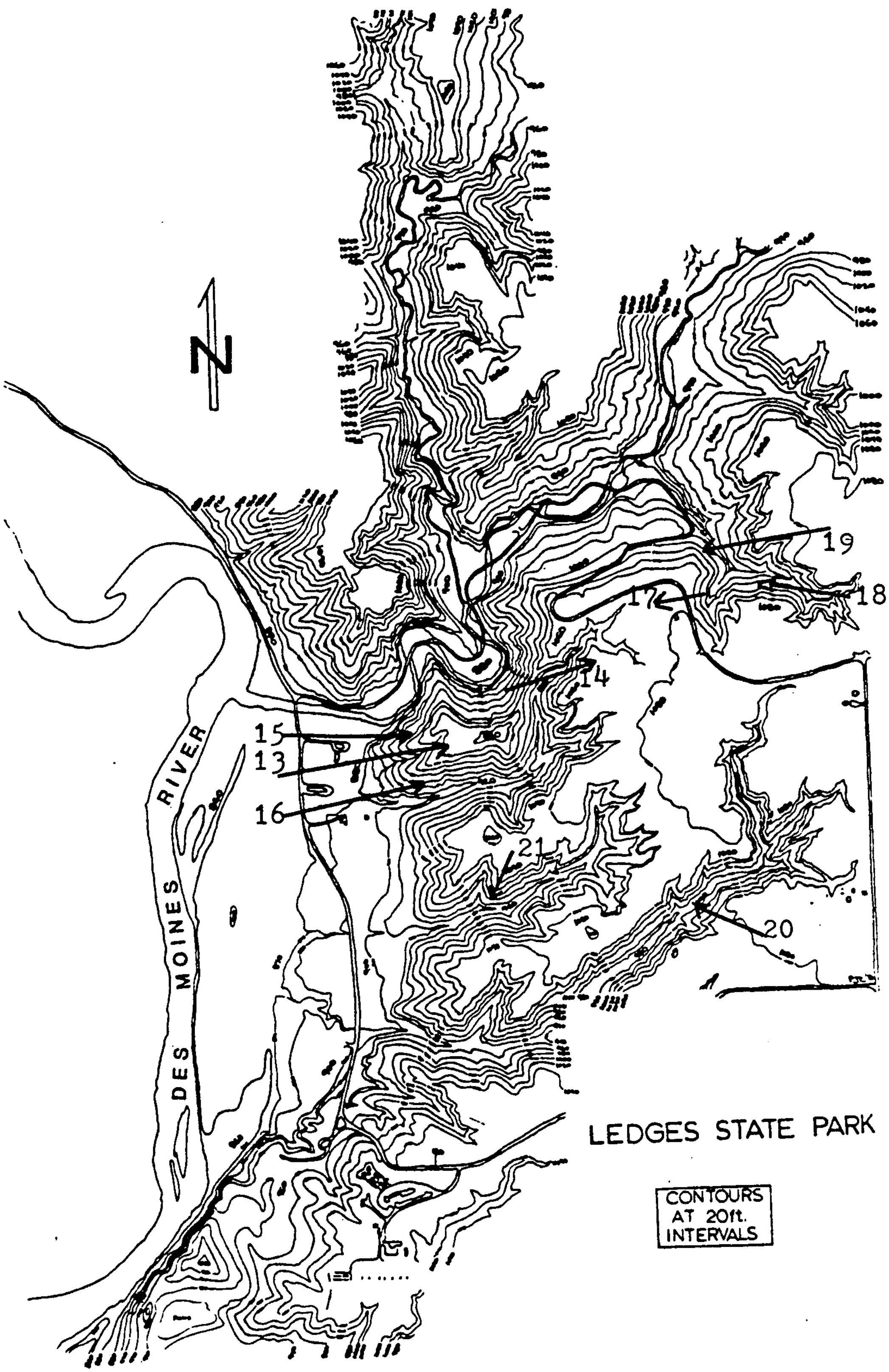
The area is rich in forest species represented on all slope aspects. Herbaceous plants are plentiful, beginning in the spring with the bloom of the woodland ephemerals. Nine study plots were located within the Ledges, typifying the Hayden-Storden soil association (USDA, Soil Conservation Service, 1976). The legal description of the park is Boone County, Worth Township: T83N, R26W, sect. 16 and sect. 21 with a latitude of $42^{o}31'$ and longitude $93^{o}55'$ (see Figure 6).

Pammel Woods - Pammel Woods is a relatively undisturbed native woodland, 15.2 hectares in size (38 acres), located on the Iowa State University campus. The University Golf Course borders on the east, Hyland Avenue on the west, the University cemetery on the south, and the Central and North Western Railroad on the north (Figure 2). Previously belonging to a larger tract of land called the North Woods, the land had been set aside for forestry and park purposes by the Board of the Iowa State Agricultural College in 1894-95. Subsequently, it was renamed College Park (Aikman and Smelzer, 1938).

In 1941, this hilly, brook-dissected tract was rededicated to Louis H. Pammel, a noted conservationist who headed the botany department from 1889-1929. Despite the removal of diseased trees, and the erosion from the adjacent construction and class use, Pammel Woods is still rich in a variety of native trees, shrubs, herbs, and fungi. It is located in the

Figure 6. Ledges State Park

Sample No.	Aspect	Elevation ft/m
13	Level	1060/323
14	NW	950/289
15	W @ 285°	1020/311
16	S @ 160°	950/289
17	E @ 100°	1040/317
18	NW	1040/317
19	NE @ 45°	1030/314
20	E @ 115°	1000/305
21	SW	990/302


N
19
18
17
14
15
13
16
21
20
DES MOINES RIVER
LEDGES STATE PARK
CONTOURS AT 20ft. INTERVALS

Story County township of Washington: T83N, R24W, sect. 4, latitude at 42°02', longitude at 93°39'30". There were five sample plots located here, numbered 22 through 26 in Figure 7. The land is in the Hayden-Storden soil association (USDA, Soil Conservation Service, 1981).

Silvers-Smith Woods - This area comprises 8 hectares (20 acres) of The Nature Conservancy-owned woods located in Dallas County and deeded in 1976 by two family property owners, Cleece M. and Renee Silvers and Richard L. and Betty A. Smith (Landers, 1976; Glenn-Lewin, 1980). The land is bordered on the west by Hickory Creek. Two ravines within the property provide drainage to the N. Raccoon River, which borders the southwest corner. The ravines expose sandstone and shale as does the river shoreline; stones lining the channel, however, are of glacial origin (Landers, 1976).

Silvers-Smith is in the Adel Township: T79N, R27W, S.W. ¼ sect. 21 with a latitude at 41°38' and a longitude at 93°59'40" (Booth, 1974). Figure 8 shows the location of the two plots in this study area, which are in the Clarion-Nicollet-Webster soil association (USDA, Soil Conservation Service, 1980).

Woodman Hollow State Preserve - This 32 hectare (80 acre) preserve is situated on the west side of the Des Moines River, south of Fort Dodge and just east of the center of Webster County. Kalo is to the north, Otho to the east, and Lehigh about 14.5 km (9 miles) southeast. In the township of Otho, it is legally described as the southern ½ of the northern ½ of sect. 22, T88N, R28W. Latitude is 42°24'30". Longitude is 94°06'.

Figure 7. Pammel Woods: Modified from United States Geological Survey Map, Ames West, Iowa, 1975

Sample No.	Aspect	Elevation ft/m
22	Level	1001/305
23	SE @ 150°	966/294
24	E @ 118°	976/297
25	N @ 0°	971/296
26	N @ 20°	976/297

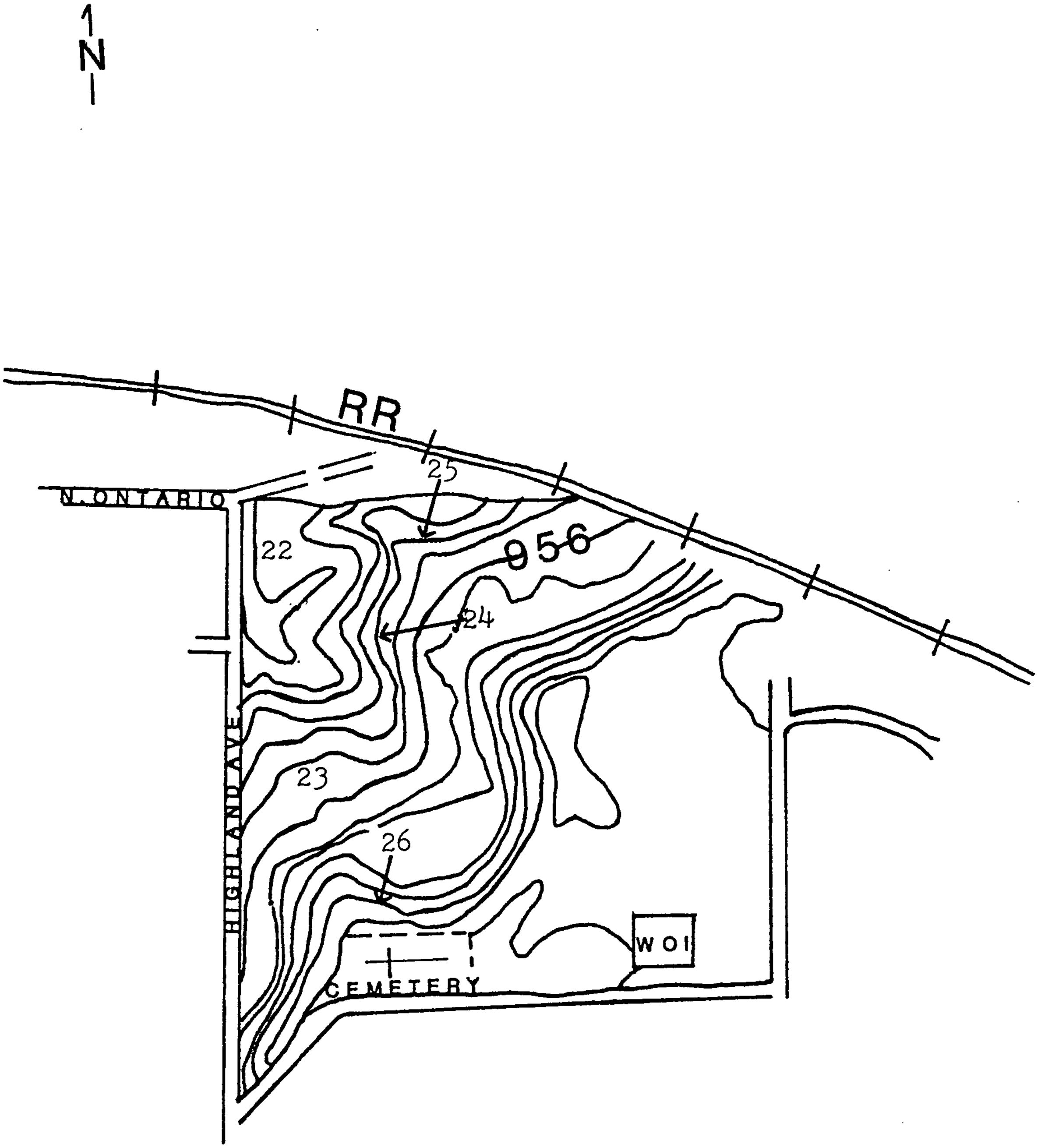
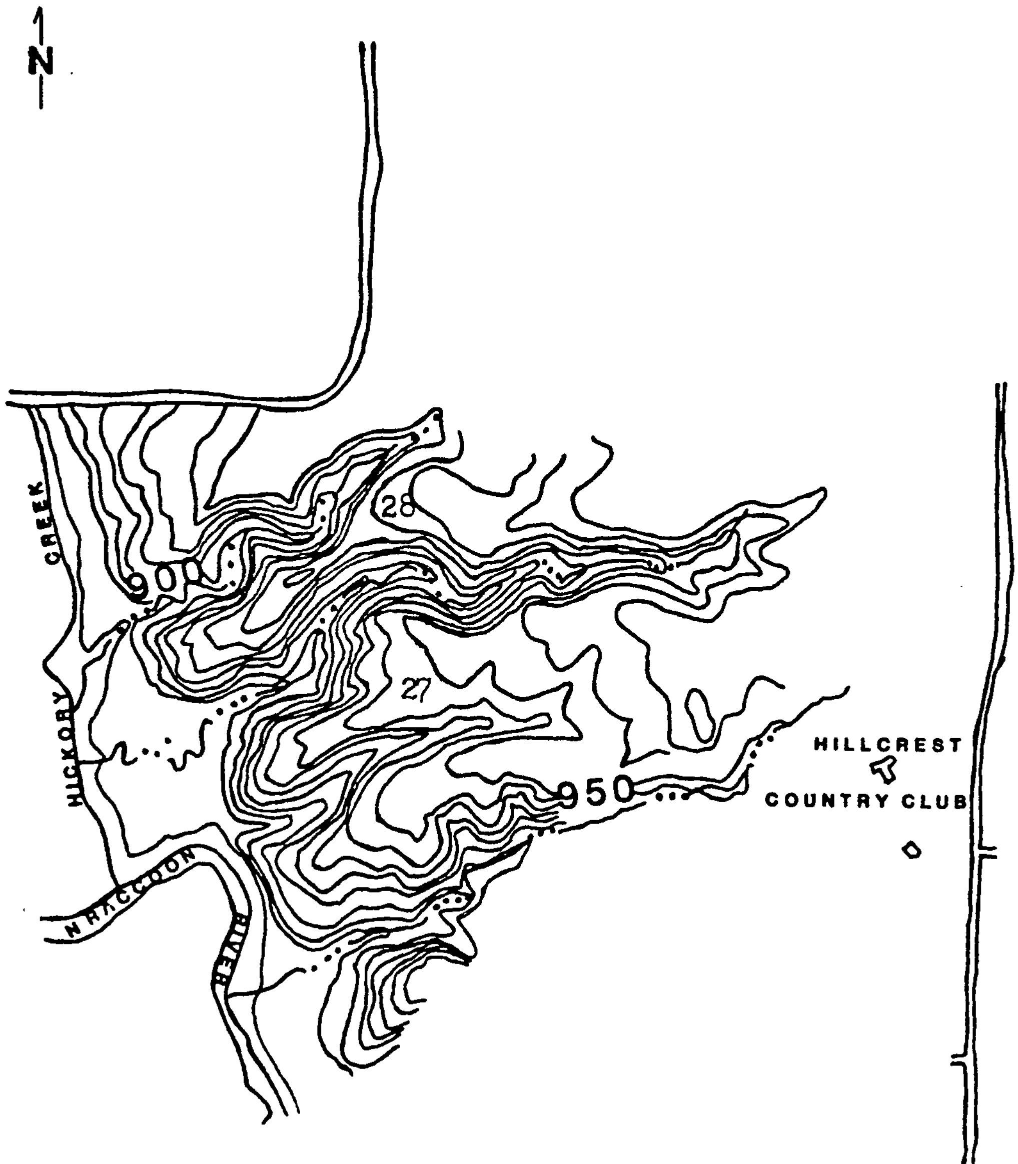

