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The Coastal Plain Floristic Element in Michigan

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THE COASTAL PLAIN
FLORISTIC ELEMENT IN MICHIGAN

by

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INTRODUCTION

The Coastal Plain Province of the eastern United States is remarkable for the presence of a large number of vascular plants with tropical affinities (Fernald, 1931). Possibly even more remarkable is the discovery of some of these Coastal Plain species in the predominantly temperate flora of the Midwest. Yet, collectors in Michigan, Indiana, Illinois, and Wisconsin are frequently rewarded with finds of disjunct Coastal Plain species. Two of the most striking examples, Eleocharis tricostata and Psilocarya nitens, are restricted to the Coastal Plain except for a single location of each in the Midwest, and both of these sites have been destroyed as a result of recent construction activities. Several other similarly disjunct species are known, and in Michigan where I have studied them they are most frequently found on certain lake shores in the southwestern corner of the state. The two most significant efforts to explain their presence in the Midwest were published in 1922 and 1932. Since then much information on these coastal species in Michigan has accumulated, and this study was begun to incorporate that material into a hypothesis explaining the history and persistence of the Coastal Plain element in the Midwest.

The Coastal Plain and Its Flora

The Coastal Plain is a physiographic province that extends from Cape Cod in the north to Mexico in the south. Except for

the peninsula of Florida and the Mississippi Embayment it is a narrow lowland. Cretaceous and Tertiary clays, silts, and sands form the distinctive soil of the Coastal Plain which is bordered on the landward side by older metamorphic rocks of the Appalachian uplands in the east and southeast and by prairies and plateaus further west (Fenneman, 1938). Although the transition from the Coastal Plain to the surrounding upland is not usually abrupt (Bowman, 1911), the soft ocean-deposited sands impart a distinctly acid soil to many areas of the coastal region. This accounts, in part, for the distinctness of its flora (Fernald, 1942a).

An enumeration of some of the more characteristic species of the Coastal Plain includes such trees as *Pinus palustris*,[1] *Pinus serotina*, *Taxodium distichum*, *Carya aquatica*, *Quercus laevis*, *Q. virginiana*, *Q. cineria*, *Asimina parviflora*, *Ilex vomitoria*, *Nyssa aquatica*, and *Fraxinus caroliniana* (Fernald, 1942a; Little, 1971) and such herbs as *Sagittaria weatherbiana*, *Panicum aciculare*, *Sacciolepis striata*, *Axonopus furcatus*, *Ctenium aromaticum*, *Manisuris rugosa*, *Scirpus divaricatus*, *Xyris flexuosa*, *Eriocaulon decangulare*, and *Lobelia elongata* (Fernald, 1942a). Others of the hundreds of characteristic species and reference to some additional features of the Coastal Plain flora have been given

[1]Author citations are omitted in the text as all names are according to the 8th edition of *Gray's Manual of Botany* (Fernald, 1950) unless otherwise indicated. The authorities for two names should, however, be corrected to read *Fuirena pumila* Spreng (cf. Voss, 1972) and *Rhynchospora macrostachya* Torr. ex Gray (cf. Rickett and Gilly, 1942).

by Bowman (1911), Braun (1950), Fernald (1937), Gleason and Cronquist (1964), Harshberger (1911), and others.

Disjunctions of the Coastal Plain Flora

There exist two basic types of westward disjunction of Coastal Plain plants (Cain, 1944). The first is the occurrence of typically lowland plants on the Appalachian uplands, and the second is the presence of Coastal Plain species in the Midwest. The former has been explained by Harper (1905) as recent inland migrations from the coastal regions where the disjunct species are now abundant. However, Braun (1937a, 1937b, 1950), Cain (1944), Fernald (1931, 1937), Harshberger (1904), Kearney (1897, 1900), Small (1924), and Steyermark (1953) feel that the Coastal Plain element on the highlands is a relict from a time when the Appalachians consisted of a peneplain and were covered by a more temperate to subtropical flora. This has been restricted to the more moderate lowlands by climatic deterioration. The second type of disjunction is not, however, amenable to such an explanation due to the existence of the disjunct species in glaciated territory. It has been discussed, at length, by Peattie (1922) and McLaughlin (1932) and mentioned by numerous others (cf. the following discussion). No analysis of the problem based on an understanding of the distribution and ecology of the species in Michigan has, however, been undertaken.

METHODS

Field studies were conducted over a period of two summers during which nine southern Michigan counties and approximately 50 lakeshores were visited. At 31 of these lakes species disjunct from the Coastal Plain were collected (Table 1). At the approximately 20 additional lakes visited the disjunct species were not found. Impressions of ecologic differences between lakes where the disjunct species are present and lakes where they are absent were, however, useful in drawing conclusions. A complete set of more than 300 collections of vascular plants made at these lakes is deposited in the Hanes Herbarium (WMU); partial sets are deposited at MICH and RM. (Herbarium abbreviations are according to Lanjouw and Stafleu [1962].) At several locations mass collections were made of fruiting portions of Coastal Plain species. Specimens of *Eleocharis melanocarpa*, *Fuirena pumila*, *Psilocarya scirpoides*, and *Rhynchospora macrostachya* were grown in the greenhouse.

Distribution data were recorded from specimens at the following herbaria: COLO, MICH, MSU, RM, and WMU. Additional distribution records were supplied by E. G. Voss. A partial list of all records seen is in Appendix 1.

Soil samples collected at nine lakes were taken at a depth of five to ten centimeters from the base of individual Coastal Plain species. Soil *pH* was determined with a La Motte soil *pH* kit, and physical characteristics of the soil were determined by scoring

Table 1. Location, glacial surface features, and elevation for 31 Michigan collection sites of Coastal Plain disjuncts.