N
RR
N. ONTARIO
HIGHLAND AVE
25
22
956
24
23
26
W O I
CEMETERY

Figure 8. Silvers-Smith Woods and vicinity: Modified from United States Geological Survey Map, Dallas Center, Iowa, 1965a

Sample No.	Aspect	Elevation ft/m
27	SW @ 250°	950/289
28	NW @ 330°	950/289


N
HICKORY CREEK
900
28
27
950
HILLCREST
COUNTRY CLUB
N RACCOON
RIVER

Originally territorial land, the property was sold to Mr. Woodman by a private citizen, the initial landowner. In 1927, the Woodman family deeded the land to the state of Iowa, which subsequently dedicated it as a state park. Peck (1980) discusses in greater detail the state acquisition and management of Woodman Hollow. In 1970, it was rededicated as a state preserve, thus excluding impact activities on the site.

The vegetational and geological richness of Woodman Hollow has been discussed by many (Hart, 1919; Pammel, 1919; Paige and Drake, 1919; Gwynne, 1959; Niemann, 1977; Stoneburner, 1971; Niemann and Landers, 1974; Peck, 1980). The prominent feature is a canyon-like valley or hollow bisecting the preserve and cut by Woodman Hollow Creek through a sequence of glacial sediment into the Pennsylvanian sandstone (Gwynne, 1959; Peck, 1980). Similar sandstone formations are present only south of the preserve on the Des Moines River. These include Dolliver Memorial State Park, Ledges State Park, Red Rock and Elk Rock (Marion County), and Cedar Creek Bluffs (Mahaska County) (Shimek, 1948; Gwynne, 1959; Peck, 1980). Water drops about 3.7 m at the western boundary of the preserve and the creek meanders through the entire length of the hollow to join the river. Niemann (1977) and Niemann and Landers (1974) report 358 vascular plant species. Peck (1980) reports 142 bryophyte species in Woodman Hollow. Figure 9 shows the location of the two samples (labeled 29 and 30) which were in the Storden-Hayden-Wadena soil association (Koppen, 1975).

Figure 9. Woodman Hollow State Preserve: Modified from United States Geological Survey Map, Evanston, Iowa, 1965b

Sample No.	Aspect	Elevation ft/m
29	SE @ 140^{o}	1075/327
30	S @ 160^{o}	1050/320


FORT DODGE
OTHO
N
1100
1000
29
30
DES MOINES RIVER

Field Methods

Collection of the field data began in June, 1979, and continued throughout that summer into early fall. Plots were revisited in early mid-fall to collect fruits from various oak trees (to clarify species) and to identify any late-blooming plants. During spring and summer 1980, spring ephemerals were identified and identifications of previously unidentified species were made. A check of all sites was conducted to note any natural catastrophes (storm damage, windfall, etc.) or human impact that may have altered the sites within the previous year.

At each study area, the selection of individual sample plots was based on the following criteria: 1) Vegetation representative of a mesophytic forest community that was not a floodplain, gallery forest, or prairie-forest border. 2) A single, relatively homogeneous sample such that no trend of change in topography or vegetation exists from one edge of the sample to the other. 3) Appropriate in size to accommodate the dimensions of the sampling technique. 4) No evidence of recent human disturbance, e.g., logging, vandalism, seeding, planting, etc. 5) Position on the slope for representing low, low-mid, mid, mid-high, high, and level upland positions. 6) Aspect or compass direction to represent forest communities on N-, NE-, E-, SE-, S-, SW-, W-, and NW-facing slopes.

At each selected sample area, a one-tenth hectare (.25 acre) quadrat was erected by laying down a 50-meter tape parallel with the contour of and perpendicular to the direction of the slope. A rectangular plot, 50 m x 20 m, was constructed extending 10 meters upslope and downslope from the center tape. Data were collected in the order described below to minimize damage to ground cover from excessive walking through the quadrat. At alternate meters along the 50-meter tape (total of 25), a 1 m^2 subquadrat was laid down. All herbs within this grid were recorded by species and by estimated percent cover. The herb stratum included vascular herbaceous plants and lianas, but not low shrubs or young tree seedlings. Trees and shrubs were measured in three strata (shrub, understory, and canopy) for individual species and for their intercept coverage over the 50-meter tape. Any tree with a diameter at breast height (DBH = height of 1.3 m above ground) of less than 5.5 cm was included in the shrub stratum. All trees (DBH greater than or equal to 5.5 cm) rooted within the quadrat were tallied and the DBH recorded. Finally, the plot was searched for "rare species"; that is, any species present but not represented by one of the above measurements. The species' name and estimated cover in dm^2 or m^2 was recorded. Before dismantling the quadrat, information such as the date, slope aspect, inclination in percent and degrees, and position of the plot on the slope was written down. Data from a total of thirty (30) sample plots at eight different study areas were taken, using this procedure.

Whittaker and Niering (1965) have found the tenth hectare quadrat method to be effective for measuring density, coverage, and frequency in a wide range of vegetation types. The technique is suitable for forest, woodland, grassland, and desert vegetation sampling, making modifications where needed (Whittaker and Niering, 1965; Gauch, 1977).

Data Analysis

Prior to detailed analysis, raw field data were reduced to the following: 1) total cover (in meters) for shrub, understory tree, and canopy tree species. Multiplication by a factor of two (2) yields percent cover; 2) percent cover for herbs; 3) herb frequency (%); the percent of 25 subquadrats in which a given species was present; 4) basal area (cm^2/0.1 ha) for each tree species; and 5) tree density (stems/0.1 ha). Soil maps and U.S. Department of Agriculture Soil Surveys for each county included in the study (Figure 1) were consulted and information regarding each sample plot was summarized (see Appendix B). U.S. Geologic Survey topographic maps were used to obtain elevation levels, latitude and longitude measures, and the study area maps (Figures 2 through 9).

The structure and variation of this vegetation data were then studied using direct and indirect gradient analysis. With direct gradient analysis, samples can be arranged and studied according to a known index of position (magnitude) along an environmental or phytosociological gradient which is accepted as a basis of study (Whittaker, 1967). Soil survey information, elevation levels, percent slope, position, and slope aspect were all used for direct gradient analysis.

Vegetation samples can be compared with one another in terms of degree of differences in species composition and thus can be arranged along axes of variations. This approach to studying plant communities is called indirect gradient analysis (Curtis, 1959). The axes may or may not correspond to environmental gradients. The process of arranging samples or species according to one or more axes of variation or gradients is ordination (Whittaker, 1967; 1973). It is a spatial arrangement in which position of a stand or species reflects its similarity to other stands or species. Therefore, ordinations derived from direct or indirect gradients provide a framework for comparison of species with phytosociological and environmental factors. Hypotheses can then be drawn regarding the cause and effect of these relationships (Chapman, 1976).

A computer program, CEP-5 (Cornell Ecology Program for Resemblance or Distance Matrix) was used to calculate similarity matrices needed in ordinations for shrub, understory tree, canopy tree, and basal area data. Sorensen's index, or coefficient of community (CC), percentage similarity (PS), and average similarity (or distance) between each plot were the three most useful indices (Whittaker, 1970; Mueller-Dombois and Ellenberg, 1974). Euclidean distance (ED) was also calculated but not useful due to the large values generated, adding increased computer memory space and unnecessary costs to ordination programs. A second program, ORDIFLEX, written by Gauch (1977), was chosen for ordinating the central Iowa data, since it contained four techniques desired: Weighted Averages (WA), Polar Ordination (PO), Principal Components Analysis (PCA), and Reciprocal Averaging (RA).

Weighted Averages - This is the simplest ordination technique and is an example of direct gradient analysis developed and presented independently by Ellenberg in 1948, Whittaker in 1948, and Curtis and McIntosh in 1951 (Curtis and McIntosh, 1951; Gauch, 1977). Whittaker

(1967, 1973) described the method, using moisture preferences of species to ordinate stands. Various factors known to affect the moisture conditions of sites are combined into a "topographic moisture" index and each species is weighted accordingly.

Basal areas and total cover (understory and canopy cover) were analyzed using weights derived from elevation, percent slope, aspect, and position of each sample. A moisture preference weight for stands was also calculated, using climax adaptation species weights determined from information in previous studies (Curtis, 1959; U.S.D.A., 1965; Sanders, 1967; Cahayla-Wynne, 1976).

Polar Ordination (Bray-Curtis Ordination) - Bray and Curtis (1957) devised a method that uses two reference stands (samples) which serve as endpoints or "poles" for ordinating all other stands (samples). The distances between pairs for central Iowa data were computed using percentage distance (PD); however, ED and CD are acceptable. The sample pair with the greatest dissimilarity (PD = 100 - PS, where PS = percent similarity) is chosen as endpoints. ORDIFLEX applies a double standardization to the data matrix prior to ordination as suggested by Bray and Curtis (1957). The length of the x-axis equals the dissimilarity index of the two endpoints. Each remaining stand is positioned along the axis by its perpendicular projection from the point of intersection of the two arcs, which represent the dissimilarity of that stand from the reference points.

The pair of stands within the center fifth of this axis having the maximum difference serve as endpoints for a second axis. The remaining stands are, once again, ordinated by their dissimilarity to these points. Likewise, species can be ordinated. ORDIFLEX can automatically generate the endpoints for two axes using the procedure described or endpoints may be specified. When the same data set is used, endpoints from the first axis of RA or PCA can also be designated for PO and the second axis can then be determined.

A two-axis PO was used for basal area and total tree cover data with endpoints generated automatically and also specified from RA and PCA. In addition, endpoints were specified employing the criteria of Mueller-Dombois and Ellenberg (1974). According to this modification, the first reference stand is that with the lowest sum of similarity indices, the second endpoint being the most dissimilar to the first. All reference stands must have at least three (3) stand comparisons with 50% or greater dissimilarity. A second axis was constructed manually, again employing the 50% or greater dissimilarity rule.

Principal Components Analysis - This technique is a form of indirect gradient analysis introduced into phytosociology in 1954 and described in statistical and ecological work (Morrison, 1967; Orloci, 1975; Pielou, 1977; Gauch, 1977). Using the basal area data to illustrate the concept of PCA, this represents a 29 x 30 species by stand matrix. If $axis_1$ and $axis_2$ correspond to $stand_1$ and $stand_2$, a cloud of twenty-nine points would denote the position of each species with respect to these stands. By rotating these axes orthogonally, a new $axis_1$ (Y_1) passes through the largest spread of this cloud and a new $axis_2$ (Y_2) passes through the largest width. Y_1 and Y_2 represent the first and second axes of principal components. The perpendicular projection of each point onto Y_1 and Y_2 represents the arrangement of species in the first and second axes. The variance on a PCA axis is called the eigenvalue and cumulative eigenvalues for axis 1-30 can be compared with the total variance. Thus, PCA is an eigenanalysis "for projecting a multidimensional cloud of points into a space of fewer dimensions, using rigid rotation to derive successive orthogonal axes which maximize variance accounted for. . . . Both species and sample ordinations results from a single analysis" (Gauch, 1977).

Basal area, total cover, and canopy tree cover data were analyzed using nonstandardized PCA. Pielou (1977) has suggested that standardization is not necessary for botanical work when the units of measure are consistent for all species in a sample. However, PCA-centered and PCA-centered and standardized were run for basal area data. Results differ significantly when the data have been standardized prior to PCA and after the principal component is found.

Reciprocal Averaging - Hill (1973) has presented an algorithm for generating a unique one-dimensional ordination both for species and stands. It is called Reciprocal Averaging (RA) because the process involves repeated cross-calibration using averaged species scores for stand scores and reciprocally averaged stand scores for species scores. RA is an eigenanalysis and, therefore, related to PCA. Because the results are weighed, RA also resembles WA. The final scores, however, do not depend on initial scores, nor is prior environmental or phytosociological knowledge required. Thus, this form of indirect gradient analysis has been suggested for initial evaluation of data sets (Gauch, 1977).

Basal area, total cover, canopy tree, and understory tree cover were ordinated by RA. Plots were constructed using the first three axes, though ORDIFLEX gives up to seven axes. Outliers, i.e., species or stands very unlike others, were removed from basal area and total cover data sets and the technique was repeated.