Location	Geologic formation #	Elevation in feet *
Augustine Lake Mason Co. T17N, R15W, N½ sect. 36	moraine	740
Houseman Lake Newaygo Co. T16N, R14W, SE¼ sect. 9	outwash plain	854
unnamed lake, Merrill Twp. Newaygo Co. T15N, R13W, W½ sect. 36	outwash plain	950
Fry Lake Newaygo Co. T13N, R12W, W½ sect. 23	moraine	875
Wood Lake Muskegon Co.	outwash plain	670
Pine Island Lake Muskegon Co. T12N, R15W, S½ sect. 19	outwash plain	689
drying lakebed, Holton Twp. Muskegon Co. T12N, R15W, N½ sect. 30	outwash plain	690
Deer Lake (Unger Lake) Muskegon Co. T12N, R15W, N½ sect. 29	outwash plain	681
Burns Lake Muskegon Co. T12N, R16W, SE¼ sect. 25	outwash plain	678

Table 1. Continued

Location	Geologic formation #	Elevation in feet *
Little Blue Lake Muskegon Co. T12N, R16W, NW¼ sect. 33	outwash plain	660
Twin Lakes Muskegon Co. T11N, R16W, N½ sect. 12	outwash plain	676
Arbutus Lake (Hidden Lake, Lost Lake) Muskegon Co. T10N, R17W, SW¼ sect. 16	interdunal (on bed of Lake Algonquin)	600
Carr Lake Muskegon Co. T10N, R15W, NW¼ sect. 32	bed of Lake Algonquin	657
One of "Five Lakes", east of Carr Lake Muskegon Co. T10N, R15W, N½ sect. 32	bed of Lake Algonquin	657
Little Bostwick Lake Kent Co. Cannon Twp. sect 14	moraine	---
Dean Lake Kent Co. T8N, R11W, SW¼ sect. 34	at edge of Grand River drainage channel	705
"East Beltline Pond" Kent Co. T7N, R11W, NW¼ of SW¼ sect. 2	moraine	750
Daggett Lake (Ludlow Lake) Barry Co. T2N, R10W, NW¼ sect. 1	moraine	939

Table 1. Continued

Location	Geologic formation #	Elevation in feet *
Otis Lake Barry Co. T3N, R9W, NE¼ sect. 31	moraine	855
Mud Lake Barry Co. T1N, R9W, SE¼ sect. 8	moraine (on edge of outwash plain)	928
drying lake bed, Clyde Twp. Allegan Co. T2N, R15W, S½ sect. 24	bed of Lake Algonquin	680
Ely Lake Allegan Co. T2N, R15W, NE¼ sect. 26	bed of Lake Algonquin	675
Crooked Lake Allegan Co. T2N, R15W, SE¼ sect. 25 & NE¼ sect. 36	bed of Lake Algonquin	670
Stony Lake Kalamazoo Co. T1S, R9W, Sect. 15 & Sect. 25	outwash plain	852
Eagle Lake Kalamazoo Co. T3S, R12W, NW¼ sect. 16	outwash plain	898
Pretty Lake Kalamazoo Co. T3S, R12W, NE¼ sect. 20	outwash plain	901
Austin Lake Kalamazoo Co. T3S, R11W, sect. 36.	outwash plain (on edge of ponded glacial lake)	855

Table 1. Continued

Location	Geologic formation #	Elevation in feet *
Keeler Lake Van Buren Co. T4S, R16W, E½ sect. 23	outwash plain	778
Bankson Lake Van Buren Co. T4S, R13W, N½ sect. 14	moraine	898
Dewey Lake Cass Co. T5S, R16W, N½ sect. 9	moraine (on edge of outwash plain)	764
Island Lake Washtenaw Co. T1S, R3E, sect. 23	moraine	950

Data from Martin (1955).

* Data from United States Geologic Survey topographic maps.

samples as pure sand, 25% peat, 50% peat, 75% peat, or pure peat. Water hardness was determined at one location using a Hach portable water engineer's laboratory.

A community ordination was constructed using presence/absence data in the 2W/(a+b) formula described by Bray and Curtis (1957), Cox (1972), and Greig-Smith (1964). Eleven species (cf. Appendix 2) were chosen on the basis of literature reports, herbarium records, and field experience as being common on shores with disjunct Coastal Plain species and rare elsewhere in Michigan, and presence of these was used in computing dissimilarity values. The matrix of dissimilarity values for the ordination was generated by a BASIC computer program (Appendix 2) on a time-sharing SIGMA 7 computer. Ten of the 31 communities visited were not used in the ordination as it was determined that they were consistently very dissimilar to other communities and that this dissimilarity was an artifact of a lack of collecting on their shores.

HISTORICAL AND LITERATURE REVIEW

Reports of Coastal Plain Plants in the Midwest

The first record of a midwestern disjunction of a Coastal Plain species was Fuirena squarrosa from Cass County, Michigan (Wright, 1839, cf. Fuller, 1928). The significance of this report was, however, not recognized until 1899 when Hill reported the association of several similar disjuncts near the south end of Lake Michigan in Indiana. He noticed the apparent anomaly of this distribution pattern and the affinity of the species with the Atlantic Coastal Plain flora. Among the species reported by Hill were Eleocharis melanocarpa (first reported a year earlier by Hill), Panicum verrucosum, Scleria torreyana Walp. (a synonym for S. muhlenbergii), Psilocarya nitens, P. scirpoides, Rhynchospora macrostachya, Fuirena squarrosa (Midwestern plants are the annual phase F. pumila.), and Juncus scirpoides. This report also listed Scleria reticularis, but Hill did not mention its disjunct nature.

The same year that Hill reported these Indiana stations additional records of Coastal Plain species in Michigan began to appear. Wheeler (1899) cited a collection of Psilocarya scirpoides by Emma Cole in Kent County. Rhynchospora macrostachya and Fuirena pumila were also collected but not reported until the publication of Grand Rapids Flora (Cole, 1901). For the next thirty years, however, the record of Coastal Plain plants in Michigan was relatively stagnant. Table 2 summarizes the Michigan record for

Table 2. Records of the occurrence of five Coastal Plain species in Michigan.

Species	Counties												
	Allegan	Barry	Berrien	Cass	Emmett	Kalamazoo	Kent	Macomb	Mason	Muskegon	Newaygo	Van Buren	Washtenaw
<u>Eleocharis</u> <u>melanocarpa</u>	0	0		X		0	x			x	0	x	
<u>Fuirena</u> <u>pumila</u>	0	0		X		0	X	X?		0		0	0
<u>Psilocarya</u> <u>scirpoides</u>	0	0			x	0	X			x	0	0	0
<u>Rhynchospora</u> <u>macrostachya</u>	0	0	X	x		0	X		0	0	0	X	
<u>Scleria</u> <u>reticularis</u>	0		0?										

0 Recorded since 1930
x Recorded by herbarium specimen before 1930
X Recorded in literature before 1930
? Questionable record

Sources: Beal, 1908; Wright, 1839 cf. Fuller, 1928; Wheeler & Smith, 1881; Cole, 1901.

five disjunct Coastal Plain species until 1930 and indicates the relative abundance of collections in the following years. It shows that for the 1900 to 1930 period only three additional records of the five species were reported in the literature (Beal, 1908). The Macomb County record for Fuirena pumila given by Wheeler and Smith (1881) is not supported by a known herbarium record and is not reported in Part 1 of the Michigan Flora (Voss, 1972).

In the 1930's Hanes and Bazuin began active field work in southwestern Michigan and added much to our present knowledge of Coastal Plain species in the Midwest. Hanes (1942) listed 54 members of the Atlantic Coastal Plain element in Kalamazoo County but was strongly criticized by Fernald (1942) for certain inaccuracies and for dubious phytogeograpic judgement. In 1947 he was more conservative and named considerably fewer plants as members of this element (Hanes and Hanes, 1947). In addition to adding to an understanding of the extent of Coastal Plain species in Kalamazoo County and providing many distribution records for Michigan, Hanes (1947; Hanes and Hanes, 1947) gives a clear description of the habitat of Rhynchospora macrostachya and recognizes its requirement for a fluctuating water level. Bazuin (1947, 1948) who collected Coastal Plain species in Kent, Muskegon, and Allegan Counties added substantially to the record of these rare species by reporting both his own collections and overlooked records in Michigan herbaria. No other work either deals specifically with these plants in Michigan or discusses them in any detail. However, Voss (1957a, 1957b, 1972) has commented at

length on their distribution within the State and noted some of their ecologic peculiarities.

Discussions of the Coastal Plain species in Indiana have been more numerous. Hill (1899) listed some of them and recognized their affinities. In 1922 Peattie listed 60 Coastal Plain plants occurring in the Indiana dunes area and gave a widely accepted interpretation of their arrival and persistence. Three years later Deam indicated that northwestern Indiana contained 21 Atlantic coast species; he listed 14 of these. Hoober (1934) gave their number in the Indiana dunes area as 74 species. Parker (1936) named 15 Indiana species with Coastal Plain affinities. These reports, through 1936, were summarized by Friesner (1937). Lamerson (1950), combining lists of plants given by seven others, listed 207 species, varieties, and forms of Coastal Plain plants found in Indiana most of which are in the dunes and lakes area of the northwest corner of the state!

Few of these reports of the Indiana flora, however, are more complete or accurate than the record of these species as provided by Hill (1899), Deam in Indiana Flora (1940), and Swink in Plants of the Chicago Region (1969). Although Deam and Swink do not address themselves directly to phytogeographic problems, their maps and comments under the various species are invaluable for understanding the distribution and ecology of these plants.

Two additional works deserve special mention in relation to the Indiana dunes area. Both Peattie (1930) and Pepoon (1927) mention the Coastal Plain element and include specific localities

for the species. Pepoon, in a thorough discussion of the interdunal lakes, made a significant contribution by providing information on the conditions necessary for the survival of such species as Eleocharis melanocarpa, Scleria reticularis, Rhynchospora macrostachya, and Psilocarya scirpoides, some of the most strikingly disjunct Coastal Plain plants.

Beyond the burst of interest in the Coastal Plain plants expressed in the 1930's and 1940's few writers have shown more than a passing interest in the arrival, persistence, and distribution of this element in the Midwest. Cain (1944) and Cushing (1965) summarized the situation and Curtis (1959) devoted a few lines to the subject but none of these added anything new. Most recently Harvill (1969) listed 25 species present in Virginia with disjunct populations in the Midwest. A few others have cited newly discovered Coastal Plain species in the Midwest: Winterringer (1959) reported Lipocarpha maculata associated with Scleria reticularis in Cass County, Illinois, and commented briefly on its ecology. Hartley (1965, 1966) discussed Thelypteris simulata in the Driftless Area of Wisconsin and gave some credibility to the possibility of arrival via long distance dispersal. And Hagenah and Wagner (1971) in a paper presented at the 75th annual meeting of the Michigan Academy of Science discussed Lycopodium appressum in Michigan.

Explanation of the Phenomenon

Based only on the scanty distribution records of the period

prior to 1930 (cf. Table 1) two workers attempted to explain the presence of the Coastal Plain plants in the Midwest (Peattie, 1922; McLaughlin, 1932). Peattie based his discussion on two premises: first, that Coastal Plain species occur on the shores of extant or extinct glacial Great Lakes and/or on glacial drainage channels, and, second, that a single explanation can account for the presence of all of the Coastal Plain species in the Midwest. McLaughlin agreed with both of these ideas.

Peattie came to the first premise by noting the presence of Coastal Plain species (1) on or near the dune formations at the southern end of Lake Michigan, (2) on the former Grand River drainage channel of Glacial Lake Chicago, (3) at the outflow of Lake Huron near Port Huron, (4) near the shores of Saginaw Bay in the vicinity of the St. Claire River outlet which served all of the glacial Great Lakes systems, (5) along the Illinois and Kankakee Rivers, and (6) in the Ottawa River Valley. His second premise was that a single explanation can account for the distribution of species as ecologically diverse as Euphoriba poygonifolia and Eleocharis melanocrapa. The former species is a plant of "sea strands" which also "occurs in a general way around the Great Lakes" (Peattie, 1922:59) but only on Great Lakes beaches, while the latter was known to Peattie only from the ponds and "sloughs" in the dunes at the southern end of Lake Michigan and from similar ponds on the Coastal Plain.

McLaughlin (1932) attempted to explain the presence of several Coastal Plain species in the Barrens Lake region of northwestern

Wisconsin by accepting Peattie's hypothesis and expanding it in two ways. First, he more firmly stated that glacial drainage features were the probable migratory routes, and that the species were distributed by water via "marginal eddy currents which may carry drift for considerable distances upstream" (McLaughlin, 1932:368). Second, he presented a description of some of the ecological factors necessary for the survival of Coastal Plain species and an explanation of local distribution patterns based on those requirements.