Another approach to interpreting vegetation data, rather than ordination, is classification. This is grouping together of a number of samples into abstract units or classes, according to shared characteristics (Whittaker, 1973). The units are called community-types. There are several characteristics upon which they can be based (Whittaker, 1970). Classification by dominant species is one such method. Another method, Orloci agglomerative, is a quantitative approach and a form of cluster analysis that groups samples by their relative similarities (Orloci, 1967).

A FORTRAN program adapted from Orloci (1967) and written by Nichols and Wittie at the University of Wisconsin was used for the agglomerative approach. Basal area, total cover, canopy tree, and understory tree cover data were analyzed this way. Also, basal area and total cover data were classified by species dominance-types.

In addition to the similarity indices provided by CEP-5, calculations of two diversity indices, species richness and beta diversity, were computed. Beta diversity, or between-stand diversity, is the degree of change in floristic composition of communities or samples along a gradient (Whittaker, 1970; Peet, 1974; Pielou, 1977). The equation is:

$$BD = \frac{\log a - \log z}{\log 2}$$

where a is the largest value of CC and z is the smallest value of CC. Species richness was calculated as the total number of species per sample (Peet, 1974). Basal area data were used for calculating diversity indices. Finally, an overall correlation and correlation by stand and by species for these two data sets were statistically determined.

RESULTS

Appendix A is a summary of the recorded and calculated information for each of the thirty sample plots, including data on elevation, slope, aspect, and soil types. With this and the individual study area maps (Figures 2-9), each stand can be relocated in the field. Total basal area (cm^2/0.1 ha.) data for all the species in each stand are presented in Appendix B. The importance of Quercus alba and Q. borealis is seen in the magnitude of area accounted for by these two species.

Ordination and Orloci agglomerative classification results presented herein are based on tree species basal area. In agreement with Cahayla-Wynne (1976), basal area data more accurately represent the vegetation. However, cover data are useful for interpreting dominance and species importance in each layer of the forest; canopy, understory, and shrub.

The classification of stands by dominance type is also given in Appendix A. Dominance is best expressed by seven species: Q. alba, Q. borealis, Q. macrocarpa, Q. muhlenbergii, Tilia americana, Fraxinus americana, and Acer nigrum. Codominance exists where the most important tree species in a stand have basal area measures within 15% of each other (Cahayla-Wynne, 1976). On mesic sites, Q. borealis is codominant with A. nigrum or T. americana, as in stand 14 or 17. Stand 6 is the most mesic stand, located on a north facing slope and dominated by A. nigrum, with Q. borealis also an important species. On slopes of medium to xeric moisture, Q. alba and Q. borealis are admixed. Such is the case with stands 2, 3, 7, and 11. The more xeric conditions exist where

Q. alba is the dominant tree species. Considering the frequency of stand occurrence and basal area, the number of dominant species can be reduced to four: Q. alba, Q. borealis, T. americana, and A. nigrum (see Appendix B).

The results of Orloci agglomerative classification are presented as a dendrogram in Figure 10. Those stands in which Q. borealis is dominant or codominant fall to the left (stands 6, 10, 12, 14, 15, 16, 17, 18, 19, 20, 21, 25, 26, 28). Stand 6 can be included in this group based on species composition and moisture level. Stands dominated by Q. alba form a group to the far right (stands 1, 13, 22, 23, 24, 27, 29, 30). A third cluster consists of stands in which Q. alba and Q. borealis are admixed (stands 2, 3, 7, and 11). Remaining stands fall to the center and represent those plots of mixed dominance, as in stand 8, or those in which F. americana, Q. muhlenbergii, or Q. macrocarpa are dominant or codominant.

In the understory layer, central Iowa forests have an ubiquitous distribution of Ostrya virginiana. Carpinua caroliniana is present in limited moist areas, particularly Ledges State Park.

For the shrub stratum, F. americana (constancy = 77%), O. virginiana (66%), Ribes missouriensis (66%), Ulmus americana (60%), T. americana (50%), and A. nigrum (50%) were the most important species. On the more mesic sites, A. arborea (43%) and C. cordiformis (43%) occurred.

In the herb stratum, Parthenocissus quinquifolia (100%) was ubiquitous. Amphicarpa bracteata (70%), Toxicodendron radicans (63%), Sanguinaria canadense (63%), Desmodium glutinosum (63%), Carex

Figure 10. Orloci (1967) agglomerative classification dendrogram of samples from central Iowa forests using basal area. The number of clustering passes corresponds to stand group dissimilarity

Stand Dominance Type:

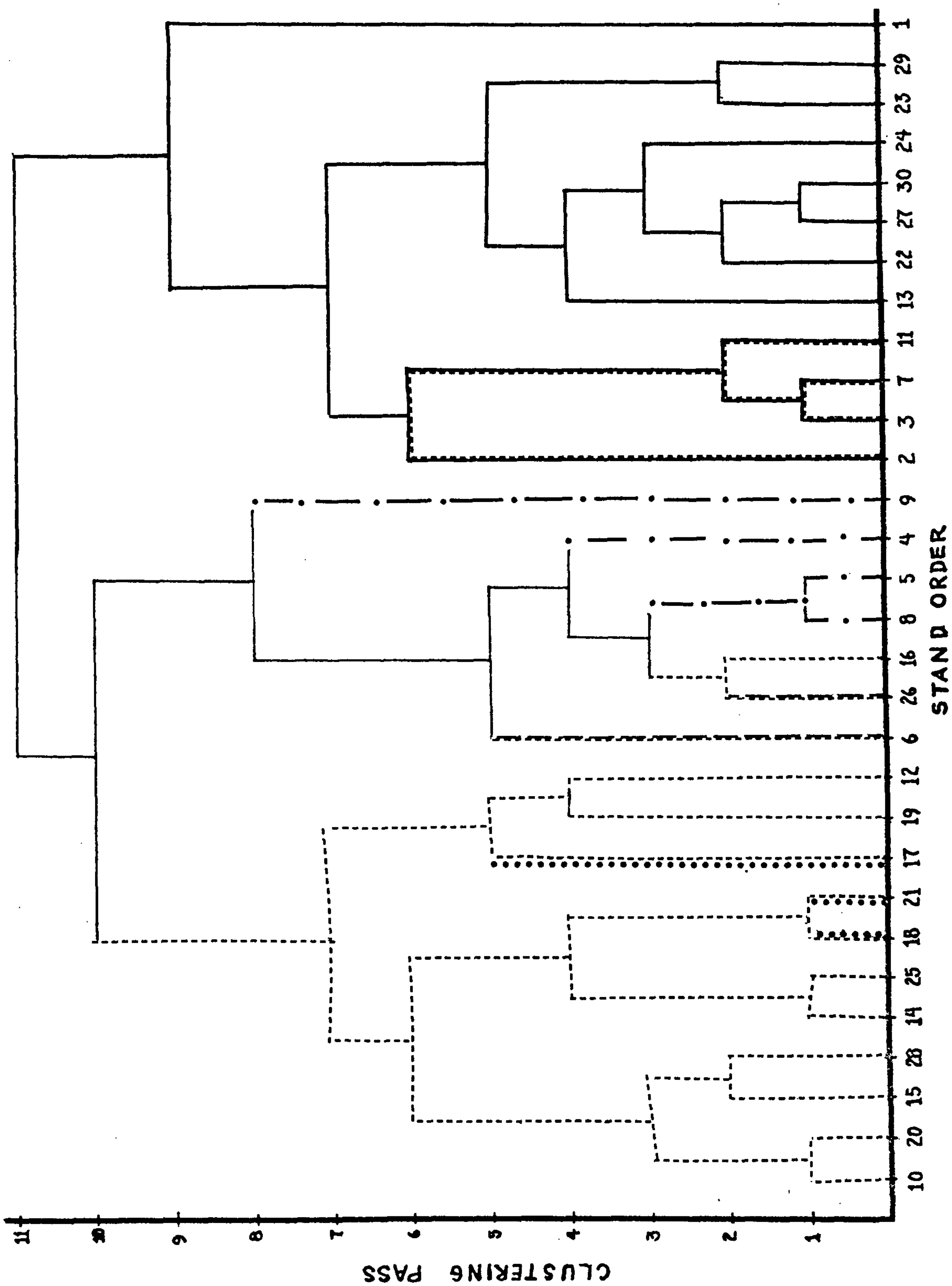
______ *Quercus alba*

-------- *Quercus borealis*

.... *Tilia americana*

.—.—. *Acer nigrum*

—.— Other (see Appendix A)


STAND ORDER
1 29 23 24 30 27 22 13 11 7 3 2 9 4 5 8 16 26 6 12 19 17 21 18 25 14 28 15 20 10
CLUSTERING PASS
1 2 3 4 5 6 7 8 9 10 11

pennsylvanicum (60%), Phyrma leptotachya (57%), and Hydrophyllum virginianum (57%) were also common. Podophyllum pelatatum, Phlox divaricata, Hepatica acutiloba, Adiantum pedatum, and Asarum canadense were characteristic of moist slopes dominated by A. nigrum, T. americana, and Q. borealis. On xeric sites, Carex spp., Galium spp., and Sanicula spp. were common.

The two-dimensional ordination presented in Figures 11a, 11b, and 11c are the first three axes of RA. Three groups are evident in Figures 11a and 11b corresponding to those stands dominated by Q. alba, Q. alba and Q. borealis admixed, and Q. borealis and/or T. americana and A. nigrum. Notice that stands 4, 5, and 9 do not fit these groups.

The relative importance of Q. alba, Q. borealis, T. americana, and A. nigrum are plotted against the first axes of RA in Figure 12. The coenoclines (patterns of distribution) indicate that Q. borealis and Q. alba are the two most dominant species in central Iowa forests. The relative abundance of T. americana and A. nigrum decrease with the increasing importance of Q. alba. The distribution of Q. alba increases from left (red oak group) to right (white oak group) as the distribution of Q. borealis decreases and as stand order changes from mesic to more xeric sites. Stand 9 is the most xeric stand, located on a southeast-facing slope where Q. macrocarpa has the greatest relative abundance. Stand 8 shows nearly equal amounts of Q. borealis and Q. alba with a small amount of A. nigrum. Therefore, this stand lies close, yet still between, the intermediate oak and red oak group.

Weighted averages ordination using climax adaptation numbers is

Figure 11a. Two-dimensional Reciprocal Averaging ordination based on tree basal area. Abscissa is axis 1; endpoints are stand 6 and stand 1. Ordinate is axis 2; endpoints are stand 28 and stand 9

——— *Quercus alba* (White Oak) group

-------- *Quercus borealis* (Red Oak) group

— — — Intermediate group: *Q. alba* and *Q. borealis*

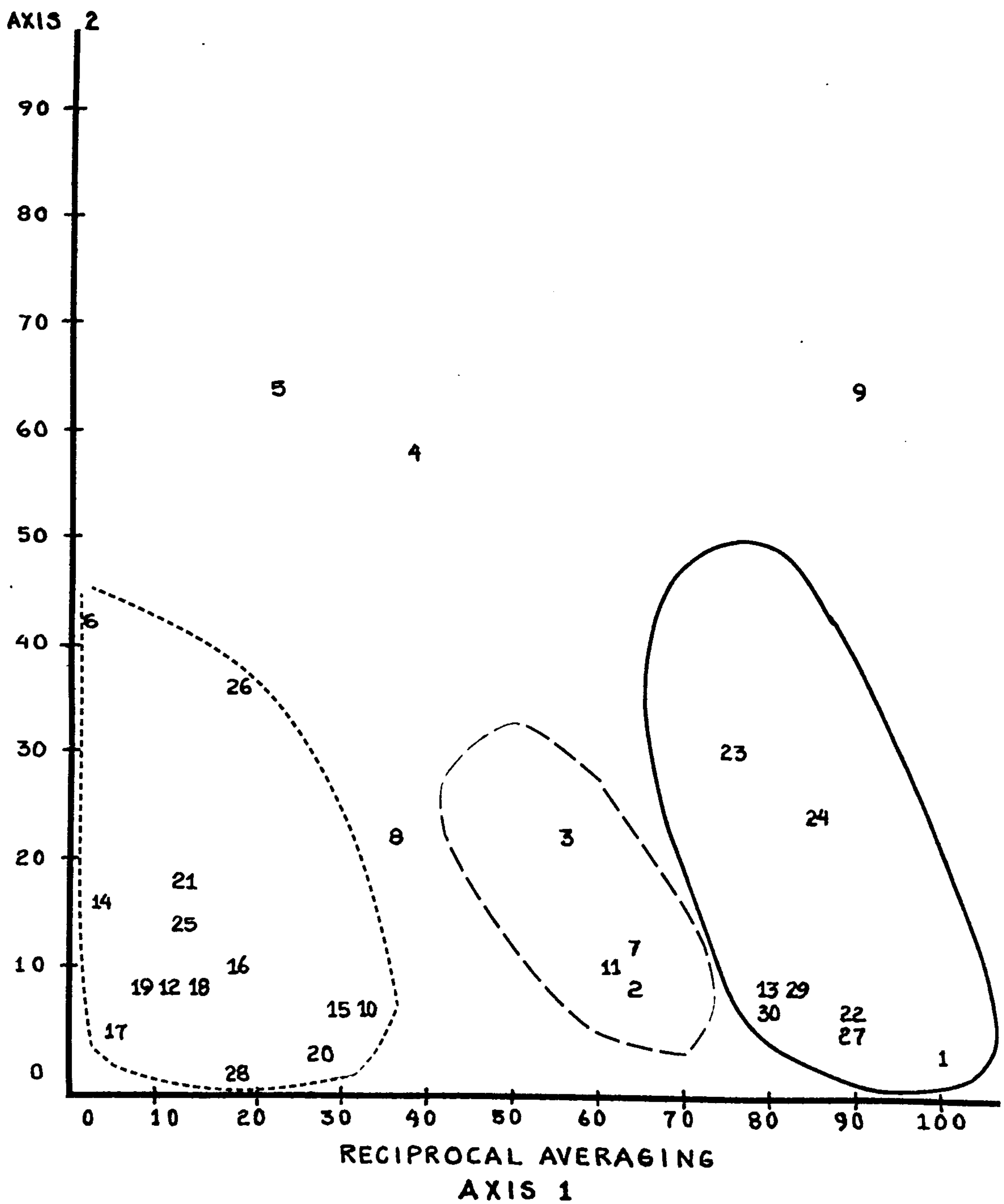

AXIS 2
90
80
70
60
50
40
30
20
10
0
5
4
9
6
26
8
3
23
24
14
21
25
16
19 12 18
17
15 10
20
28
7
11
2
13 29
30
22
27
1
0
10
20
30
40
50
60
70
80
90
100
RECIPROCAL AVERAGING
AXIS 1