Criticism of the Explanations

In 1942 Fernald leveled a criticism at various attempts to explain the presence of Coastal Plain species in the Midwest. The basis of his criticism is brief enough and important enough to an understanding of Peattie's and McLaughlin's hypothesis that a detailed summary is appropriate. With his usual candor, Fernald (1942a:242) stated that most discussions of "Atlantic Coastal Plain Plants in the Flora of 'Here-and-There'" have erred by including species of other affinities. He indicated that the phytogeographic histories of the species included are probably as varied as the floristic elements that they represent.

Some of the plants discussed by others as Coastal Plain species, but without Coastal Plain affinities are (1) northern plants, some circumboreal, with southern extensions on the Coastal Plain; e.g., <u>Lycopodium inundatum</u>, <u>Muhlenbergia uniflora</u>,

Rhynchospora fusca, R. alba, Eriocaulon septangulare, Juncus pelocarpus, J. articulatus, and J. balticus var. littoralis; (2) rather generally distributed plants of the eastern United States appearing wherever suitable habitats occur both off and on the Coastal Plain; e.g., Stipa avenacea and Echinochloa walteri; (3) plants entirely absent from the Coastal Plain; e.g., Eleocharis pauciflora and Carex richii; (4) plants of halophytic soils distributed throughout the United States; e.g., Eleocharis rostellata; (5) plants generally distributed in the United States but more common on the Coastal Plain; e.g., Hemicarpha micrantha; and (6) plants found on granitic rock of higher elevations and latitudes than the Coastal Plain; e.g., Juncus greenii.

Table 3 lists 24 species that were considered by Peattie as Coastal Plain species but which have other phytogeographic affinities. This list represents more than one-fourth of the 90 species Peattie listed as members of the Coastal Plain element. It also represents high percentages of the species supposed to be relicts of migration of the Coastal Plain flora along glacial drainage features: for Lake Ontario 86%; for Lake Erie 33%; for the Detroit and St. Clair Rivers, Lake St. Claire, and Port Huron 79%; and for Saginaw Bay 58%. In fact, the number of Coastal Plain plants at all of these locations is much lower than that suggested by Peattie.

In addition to those in Table 3, there are in Peattie's list of 90 Coastal Plain species others like Linaria canadensis and Hydrocotyle umbellata which appear basically to have a Coastal

Table 3. Distribution patterns of some species listed as Coastal Plain species by Peattie (1922).

species	actual distribution pattern	source of distribution data
Woodwardia virginica	eastern U. S.	Fernald, 1950
Echinochloa walteri	eastern U. S.	Gould et al., 1972
Ammophila breviligulata	littoral	Fernald, 1950 Guire and Voss, 1963
Eleocharis quadrangulata	eastern U. S.	Svenson, 1939
Fimbristylis autumnalis	eastern U. S.	Kral, 1971
Scirpus Smithii	eastern North America	Fernald, 1950 Muenscher, 1944
Hemicarpha micrantha	throughout U. S. and South to tropics	Fernald, 1942a
Rhynchospora fusca	northern	Fernald, 1942a
Carex exilis	northern	Fernald, 1942a
Peltandra virginica	eastern North America	Fernald, 1950 Muenscher, 1944
Juncus balticus var. *littoralis*	northern	Fernald, 1942a
Juncus articulatus	northern	Fernald, 1942a
Juncus pelocarpus	northern	Fernald, 1942a
Quercus prinoides	eastern U. S.	Fernald, 1950
Nelumbo lutea	eastern U. S.	Fernald, 1950 Muenscher, 1944
Cakile edentula	littoral	Fernald, 1950
Drosera longifolia	eastern U. S. and Europe	Fernald, 1942a, 1950

Table 3. Continued

species	actual distribution pattern	source of distribution data
Lupinus perennis	eastern North America	Fernald, 1950
Lathyrus maritimus var. *glaber*	littoral	Fernald, 1950 Guire and Voss, 1963
Euphorbia polygonifolia	littoral	Fernald, 1950 Guire and Voss, 1963
Rotala ramosior	eastern North America	Fernald, 1950
Gerardia purpurea	eastern U. S.	Fennell, 1935
Utricularia resupinata	northern and southward on coastal plain	Fernald, 1950
Bidens discoides [sic]	eastern North America	Fernald, 1950

Plain - Midwest pattern but also have numerous other stations scattered off the Coastal Plain. Such diffuse distribution patterns only serve to make an interpretation of their appearing in the Midwest via the same mode as the less diffusely dispersed Eleocharis melanocarpa, for instance, uncertain.

Fernald criticized both of Peattie's premises. The first, that there are relicts of a post glacial migration along drainage features, he has criticized by indicating that these populations of supposedly Coastal Plain species are largely composed of members of other floristic elements. The second, that the presence of several species can be attributed to a single set of phenomena, he has criticized by showing that the species subjected to that analysis have diverse phytogeographic and ecologic affinities. These criticisms apply equally well to McLaughlin's analysis.

Other Hypotheses

The only alternatives appearing in the literature, to the Peattie-McLaughlin theory are those proposed by Fernald (1931, 1937), who is supported by Pennell (1935) and Svenson (1943), and by Gleason and Cronquist (1964). The Fernaldian theory is that the Coastal Plain plants have survived various geologic catastrophies in relict colonies on the Appalachian highlands (cf. the discussion above under "Disjunctions of the Coastal Plain Flora") and have migrated north and west from these refugia, as well as south and east. This theory is not, however, supported by much evidence and is not elaborated beyond a statement of a few sentences.

Northwestward migration would have occurred recently, since the retreat of the glaciers, and across the relative lowlands of Kentucky, Ohio, and southern Indiana. The evidence is a group of plants that have been reported from a few locations in the Appalachians and in the Midwest but that have the major portion of their range on the Coastal Plain. (Fernald [1931] shows maps of Woodwardia aerolata and Xyris torta, two species with such a pattern.) Two objections to Fernald's idea are that many plants with the Coastal Plain - Midwest pattern are not known from the Appalachian highlands and that no traces of their migration have been left in the form of relict populations in the Kentucky, Ohio, southern Indiana area; cf. patterns mapped in figures 1 - 5.