Figure 11b. Two-dimensional Reciprocal Averaging ordination based on tree basal area. Abscissa is axis 1; endpoints are stand 6 and stand 1. Ordinate is axis 3; endpoints are stand 5 and stand 9

______ *Quercus alba* (White Oak) group

-------- *Quercus borealis* (Red Oak) group

-·—·— Intermediate group: *Q. alba* and *Q. borealis*

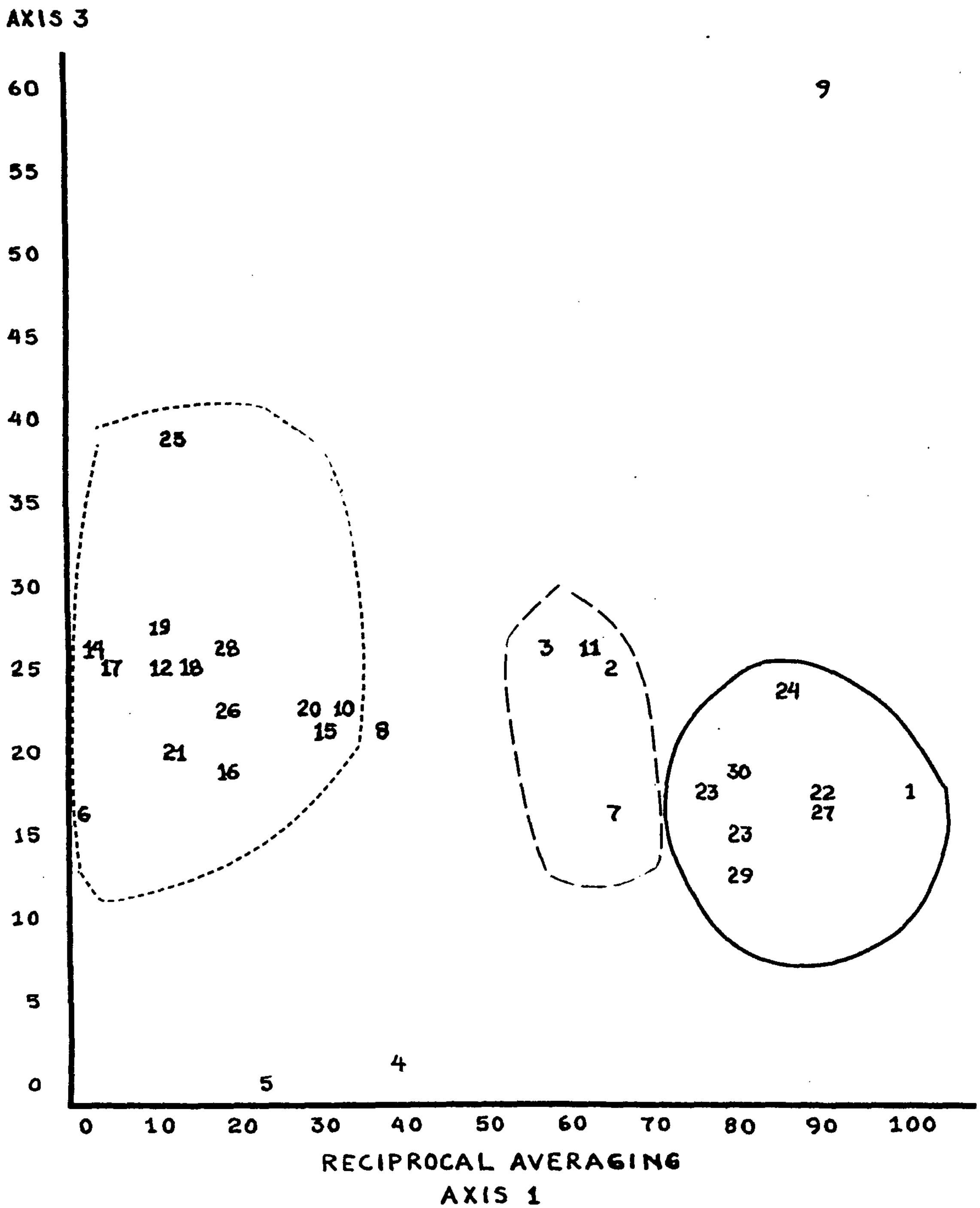

AXIS 3
60
55
50
45
40
35
30
25
20
15
10
5
0
9
25
19
14
17
12
18
28
26
20
10
15
8
21
16
6
3
11
2
7
24
30
23
22
27
1
23
29
4
5
0
10
20
30
40
50
60
70
80
90
100
RECIPROCAL AVERAGING
AXIS 1

Figure 11c. Two-dimensional Reciprocal Averaging ordination based on tree basal area. Abscissa is axis 2; endpoints are stand 28 and stand 9. Ordinate is axis 3; endpoints are stand 5 and stand 9

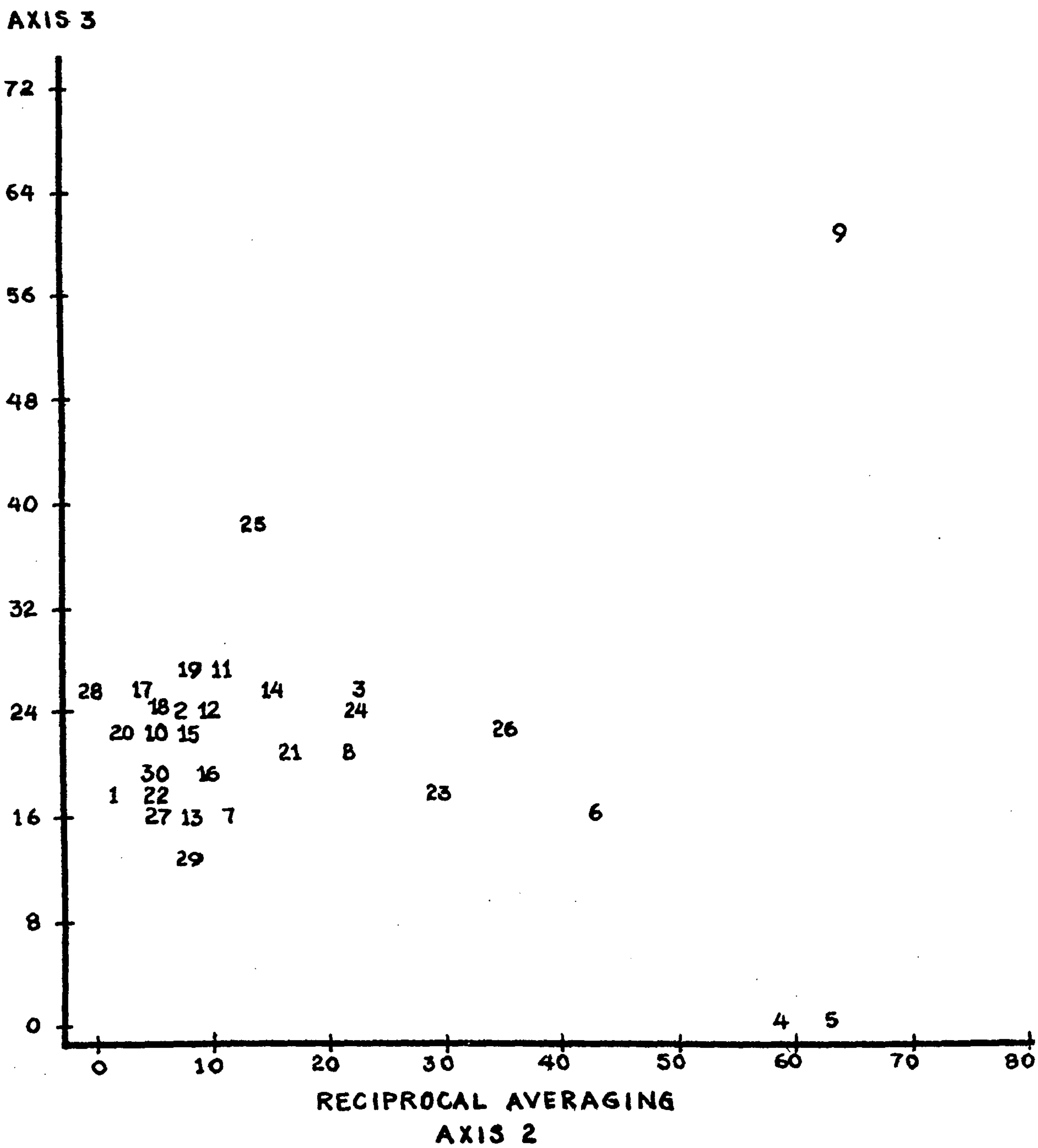

AXIS 3
72
64
56
48
40
32
24
16
8
0
9
25
19 11
28 17 14 3
18 2 12 24
20 10 15 26
21 8
30 16
1 22 23
27 13 7 6
29
4 5
0 10 20 30 40 50 60 70 80
RECIPROCAL AVERAGING
AXIS 2

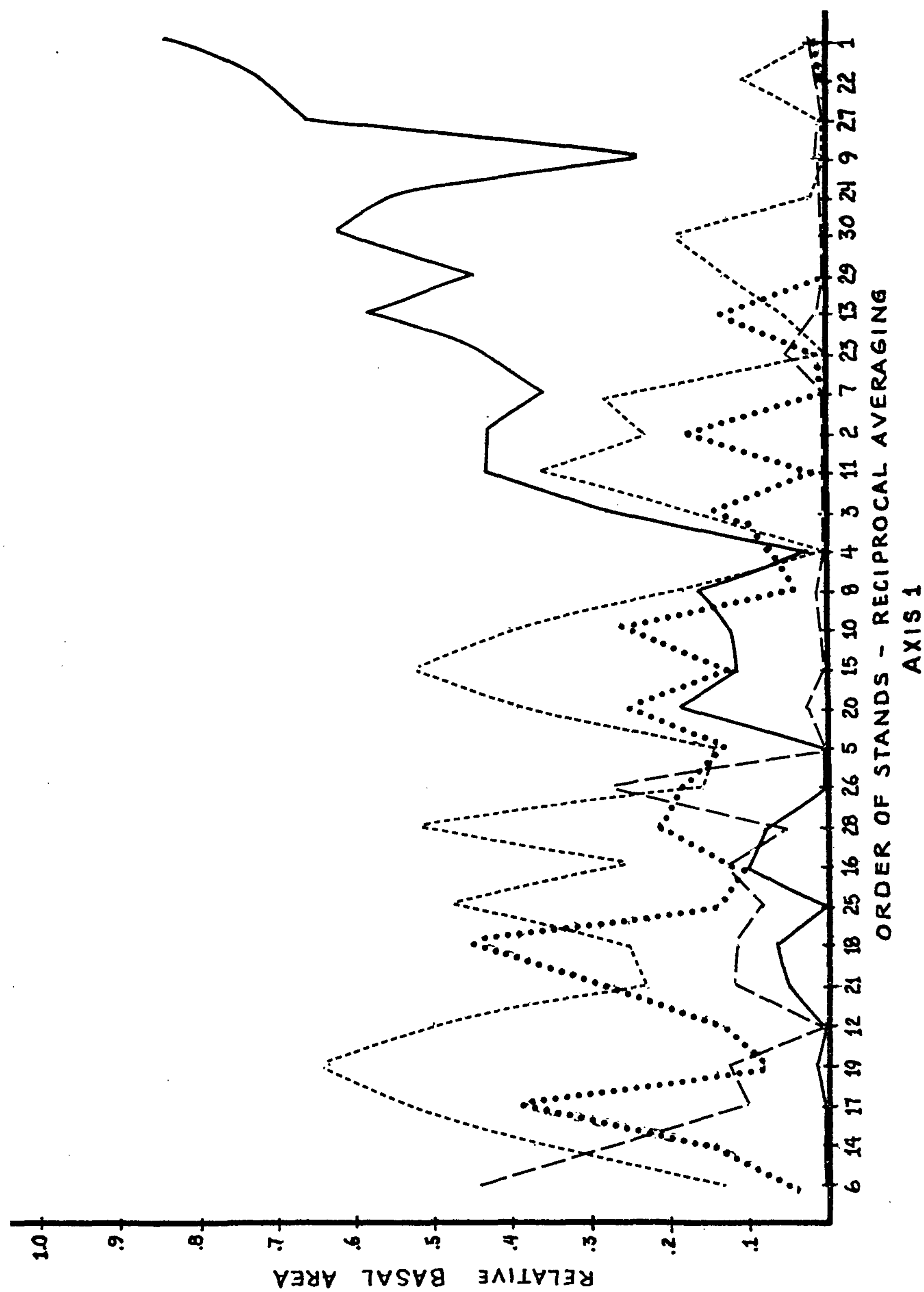
Figure 12. Relative basal area curves of the four most dominant tree species along the first axis of Reciprocal Averaging ordination. Abscissa is the order of stands on axis 1; the ordinate is relative basal area

- - - *Acer nigrum*

——— *Quercus alba*

-------- *Quercus borealis*

.... *Tilia americana*



RELATIVE BASAL AREA
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
6 14 17 19 12 21 18 25 16 28 26 5 20 15 10 8 4 3 11 2 7 23 13 29 30 24 9 27 22 1
ORDER OF STANDS - RECIPROCAL AVERAGING
AXIS 1

shown in Figure 13. Species within a stand are weighted according to how well they coexist with A. nigrum in the natural undisturbed forest (Table 1). Values for each stand are listed in Appendix A. In central Iowa, A. nigrum is assumed to be the most successful in the terminal forest, having a climax adaptation number of 10 (Curtis, 1959). Q. macrocarpa and Q. muhlenbergii are seen at the far extreme with values of 1.0. Comparisons of these numbers with shade tolerance ratings of foresters indicate they are roughly parallel (Curtis and McIntosh, 1951). A. nigrum is considered to be the most mesic tree species in central Iowa; Q. muhlenbergii and Q. macrocarpa indicate xeric conditions (Aikman and Smelzer, 1938).