Gleason and Cronquist (1964) propose, as an alternative, that migration may have occurred along a route north of the present distribution of the species during the Hypsithermal interval of ca. 8,000 B.C. Again, many disjunct species do not show northern outliers nor intermediate stations between the Coastal Plain and Midwest along the hypothesized route. There are, on the other hand, northern records for several Coastal Plain species in Nova Scotia well north of the present day tension zone (Fernald, 1921, 1922). In addition the tension zone which seems to limit the northward distribution of many Coastal Plain species may have been 100 miles north of its present position during the xerothermic interval (Curtis, 1959). If this hypothesis of a northern route were, in fact, correct then the populations of Coastal Plain species in northern Michigan, e.g., Juncus Militaris and Panicum

Figure 1. Distribution of Eleocharis melanocarpa

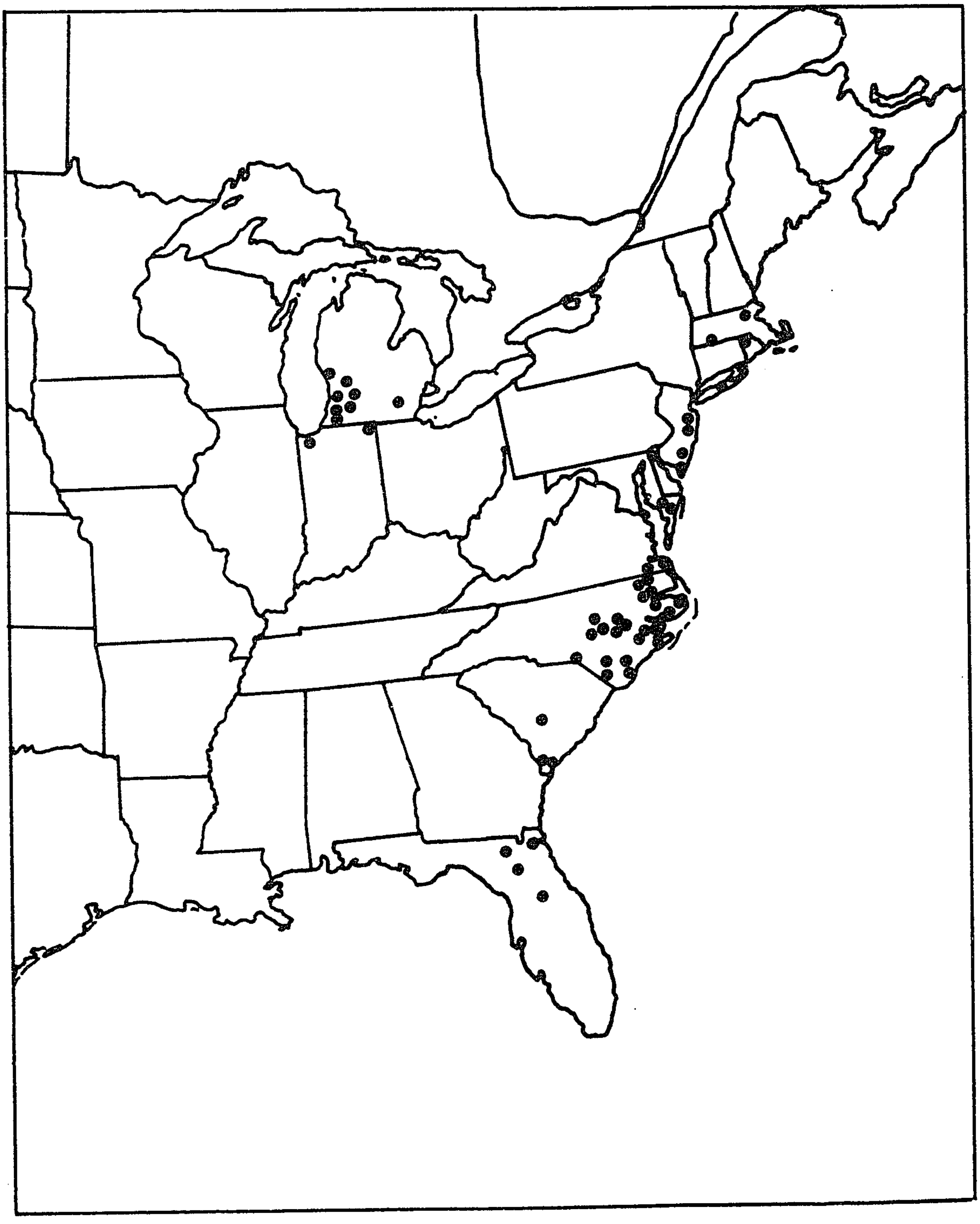


Figure 2. Distribution of Fuirena pumila.