Single axis ordination for RA, PO, PCA, and WA-climax adaptation is presented in Figure 13, along with the Orloci agglomerative classification results for comparison. All four ordination methods separate stands of the red oak group from those dominated by white oak. White oak stands group together in each ordination technique with the exception of WA-climax adaptation, in which stands 4, 11, and 23 are displaced. RA, PO, and PCA results cluster stands 2, 3, 7, and 11 as does the classification method.

Note that the second axis of nonstandardized PCA is presented in Figure 13 rather than axis 1. Examination of PCA results shows that the first axis of nonstandardized PCA ordinates by total stand magnitude. This is indicated by high Spearman-ranked correlation coefficients for total basal area ($r_s = .74$, $p < .0001$) and total cover ($r_s = .77$, $p < .0001$) data. PCA-centered results, however, are clearer for axis 1

Figure 13. Orloci agglomerative classification (A) and single-axis ordinations using tree basal area: Reciprocal Averaging-axis 1 (B), Polar Ordination-endpoints designated (C), Weighted Averages-climax adaptation (D), centered PCA-axis 1 (E), nonstandardized PCA-axis 9 (F)

——— *Quercus alba* (White Oak) group

.... *Quercus borealis* (Red Oak) group

— — — Intermediate group: *Q. alba* and *Q. borealis*

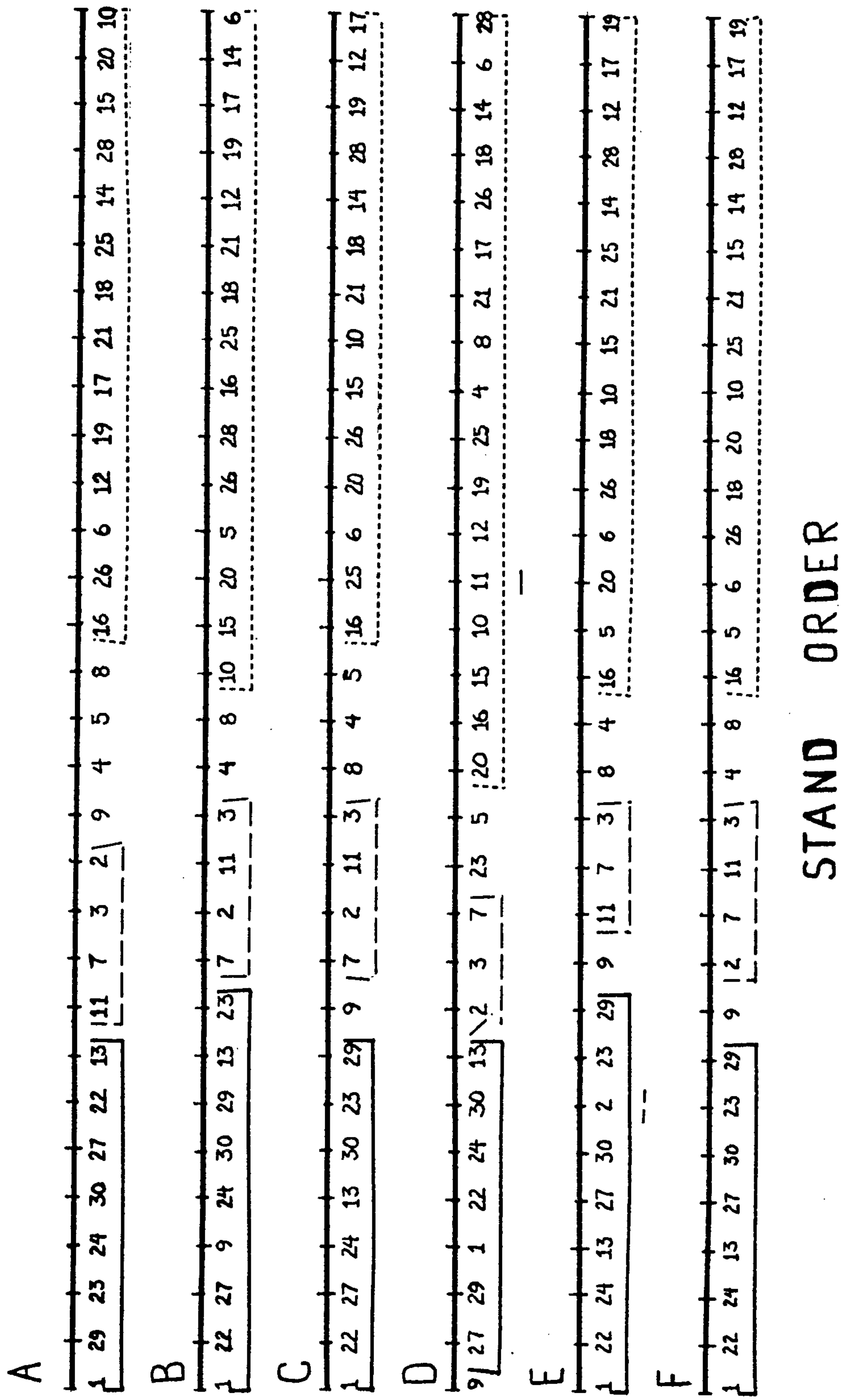

A 1 29 23 24 30 27 22 13 11 7 3 2 9 4 5 8 16 26 6 12 19 17 21 18 25 14 28 15 20 10
B 1 22 27 9 24 30 29 13 23 7 2 11 3 4 8 10 15 20 5 26 28 16 25 18 21 12 19 17 14 6
C 1 22 27 24 13 30 23 29 9 7 2 11 3 8 4 5 16 25 6 20 26 15 10 21 18 14 28 19 12 17
D 9 27 29 1 22 24 30 13 2 3 7 23 5 20 16 15 10 11 12 19 25 4 8 21 17 26 18 14 6 28
E 1 22 24 13 27 30 2 23 29 9 11 7 3 8 4 16 5 20 6 26 18 10 15 21 25 14 28 12 17 19
F 1 22 24 13 27 30 23 29 9 2 7 11 3 4 8 16 5 6 26 18 20 10 25 21 15 14 28 12 17 19
STAND ORDER

Table 1. Climax-adaptation numbers used as moisture preference weights for tree species[a]

Species	Climax-adaptation number
Acer nigrum	10.0
Ostrya virginiana	9.0
Carya cordiformis	8.5
Amelanchier arborea[b]	8.0
Carpinus caroliniana	8.0
Celtis occidentalis	8.0
Fraxinus americana	8.0
Tilia americana	8.0
Ulmus rubra	8.0
Morus rubra[b]	7.5
Ulmus americana[b]	7.0
Fraxinus nigra	6.0
Quercus borealis	6.0
Fraxinus pennsylvanica	5.0
Juglans nigra	5.0
Aesculus octandra[c]	4.5
Gleditsia triancanthos[b]	4.0
Prunus virginiana[d]	4.0
Quercus alba	4.0
Carya ovata	3.5
Prunus serotina	3.5
Crataegus sp.[b]	2.5
Quercus velutina	2.5
Juniperus virginiana	2.0
Populus tremeloides	2.0
Populus deltoides[b]	1.5
Acer negundo	1.0
Quercus macrocarpa	1.0
Quercus muhlenbergii	1.0

[a]After Curtis (1959).

[b]After Sanders (1967).

[c]Species for which tentative climax-adaptation numbers were assigned.

[d]After Cahayla-Wynne (1976).

(Figure 13).

Other weighted average ordinations were performed using elevation, percent slope, aspect, and position data. These were then correlated with the first axis of ordination RA and PO. Elevation levels varied insignificantly from one stand to another and thus did not help interpret ordination results. Weighted averages-percent slope, however, showed a Spearman-correlation coefficient of -.57 ($p < .001$) with PO results and a value of -.54 ($p < .001$) with RA (Table 4). Table 2 gives the weighted average used for the position x aspect (Appendix A, ASPO = weighted average ordination using aspect weights x position weight). WA-ASPO has a correlation coefficient of .44 with RA (Table 4). A graph of this as presented in Figures 15a and 15b shows again white oak separated from red oak stands. Ordination results for RA and PO have a correlation coefficient of .94 ($p < .001$).

An examination of species-composition, classifications, and ordination results suggested that stands 4, 5, 8, and 9 were possible outliers. Therefore, ordination techniques were repeated, eliminating these stands from the data set. Single axis ordination results appear in Figure 14. The pattern of the three oak--*Q. alba*, *Q. borealis*, and mixed *Q. alba* and *Q. borealis*--is clearly apparent. Two-dimensional reciprocal averaging ordinations are presented in Figures 15a and 15b. Endpoints for axis 1 are the same as those prior to the removal of the outliers; the grouping of stands by oak type persists.

Stand 4 is dominated by *F. americana*, with *C. cordiformis* and *C. ovata* as important canopy species. It has a dense understory of O.

Table 2. Assignment of weight by position on slope

Position	Weights
low-slope	3.0
low-mid slope	2.5
mid-slope	2.0
mid-upper slope	1.5
upland	1.0

Table 3. Assignment of moisture numbers by aspect[a]

Aspect	Moisture number
N, NNE, NE	1
NNW	2
NW	3
E	4
W	5
SE	6
S	7
SW	8
Level	9

[a]After Whittaker (1973).

Table 4. Spearman rank correlation (r_s) of single axis ordination

	r_s[a]
Reciprocal averaging$_{axis\ 1}$ -Polar ordination$_{axis\ 1}$	.94
Reciprocal averaging$_{axis\ 1}$-Weighted Averages-ASPO	.44
Reciprocal averaging$_{axis\ 1}$-Weighted Averages-percent slope	-.54
Polar ordination$_{axis\ 1}$ -Weighted Averages-percent slope	-.57
Nonstandardized PCA$_{basal\ area}$ -total basal area data	.74
Nonstandardized PCA$_{total\ cover}$ -total cover data	.77

[a]All values significant at $p < .001$ level.

virginiana. F. americana is also an important tree species in stand 5, in addition to several species indicative of disturbance (Gleditsia triacanthos, Morus rubra, Populus tremeloides, and Crataegus spp.). Soil profiles of each stand showed nothing unusual for stand 4; however, compaction of the A and B horizon was pronounced in stand 5. The disturbance was assessed as a minor one by Dr. Donald Wysacki at the Department of Agronomy, Iowa State University, occurring as long as fifty years ago. A lightweight vehicle may have been used when the man-made

Figure 14. Single-axis ordinations using tree basal area and omitting outlier stands 4, 5, 8, and 9. A) Reciprocal Averaging-axis 1, B) Polar Ordination-axis 1, c) nonstandardized PCA-axis 2