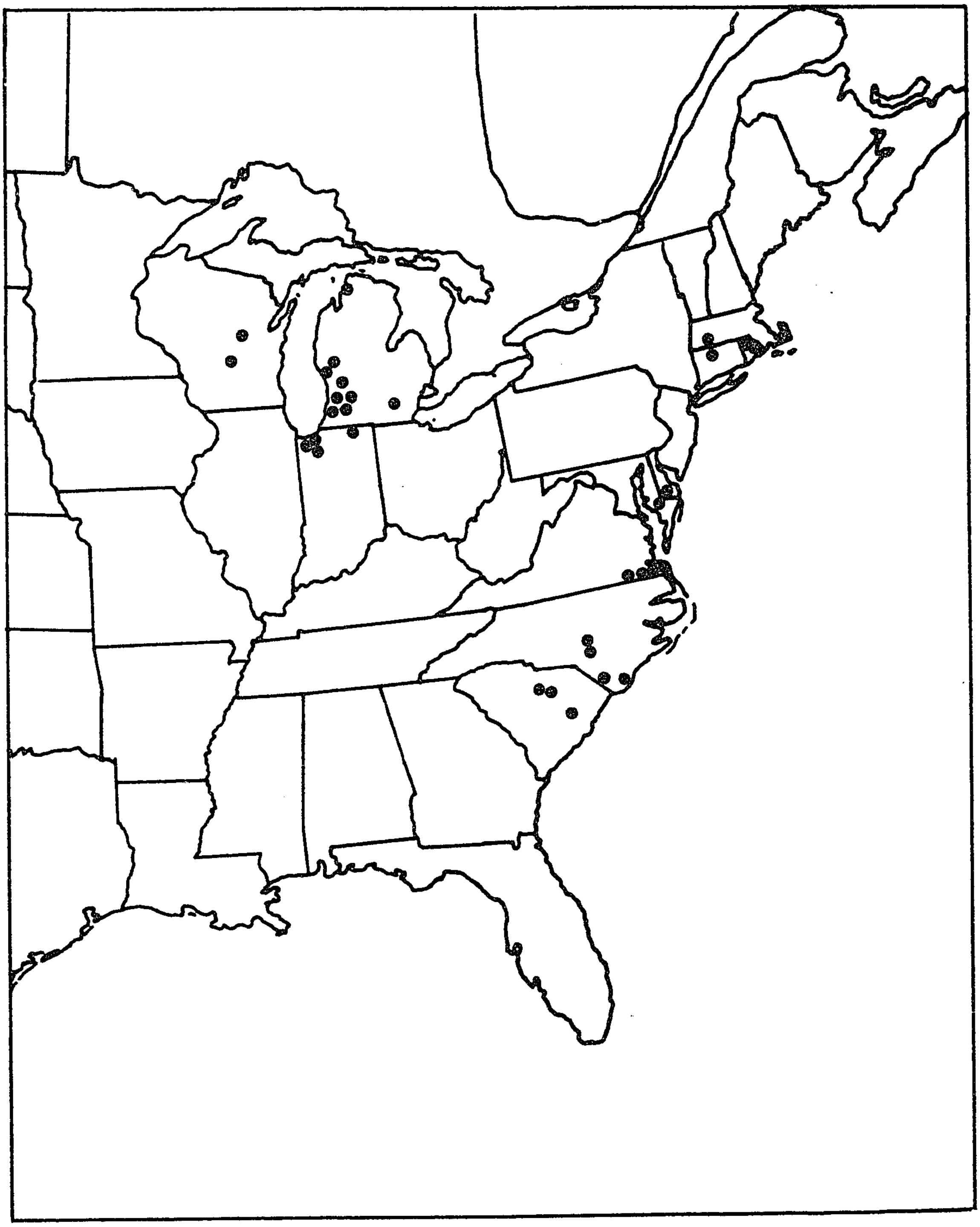


Figure 3. Distribution of Psilocarya scirpoides.

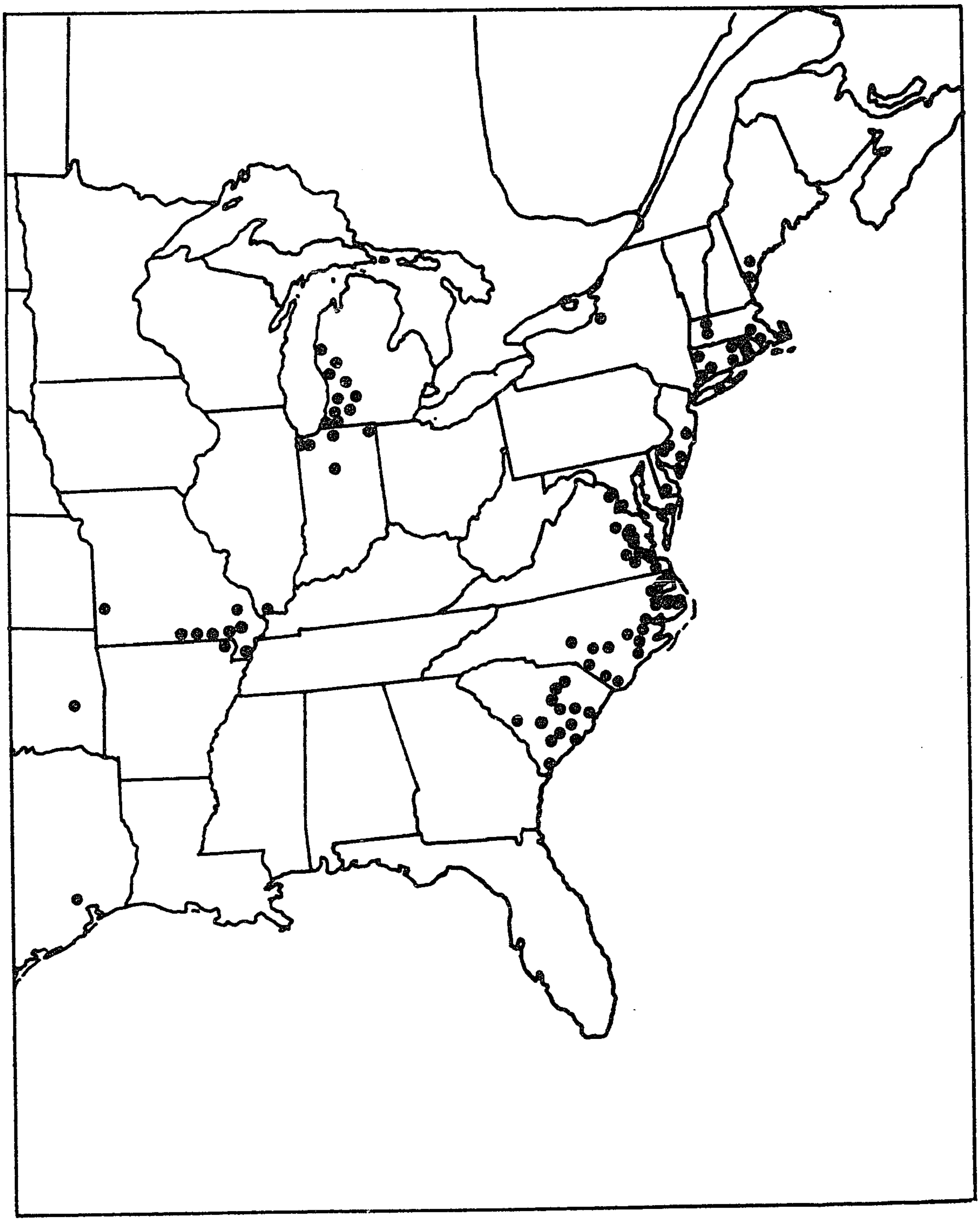


Figure 4. Distribution of Rhynchospora macrostachya.

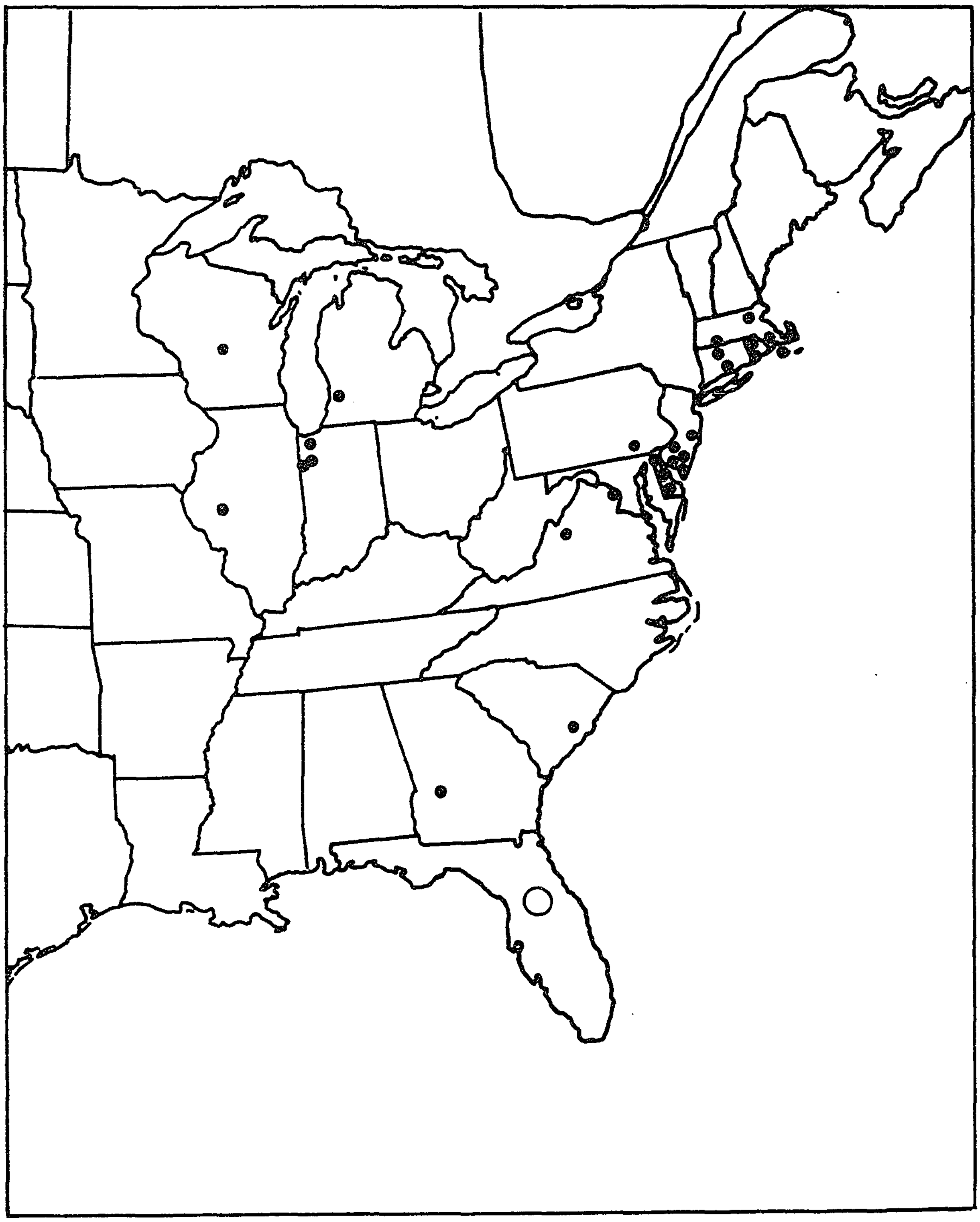


Figure 5. Distribution of Scleria reticularis in the United States. Reported from Florida (Core, 1936) but without a county indicated ○.

spretum in Presque Isle and Cheboygan Counties and *Psilocarya scirpoides* in Emmett County, take on new meaning and are seen as relictual population rather than as anomalous northward dispersals.

LIMITATION OF THE PROBLEM

Definition of "Coastal Plain Disjunct"

One species, Eleocharis melanocarpa, has been consistently cited as a typical example of a Coastal Plain species disjunct in the Midwest (Cain, 1944; Deam, 1940; Fernald, 1937, 1942a; Harvill, 1969; McLaughlin, 1932; Peattie, 1922; Swink, 1969; Voss, 1957b, 1972). In southwestern Michigan, often with Eleocharis melanocarpa, are other species that have a similar disjunct distribution pattern, e.g.: Fuirena pumila, Psilocarya scirpoides, Rhynchospora macrostachya, Scleria reticularis, Juncus scirpoides, and Stachys hyssopifolia. Several sources indicate that these species are commonly associated with one another in Indiana and on the northern part of the Coastal Plain as well (Hill, 1899; Pepoon, 1927; Sinnott, 1912; Swink, 1969). These disjunct species are commonly associated with several others which confirm floristic and ecologic uniformity among the lakes on which disjuncts are found. Some examples are Panicum meridionale, Cyperus rivularis, Rhynchospora capitellata, Cladium mariscoides, Fimbristylis autumnalis, Pontederia cordata, Eriocaulon septangulare, Xyris difformis, Hypericum virginicum, Viola lanceolata, Rhexia virginica, Lycopus americanus, Cephalanthus occidentalis, and Solidago remota.

Although this list of associates and the lists appearing in the literature cited above would be likely to include most of the Coastal Plain element in the Midwest, clarity is best served by

selecting a smaller more uniform assemblage on which to base an analysis.