———— *Quercus alba* (White Oak) group

········ *Quercus borealis* (Red Oak) group

— — — Intermediate group: *Q. alba* and *Q. borealis*

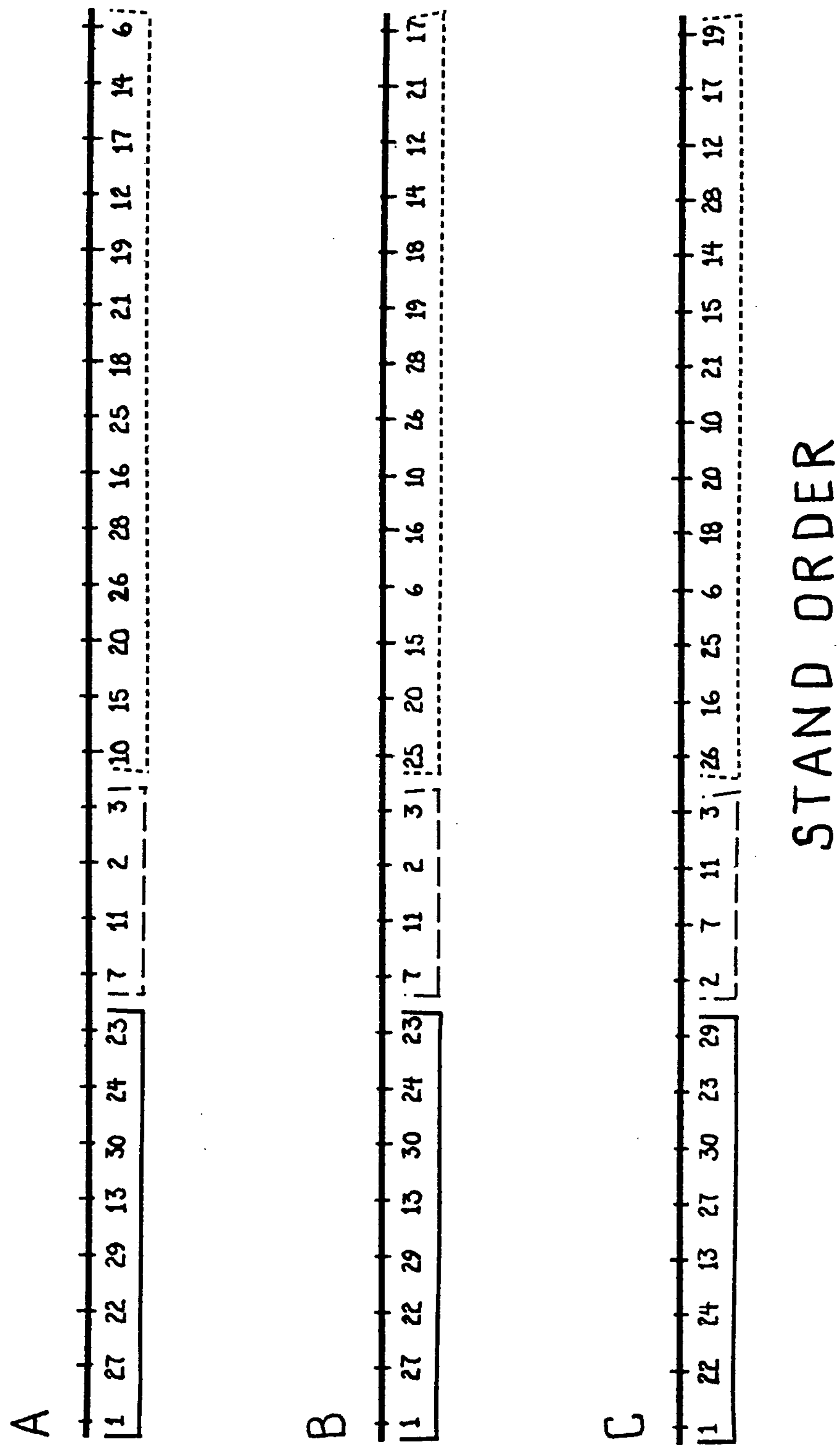

A
1 27 22 29 13 30 24 23 7 11 2 3 10 15 20 26 28 16 25 18 21 19 12 17 14 6
B
1 27 22 29 13 30 24 23 7 11 2 3 25 20 15 6 16 10 26 28 19 18 14 12 21 17
C
1 22 24 13 27 30 23 29 2 7 11 3 26 16 25 6 18 20 10 21 15 14 28 12 17 19
STAND ORDER

Figure 15a. Two-dimensional Reciprocal Averaging ordination using tree basal area. Outlier stands (4, 5, 8, and 9) have been removed. Abscissa is axis 1 with endpoints at stand 6 and stand 1. Ordinate is axis 2 with endpoints at stand 12 and 25

______ Quercus alba (White Oak) group

.... Quercus borealis (Red Oak) group

_ __ __ Intermediate group: Q. alba and Q. borealis

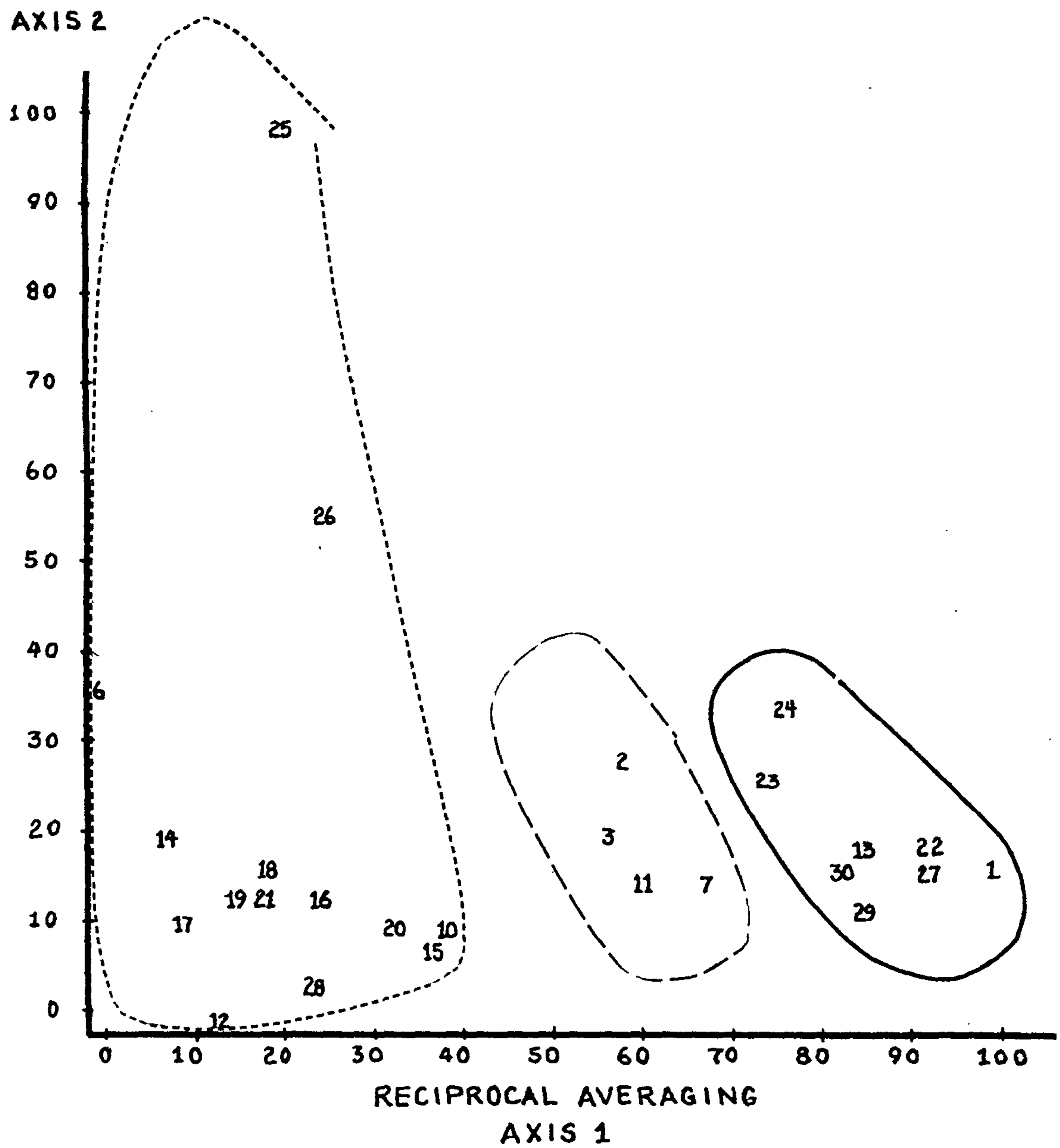
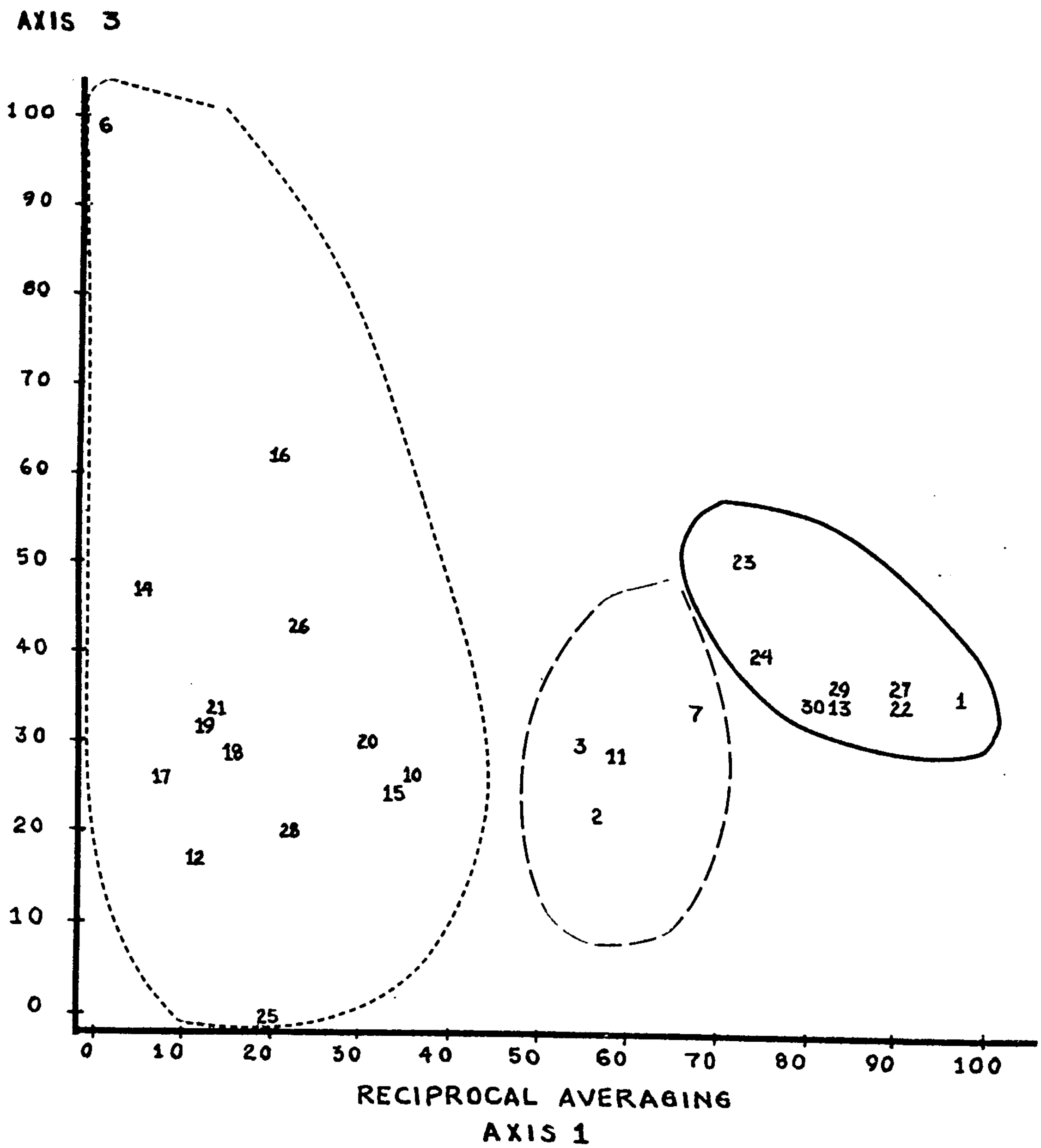

AXIS 2
100
90
80
70
60
50
40
30
20
10
0
25
26
6
14
18
19 21
16
17
20
10
15
28
12
2
3
11
7
24
23
13
22
30
27
1
29
0
10
20
30
40
50
60
70
80
90
100
RECIPROCAL AVERAGING
AXIS 1

Figure 15b. Two-dimensional Reciprocal Averaging ordination using tree basal area. Outlier stands (4, 5, 8, and 5) have been removed. Abscissa is axis 1 with endpoints at stand 6 and stand 1. Ordinate is axis 3 with endpoints at stand 25 and stand 6

———— *Quercus alba* (White Oak) group

.... *Quercus borealis* (Red Oak) group

— — — Intermediate group: *Q. alba* and *Q. borealis*


AXIS 3
100
90
80
70
60
50
40
30
20
10
0
6
16
14
26
21
19
18
17
12
28
20
10
15
25
23
24
29
27
1
30
13
22
7
3
11
2
0
10
20
30
40
50
60
70
80
90
100
RECIPROCAL AVERAGING
AXIS 1

pond, located southeast of the stand, was dug.

Further investigation and consultation regarding stand 8, located at Dolliver State Memorial Park, revealed that the area of the park had been the location of a Dutch elm disease outbreak. Storm damage also occurred during the summer of 1978 (James Farnsworth, Park ranger, personal comments). A low total basal area value, infectious elm canopy trees, and increased understudy cover (O. virginiana) indicated this history.

Stand 9 is a southeast-facing plot located on a mid to upper slope. Based on species composition, it is the most xeric site. Q. macrocarpa is the dominant canopy species, with Q. alba present to a lesser degree. Of all thirty samples, it has the lowest climax adaptation number. Therefore, it is reasonable that in ordination analysis, this stand is either an endpoint or groups with xeric white oak stands.

In addition to the ordination and classification techniques used, species richness was determined for each stand (Appendix A). In general, east-facing slopes had the greatest average number of species (average = 49.3), and west-facing slopes had the lowest average (39). A beta diversity of 1.6 was calculated for basal area data.

Finally, basal area and total cover data sets were analyzed in each stand according to species importance. Correlation coefficients were calculated but did not provide a basis for comparison. Evaluation of ordination results using both data sets showed that basal area data represented stand composition better, while cover data tended to miss many species.

DISCUSSION

Central Iowa forest data were initially analyzed by classification techniques. This and stand similarity indices gave an indication of stand group. Only the most important tree species were used in dominance-type classification based on basal area, total cover, and field observations. Dominance-type distinguished those stands in which Q. alba and/or Q. borealis were important from those in which other species, such as F. americana, Q. muhlenbergii, and Q. macrocarpa, were important. Orloci agglomerative also separated white oak stand from more mesic sites and clustered those having a mixed oak composition (stands 2, 3, 7, and 11). Stands which did not fit any of these three oak patterns were left toward the center. Though dominance-type classification is subjective, when used with the agglomerative technique it is helpful in depicting general trends in the species composition of central Iowa forest.

Only tree species were used for classifications and ordinations since they accounted for the bulk of the biomass. Q. borealis (total area = 26%) and Q. alba (25%) accounted for just over half (51%) of the total forest tree species cover (based on basal area). A. nigrum (6%) and T. americana (12%) comprised another 18%; these species were generally admixed in the canopy with Q. borealis on mesic slopes.

In the understory, O. virginiana was ubiquitously distributed and accounted for 8% of the total tree cover. On mesic sites, A. nigrum occurred with O. virginiana; however, T. americana was very rarely found in the understory layer. C. ovata (constancy = 70%) and F. americana (constancy = 63%) were also common understory species with each covering 5% of the total area. Both species showed no particular pattern of distribution.

The distribution of herbs and shrubs has been shown to be affected by tree species (Curtis, 1959; Sanders, 1967; Cahayla-Wynne, 1976). Thus, O. virginiana and F. americana were widely distributed in the shrub layer. R. missouriensis and U. americana were also very common, but had larger cover values on xeric sites. So too, T. americana and A. nigrum were important species on mesic sites with A. arborea and C. cordiformis. Sanders (1967) found that the herbaceous layer in central Iowa followed the same trends as the tree species. In this study, certain herbaceous species were, also, characteristic of mesic situations as in northeast Iowa (Cahayla-Wynne, 1976). Likewise, there were species more common to xeric slopes. Finally, P. quinquefolia was found to be nonpreferential, occurring on all sites.

Aikman and Smelzer (1938) had said that oak-hickory communities had a greater number of dominant species than did maple-basswood communities. No patterns of species richness were readily distinguishable to support this claim. Rather, central Iowa forests seem to represent a mixture of these two communities as suggested by Braun (1947; 1950). A. nigrum and F. americana did associate on more mesic, north-facing slopes, as surmised by Aikman (1941) and Niemann (1977). Both Sanders (1969) and Kucera (1950; 1952), in studies of central Iowa, concluded that these two species admixed with Q. borealis on mesic slopes. Ordination and classification results of this study indicated the same. Studies by

Kucera (1950; 1952), Sanders (1967), and Niemann (1977) have reported Q. alba and Q. borealis admixed on xeric sites. Such was the composition of stands 2, 3, 7, and 11. This dominant effect of oak species in Iowa forest existed even prior to settlement (Dick-Peddie, 1955).

As previously stated, ordinations derived from both direct and indirect gradients provided a framework for comparison. RA was the first ordination technique applied. Results of this analysis compared well with that of PO ($r_s = .94$, $p < .0001$). Figure 13 showed that single axis ordinations for Reciprocal Averaging, Polar Ordination, Principal Components Analysis and Weighted Averages-climax adaptation also compared well. The pattern of three oak groups was apparent in direct and indirect gradient ordination techniques as well as in classification.

As suggested by Gauch, Whittaker, and Wentworth (1977), PO and RA have good results with a beta diversity of 1.6 half changes. Figure 11c presents a situation, however, that is common in ordination. Often the second axis of RA, when plotted against axis 3, causes involutions of the stand order, resulting in a clumping of samples near the origin. Though the beta diversity value is low, nonstandardized PCA and standardized PCA results did not agree with the previous two ordination techniques.

It was determined that in designating endpoints for PO, the criteria of Mueller-Dombois and Ellenberg (1974) produced clearer ordination than without the modification. In analyzing the presence of outliers (stands 4, 5, 8, and 9), PO ordinated these toward the center as was previously suggested (Gauch, Whittaker, and Wentworth, 1977). PCA ordinated these stands toward the center, too, as did RA with the exception of stand 9.

The position of other stands, however, did not seem to be much affected since upon removal of the outliers, the new ordinations were quite similar (Figure 14).

In all, PCA was not a preferred ordination technique. The need for applying standardizations and centering was both costly and time-consuming without enough benefits. It would also not be advantageous to use PCA without RA and PO, since comparisons would be necessary.

Species abundance curves (Figure 12) when plotted along the stand order for RA axis 1 supported the hypothesis of Gleason (1926; 1939) that species are distributed individualistically along gradients based on environmental characteristics and the specific properties of each species. T. americana and A. nigrum curves dropped as the relative abundance of Q. borealis decreased and Q. alba increased. Sanders (1969) and Cahayla-Wynne (1976) have found similar trends in their own studies in Iowa forest, supporting Gleason's hypothesis. As suggested by Whittaker (1967) and Curtis and McIntosh (1951), ordination results should help to demonstrate the continuum concept of vegetation and individualistic species concept of Gleason.

Aspect, position, and percent slope showed some effect on stand ordination, though elevation did not. When correlated with RA results (Table 4), WA-ASPO and WA-percent slope had values of $r_s = 44$ ($p < .0001$) and $r_s = .54$ ($p < .0001$), respectively. For PO and WA-ASPO, a correlation coefficient of $r_s = 57$ ($p < .0001$) was calculated.

Soil types and stand location with respect to the Des Moines lobe did not help explain species composition or ordination results. In fact, the Guthrie County sites and Berry Woods are located on the border and just south of the lobe. Silvers-Smith Woods is also borderline. Stands within these three sites responded independently of each other and regardless of soil type (Appendix A). For example, stand 1 from Berry Woods grouped with other xeric stands (27, 29, 30, etc.) from Woodman Hollow, Silvers-Smith Woods, the Ledges, and Pammel Woods. Stands 2 and 3, from Berry Woods, responded similarly to stand 7 and stand 11 from Dolliver State Park and Guthrie County. Though previous studies have concluded soil properties to be important factors in species composition, the soil information collected in this study perhaps was not sufficient to draw similar conclusions (Kucera, 1950; 1952).

SUMMARY

1. The vegetation of central Iowa forests was analyzed by classification and ordination techniques.

   a. Classification by dominance-type and Orloci agglomerative techniques produced similar results distinguishing stands dominated by Q. alba and/or or Q. borealis from all other stands.

   b. Reciprocal Averaging (RA), Polar Ordination (PO), Principal Components Analysis (PCA), and Weighted Averages (WA) were four ordination methods chosen. RA and PO were the most useful in describing the forest vegetation. Their results compared well, having a r_s = .94 (see Table 4). PCA was the least preferred method. Standardized-PCA and centered-PCA were not necessary to interpret the data, thus, PCA usage caused unnecessary computer expenses.

   c. Classification and ordination results distinguished stand composition by oak dominance. Three major oak groups were distinguished: stands dominated by Q. alba, stands dominated by Q. borealis, and stands in which both species were important.

   d. The three oak groups were more apparent when ordination results were repeated eliminating outlier stands 4, 5, 8, and 9.

2. The dominant effect of oak species in Iowa forests existed

prior to settlement. In this study, Q. alba, and Q. borealis comprised 51% of the total tree species cover. A. nigrum and T. americana accounted for another 18% generally occurring on more mesic sites.

3. Central Iowa tree species support the theory of Gleason (1926; 1939) that species are individually distributed along continuous gradients.

a. The relative abundance of T. americana and A. nigrum decrease with Q. borealis, as the relative abundance of Q. alba increases.

b. On mesic sites, Q. borealis is codominant with A. nigrum and T. americana. North-facing slopes dominated by A. nigrum represent the most mesic situations. On medium to xeric slopes, Q. borealis and Q. alba are codominant. The most xeric sites have Q. alba and/or Q. muhlenbergii and/or Q. macrocarpa as important species.

4. Aspect, position, and slope inclination had some effect on stand ordinations though elevation levels did not.

5. Soil information collected and stand location with respect to the Des Moines lobe did not facilitate explanation of species composition or ordination results.

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ACKNOWLEDGMENTS

The author wishes to express her thanks and appreciation to many people who have helped with the completion of this manuscript. Special thanks are extended to Dr. Robert H. Chapman and Dr. Lois H. Tiffany for their valuable advice, support, time, and encouragement throughout the course of my studies; to Dr. Sharron A. S. Bach-McCabe for her moral support; to Dr. Paul Hinz and Dr. George P. McCabe, Jr. for their statistical assistance; to Dr. Roger Q. Landers and Dr. David C. Glenn-Lewin for their advice during the early stages of my graduate career; to Dr. Glenn-Lewin for his contributions to the design of this project and loan of computer programs; and to Dean Roosa (State Ecologist), Mr. James Farnsworth (Park Ranger, Dolliver Memorial State Park), Dr. James Peck, and Dr. Donald Wysacki for providing pertinent field information.

Particular recognition is given to my fellow colleagues for their suggestions, contributions (both in the field and the lab), and support: Roger Laushman, Ann White, Howard Markus, and Mark Gabel.

Finally, sincere appreciation is extended to my family and friends for their faith in my abilities, especially my parents, Sharron, Kathie, Mac, Terry, Ann, and to Chip, for his unending confidence and patience.

APPENDIX A: STAND INFORMATION

Table A.1. Sample stands

Sample	Location	Aspect	Slope[a]	Position
1	Berry Woods	Level	7/15.6	upland
2	Berry Woods	S@ 200°	17/37.8	low-mid
3	Berry Woods	E@ 80°	11/24.4	low-mid
4	Berry Woods	NNE@ 30°	11/24.4	low-mid
5	Berry Woods	Level	5/11.1	upland
6	Diggings	N@ 355°	22/48.9	upland
7	Dolliver	S@ 200°	19/42.2	mid-slope
8	Dolliver	NW@ 300°	18/41.1	low-slope
9	Dolliver	SE@ 136°	7/15.6	mid-upper
10	Guthrie	S@ 295°	22-25/52.2	mid-slope
11	Guthrie	W@ 290°	23/51.1	low-slope
12	Guthrie	N@ 355°	13/28.9	mid-slope
13	Ledges	Level	0-6/6.7	upland
14	Ledges	NW	30/66.7	mid-slope
15	Ledges	W@ 280-290°	15-21/40	upland
16	Ledges	S@ 160°	26-28/60	upland
17	Ledges	E@ 100°	33/73.3	mid-upper
18	Ledges	NW	26/57.8	upland
19	Ledges	NE@ 45°	30/66.7	upland
20	Ledges	E@ 115°	29/64.4	low-mid
21	Ledges	SW	23/51.1	low-mid
22	Pammel	Level	8/17.8	upland
23	Pammel	SE@ 150°	10/22.2	mid-slope
24	Pammel	E@ 115-120°	15-20/37.8	mid-slope
25	Pammel	N@ 0°	17/37.8	low-slope
26	Pammel	N@ 20°	17-18/39.9	low-mid
27	Silvers-Smith	SW@ 250°	11/24.4	upland
28	Silvers-Smith	NW@ 330°	25/55.6	mid-slope
29	Woodman	SE@ 140°	9/20	mid-upper
30	Woodman	S@ 160°	38/84.4	mid-slope

[a]Degree of inclination/percentage slope.

[b]In meters.

[c]From United States Department of Agriculture, Soil Conservation Service, Soil Survey of the state of Iowa, by county.

Elevation[b]	Soil association[c]	Soil series[c]	Sample
277	Ladoga-Gara-Armstrong	Clinton	1
260	Ladoga-Gara-Armstrong	Gosport	2
253	Ladoga-Gara-Armstrong	Colo	3
260	Ladoga-Gara-Armstrong	Gosport	4
267	Ladoga-Gara-Armstrong	Gosport-Clinton	5
329	Storden-Hayden-Wadena	Hayden-Storden	6
314	Storden-Hayden-Wadena	Hayden-Storden	7
312	Storden-Hayden-Wadena	Hayden-Storden	8
305	Storden-Hayden-Wadena	Terril	9
344	Gara-Lindley	Lindley	10
344	Gara-Lindley	Lindley	11
296	Gara-Lindley	Gara	12
323	Hayden-Storden	Hayden	13
289	Hayden-Storden	Hayden-Storden	14
311	Hayden-Storden	Hayden-Storden	15
289	Hayden-Storden	Hayden-Storden	16
317	Hayden-Storden	Hayden-Storden	17
317	Hayden-Storden	Hayden-Storden	18
314	Hayden-Storden	Hayden-Storden	19
305	Hayden-Storden	Hayden-Storden	20
302	Hayden-Storden	Hayden-Storden	21
305	Hayden-Lester-Storden	Hayden	22
294	Hayden-Lester-Storden	Hayden	23
297	Hayden-Lester-Storden	Hayden	24
296	Hayden-Lester-Storden	Hayden	25
297	Hayden-Lester-Storden	Hayden	26
289	Clarion-Nicollet-Webster	Hayden-Storden	27
289	Clarion-Nicollet-Webster	Hayden	28
327	Storden-Hayden-Wadena	Hayden	29
320	Storden-Hayden-Wadena	Hayden-Storden	30

Table A.1. (Continued)

Sample	Parent material[c]	Drainage[c]	Permeability	Native vegetation
1	loess	mod-well	mod-slow	trees
2	residuum	well	very slow	trees
3	alluvium	poor	mod-slow	prairie
4	residuum	well	very slow	trees
5	loess	well-mod	very mod-slow	trees
6	glacial till	well	moderate	forest-pr[g]
7	glacial till	well-excess	mod-rapid	trees
8	glacial till	well-excess	mod-rapid	trees
9	sand residuum	well-excess	mod-rapid	trees-pr
10	glacial till	mod-well	mod-slow	trees
11	glacial till	mod-well	mod-slow	trees
12	glacial till	mod-well	mod-slow	trees-pr
13	glacial till	well	moderate	forest
14	glacial till	well	moderate	forest-pr
15	glacial till	well	moderate	forest-pr
16	glacial till	well	moderate	forest-pr
17	glacial till	well	moderate	forest-pr
18	glacial till	well	moderate	forest-pr
19	glacial till	well	moderate	forest-pr
20	glacial till	well	moderate	forest-pr
21	glacial till	well	moderate	forest-pr
22	glacial till	well	moderate	forest
23	glacial till	well	moderate	forest
24	glacial till	well	moderate	forest
25	glacial till	well	moderate	forest
26	glacial till	well	moderate	forest
27	glacial till	well	moderate	forest-pr
28	glacial till	well	moderate	forest
29	glacial till	well	moderate	forest
30	glacial till	well	moderate	forest-pr

[d]Dominance type based on basal area (cm^2/0.1 ha) and cover data. QA = *Quercus alba*, QB = *Quercus borealis*, QM = *Quercus macrocarpa*, QMu = *Quercus muhlenbergii*, AN = *Acer nigrum*, FA = *Fraxinus americana*, TA = *Tilia americana*.

[e]Weighted averages using weights for aspect (Table 3) x weights for position (Table 2).

[f]Weighted averages using weights for tree species (Table 1).

[g]Forest-prairie.

Species richness	Dominance type[d]	ASPO[e]	Climax adaptation number[f]	Sample
52	QA	9.0	4.5	1
57	QA-QB	17.5	5.2	2
50	QA-QB	10.0	5.3	3
61	FA	2.5	7.0	4
59	QB-FA	9.0	5.9	5
24	AN	1.0	8.8	6
45	QA-QB	14.0	5.4	7
54	QA-QB	9.0	7.1	8
37	QA-QM	9.0	3.3	9
35	QB-TA	10.0	6.5	10
37	QA-QB	15.0	6.6	11
42	QB	2.0	6.6	12
34	QA	9.0	5.0	13
44	AN-QB	6.0	7.6	14
45	QB	5.0	6.2	15
51	QB-QMu	7.0	6.1	16
50	QB-TA	7.0	7.2	17
52	QB-TA	3.0	7.5	18
49	QB	2.0	6.6	19
51	QB	10.0	6.0	20
47	QB-TA	20.0	7.2	21
36	QA	9.0	4.7	22
56	QA	12.0	5.5	23
46	QA	8.0	4.7	24
43	QB	3.0	6.8	25
53	QB-AN-TA	2.5	7.3	26
40	QA	8.0	4.0	27
47	QB	6.0	9.7	28
43	QA	9.0	4.4	29
43	QA	14.0	5.0	30

APPENDIX B: TREE BASAL AREA

Table B.1. Basal area data[a]

	Stand 1	Stand 2	Stand 3	Stand 4
Acer negundo				
Acer nigrum				
Aesculus octandra				1678.5
Amelanchier arborea				
Carpinus caroliniana				
Carya cordiformis		23.8		4541.5
Carya ovata	59.0			3952.4
Celtis occidentalis		157.1	300.8	
Crataegus spp.				
Fraxinus americana	1771.3		3487.9	5539.2
Fraxinus nigra				
Fraxinus pennsylvanica				
Gleditsia triacanthos				1378.9
Juglans nigra			1562.3	1281.0
Juniperus virginiana				
Morus rubra				
Ostrya virginiana		1405.1	1303.1	5289.1
Populus deltoides				
Populus tremeloides				
Prunus serotina			73.9	
Prunus virginiana		86.6		
Quercus alba	30435.8	15772.6	8663.2	346.4
Quercus borealis	2206.2	8353.3	6202.2	
Quercus macrocarpa			3087.6	
Quercus muhlenbergii				
Quercus velutina		4156.4		
Tilia americana	613.0	6188.3	4303.0	1727.4
Ulmus americana		156.4	103.5	232.4
Ulmus rubra	1042.0		69.4	
TOTAL STAND BASAL AREA:	36127.2	36299.6	30464.3	25967.7

[a] cm^2.0.1 ha.

Stand 5	Stand 6	Stand 7	Stand 8	Stand 9	Stand 10
	9261.6		243.3	331.9	
		195.2	44.2		
					51.2
	5473.7				240.5
764.7	158.4	3376.3			2770.5
95.8					
3635.2		2978.5	993.9	93.0	13.6
				105.7	
2323.2					
363.1					
881.3	2497.9	1742.1	5672.6	3975.5	2686.0
2642.1					
130.3			51.5	138.9	
		25.5			
		8140.3	2679.0	6227.8	3257.6
2828.8	2780.5	6344.8	3023.9		10886.3
228.4				12731.3	
1210.6				1824.7	
2549.8	824.7		597.3		6967.7
			3293.9	329.6	
2866.9					306.0
20157.1	20996.8	22802.7	16599.6	25758.2	26479.4

Table B.1 (Continued)

	Stand 11	Stand 12	Stand 13	Stand 14
Acer negundo				
Acer nigrum			196.2	6760.1
Aesculus octandra				
Amelanchier arborea			59.5	
Carpinus caroliniana				171.5
Carya cordiformis	846.0	611.9		
Carya ovata		452.4	3610.7	
Celtis occidentalis		814.3		
Crataegus spp.				
Fraxinus americana			1863.7	53.4
Fraxinus nigra				
Fraxinus pennsylvanica				
Gleditsia triacanthos				
Juglans nigra				886.7
Juniperus virginiana				
Morus rubra				
Ostrya virginiana	2423.0	3002.7	453.2	2761.5
Populus deltoides				
Populus tremeloides				914.5
Prunus serotina	263.0	1947.6		107.5
Prunus virginiana				
Quercus alba	10561.4		15487.2	
Quercus borealis	8999.8	17157.0	1400.5	8611.1
Quercus macrocarpa	1492.9			
Quercus muhlenbergii				
Quercus velutina				
Tilia americana		4509.2	3444.8	3397.4
Ulmus americana	5095.8	5956.6		
Ulmus rubra				
TOTAL STAND BASAL AREA:	24696.6	34451.7	26515.8	23556.2

Stand 15	Stand 16	Stand 17	Stand 18	Stand 19	Stand 20
	1806.2	3754.6	2018.1	4299.7	391.2
250.5	28.3				96.2
	1113.7	186.3			
1818.7	1185.2	224.3		158.4	
1665.2			339.8	984.2	1589.4
	56.7				
2098.4	836.1	471.0	1834.7	1011.3	371.2
2737.5	1429.6		1149.1	271.7	4764.1
12719.3	3777.2	16523.0	4713.8	23164.5	10110.4
				881.4	
	3921.9			779.3	1993.8
2696.2	1500.1	13803.4	8693.3	2803.2	6559.9
742.7		1365.7		1856.2	
25091.6	14655.0	36413.3	19202.8	36831.7	25876.2

Table B.1 (Continued)

	Stand 21	Stand 22	Stand 23	Stand 24
Acer negundo				
Acer nigrum	3530.7	70.9	980.0	1025.1
Aesculus octandra				
Amelanchier arborea				
Carpinus caroliniana				
Carya cordiformis	846.0	33.2	1403.0	1074.8
Carya ovata	363.8	1378.1	2056.4	1330.5
Celtis occidentalis				
Crataegus spp.				
Fraxinus americana	2162.5	1158.1	3086.5	
Fraxinus nigra	594.0			
Fraxinus pennsylvanica				
Gleditsia triacanthos				
Juglans nigra	978.7			1104.5
Juniperus virginiana				
Morus rubra				
Ostrya virginiana	529.3	1222.5	1949.4	2602.9
Populus deltoides				
Populus tremeloides				
Prunus serotina		70.9		107.5
Prunus virginiana				
Quercus alba	1640.0	16306.6	8887.5	14605.6
Quercus borealis	6889.9	2284.3		602.6
Quercus macrocarpa			1445.3	1513.4
Quercus muhlenbergii				
Quercus velutina				2401.8
Tilia americana	8250.3		268.8	
Ulmus americana	5095.8			70.9
Ulmus rubra				
TOTAL STAND BASAL AREA:	30881.0	22524.6	20076.9	26503.1

Stand 25	Stand 26	Stand 27	Stand 28	Stand 29	Stand 30
	142.0				
1418.1	5625.2		907.9		151.4
	730.6				
			2031.1		93.5
1818.7	1241.3	3049.9		6989.8	1426.1
	3838.8				37.4
2289.3					
					87.7
1994.0	875.0	1621.9	2300.8	835.4	2817.7
			834.7		
		12573.5	2613.4	9233.4	13836.5
8659.6	3379.9		15928.7	2682.1	3952.7
1318.2	1527.5				
2550.9	3764.7		6469.3		36.3
51.9				640.6	
18281.6	21181.6	19037.0	31085.9	20380.7	22439.3

APPENDIX C: SPECIES LIST

Nomenclature follows Gleason and Cronquist (1963) except the grasses which follow Pohl (1966).

Pteridophyta
- Ophioglossaceae
  - *Botrychium virginianum*
- Polypodiaceae
  - *Adiantum pedatum*
  - *Cystopteris fragilis*
  - *Onoclea sensibilis*

Spermatophyta
- Gymospermae
  - Cupressaceae
    - *Juniperus virginiana*
- Angiospermae
  - Monocotyledonae
    - Araceae
      - *Arisaema Dracontium*
      - *Arisaema triphyllum*
    - Cyperaceae
      - *Carex blanda*
      - *Carex Davisii*
      - *Carex pennsylvanica*
      - *Carex rosea*
    - Dioscoreaceae
      - *Dioscroea villosa*
    - Gramineae
      - *Bromus pubescens*
      - *Cinna arundinaceae*
      - *Diarrhena americana*
      - *Festuca obtusa*
      - *Glyceria striata*
      - *Hystrix patula*
      - *Panicum latifolium*
    - Liliaceae
      - *Allium tricoccum*
      - *Erythronium albidum*
      - *Polygonatum biflorum*
      - *Polygonatum pubescens*
      - *Smilacina racemosa*
      - *Smilacina stellata*
      - *Smilax herbacea*
      - *Smilax hispida*
      - *Uvularia grandiflora*

Dicotyledonae

Aceraceae

Acer negundo
Acer nigrum

Anacardiaceae

Taxicodendron radicans

Araliaceae

Aralia nudicaulis

Aristolochiaaceae

Asarum canadense

Balsaminaceae

Impatiens pallida

Berberidaceae

Podophyllum peltatum

Betulaceae

Carpinus caroliniana
Corylus americana
Ostrya virginiana

Caesalpiniaceae

Gleditisia triacanthos

Campanulaceae

Campanula americana

Caprifoliaceae

Lonicera tatarica
Sambucus canadensis
Symphoricarpos orbiculatus
Triostem perfoliatum
Viburnum Rafinesquianum

Caryophyllaceae

Silene stellata

Celastraceae

Euonymus alatus

Compositae

Antennaria neglecta
Aster cordifolius
Aster ericoides
Eupatorium maculatum
Eupatorium rugosum
Helianthus strumosus
Helianthus tuberosus
Prenanthes alba
Solidago flexicaulis
Solidago rugosa

Cornaceae

Cornus alternifolia
Cornus Drummondi
Cornus rugosa

Fabaceae

Amphicarpa bractèata
Desmodium glutinosum

Fagaceae
- *Quercus alba*
- *Quercus borealis*
- *Quercus macrocarpa*
- *Quercus muhlenbergii*
- *Quercus velutina*

Fumariaceae
- *Dicentra cucullaria*

Geraniaceae
- *Geranium maculatum*

Hippocastanaceae
- *Aesculus octandra*

Hydrophyllaceae
- *Hydrophyllum virginianum*

Juglandaceae
- *Carya cordiformis*
- *Carya ovata*
- *Juglans nigra*

Menispermaceae
- *Menispermum canadense*

Moraceae
- *Morus rubra*

Oleaceae
- *Fraxinus americana*
- *Fraxinus nigra*
- *Fraxinus pennsylvanica*

Onagraceae
- *Circeae quadrisulcata*

Oxalidaceae
- *Oxalis stricta*

Papaveraceae
- *Sanguinaria canadensis*

Phyrmaceae
- *Phyrma leptostachya*

Polemoniaceae
- *Phlox divaricata*

Portulacaceae
- *Claytonia virginica*

Ranunculaceae
- *Actaea alba*
- *Anemone cylindrica*
- *Anemone quinquefolia*
- *Anemonella thalictroides*
- *Aquilegia canadensis*
- *Hepatica acutiloba*
- *Isopyrum biternatum*
- *Ranunculus abortivus*
- *Ranunculus cymbalaria*
- *Ranunculus repens*
- *Thalictrum dioicum*

Rhamnaceae
- *Ceanothus americanus*
- *Rhamnus catharticus*

Rosaceae
- *Agrimonia pubescens*
- *Amelanchier arobrea*
- *Crataegus* spp.
- *Fragaria virginiana*
- *Geum canadense*
- *Prunus serotina*
- *Prunus virginiana*
- *Rubus allegheniensis*
- *Rubus occidentalis*

Rubiaceae
- *Galium circaezans*
- *Galium triflorum*

Rutaceae
- *Zanthoxylum americanum*

Salicaceae
- *Populus deltoides*
- *Populus tremuloides*

Saxifragaceae
- *Mitella diphylla*
- *Ribes missouriense*

Staphylaceae
- *Staphylea triflorum*

Tiliaceae
- *Tilia americana*

Ulmaceae
- *Celtis occidentalis*
- *Ulmus americana*
- *Ulmus rubra*

Umelliferae
- *Cryptotaenia canadensis*
- *Osmorhiza Claytone*
- *Osmorhiza longistylus*
- *Sanicula canadensis*
- *Sanicula gregaria*
- *Sanicula marilandica*

Urticeae
- *Boehmeria cylindrica*
- *Laportea canadensis*
- *Pilea pumila*
- *Urtica dioica*

Violaceae
- *Viola pennsylvanica*
- *Viola* spp.

Vitaceae
- *Parthenocissus quinquefolia*
- *Vitis riparia*