Criteria were selected that would limit the number of species to a few that are clearly Coastal Plain plants and are found in uniform ecologic situations. The characteristics used to define a Coastal Plain disjunct for this study were as follows:

1. The major area of its distribution must be on the Atlantic Coastal Plain.

2. The range of the species must extend northward on the Coastal Plain to Massachusetts and New York.

3. The species must occur in Michigan. (This criterion eliminated several otherwise acceptable species such as *Panicum verrucosum*, *Psilocarya nitens*, and *Ludwigia sphaerocarpa* and limited the scope of field studies to Michigan.)

4. The Midwest distribution of the species must be limited to the vicinity of the lower end of Lake Michigan.

5. The disjunction from the Coastal Plain must be distinct with few or no geographically intermediate stations.

6. The midwestern distribution must be restricted to sandy, soft water, inland lakes lacking permanent drainage.

7. The species must be found in association with others meeting these criteria.

One further criterion that the species be relatively well known in the Midwest was also taken into consideration. Five species were selected that fit all criteria: *Eleocharis melanocarpa*, *Fuirena pumila*, *Psilocarya scirpoides*, *Rhynchospora macrostachya*, and

Scleria reticularis.

A narrow definition, as presented here, has the advantage of allowing conclusions to be based on a homogeneous array of species without courting the danger of drawing conclusions that will apply to some of the species discussed and not to others, or else that do not apply in their entirety to any of the species. Voss (personal communication) in a 1955 paper presented at the American Institute of Biological Science meetings also based a consideration of disjunct Coastal Plain plants on a strict definition. He discussed the distribution of *Psilocarya scirpoides* and only included a few observations on the distribution of other species.

Two assumptions are, however, critical to the conclusions that follow. First, the five species are assumed to be homogeneous in their phytogeographic histories, and a single set of phenomena can thus be expected to account for their distribution. This is justified on the basis of the resemblance of the distributional patterns of the five to one another and on the basis of the homogeneous and rather unique ecological characteristics exhibited by the species throughout the Midwest and on the northern part of their coastal range. Second, they are similar to other species in their distribution and ecology, and this similarity is assumed to be great enough to justify generalizing the conclusions based on them and to explain the history of a larger portion of the Coastal Plain floristic element occurring in the Midwest.

A few of the species which probably could be discussed along with the Coastal Plain disjuncts, but which do not fit all of the

above considerations, are discussed below. Their failure to fit the criteria, probably due to some combination of better dispersal, a wider range of environmental tolerance, or slightly different ecological requirements as compared to the five accepted species, does not indicate that they cannot be subjected to the same analysis, but their inclusion would make analysis more complex.

Juncus scirpoides is excluded because its midwestern range is too broad. It is known from central and southern Illinois (Jones and Fuller, 1955; Mohlenbrock, 1970), Kansas (Barkley, 1968; Gates, 1940; Hermann, 1935; McGregor, 1960), and several stations in Missouri (Steyermark, 1963). In addition it is not known to be present in New England (Seymour, 1969).

Stachys hyssopifolia appears to have broader ecologic tolerances than the accepted Coastal Plain disjuncts; it often grows at some distance from them in dry, sandy fields. Swink (1969:402) says: "It is also found in sterile sandy fields with Desmodium illinoense and Hieracium longipilum." Data on labels of plants collected in Michigan concur, and I have seen it at least once in such a field. Labels on specimens at MICH show its distribution to include many lakes from which none of the five accepted species are known, as well as lakes on which those five grow. Voss (1957b) and Waterman (1960) give the known distribution of this species in Michigan.

Panicum meridionale (including P. albamarlense) is also known from diverse ecologic situations and a wide geographic range in the Midwest. It occurs on Glacial Barrens Lake in northwestern

Wisconsin (Fassett, 1951; McLaughlin, 1932) and in Minnesota (Hitchcock and Chase, 1910, 1950).

Solidago tenuifolia is reported in the Midwest (Voss, 1957b) but its presence there is doubtful. Specimens (deposited at MICH) determined by Shinners as S. tenuifolia have been redetermined by Cronquist as S. remota. Whether or not S. remota is a "neo-endemic" derivative of the former species is a question beyond the scope of this paper.

Other species such as Juncus militaris and Panicum spretum range far north of the Coastal Plain disjuncts on the east coast and in the Midwest. They are both known from Nova Scotia (Fernald, 1950) and northern Michigan (Voss, 1972). In Michigan the former has been collected in Presque Isle County (Hermann, 1936; Hermann 7015 MICH) and Cheboygan County (Wood s.n., July 10, 1951, A). The latter is known from Presque Isle County on the same lake as J. militaris (Voss 12252 MICH). Voss (1972) indicates that both species are known from both of these counties but only gives a partial list of specific localities.

Eleocharis tricostata is excluded because too little is known about it in the Midwest. Bazuin collected it near Fruitport, Michigan, at a location that subsequently became the site of a motel (Voss, 1972). This is representative of a few species that are exceedingly rare and thus poorly known in the Midwest. Psilocarya nitens, Rhynchospora globularis, Panicum verucossum, and several vascular cryptogams are also known, off the Coastal Plain, from only one or a few locations each.

The rare vascular cryptogams include Lygodium palmatum (Pippen, 1966), Woodwardia aereolata (Billington, 1952; Fernald, 1931), and Thelypteris simulata (Hartley, 1965, 1966). These along with Lycopodium appressum (Hagenah and Wagner, 1971) are found in ecologic situations very dissimilar to those for phanerogamic Coastal Plain species, and they are not associated with any of the five Coastal Plain disjuncts. The Lycopodium is apparently not so rare as the other cryptogams and has been collected at several locations in southern Michigan.

Distribution of Five Coastal Plain Disjuncts

Most earlier workers based discussions of Coastal Plain plants in the Midwest on sketchy distribution records. There are now many more locations known of Coastal Plain species in Michigan than in the 1930's (cf. Table 1). This increase is due to collections by Bazuin and Hanes in the 1930's and 1940's, by Voss in the 1950's and 1960's, and by several others; e.g., Hyypio, Kenoyer, Schuyler, and Stuckey. A few new records, including new county records in Allegan County for Fuirena pumila, and Scleria reticularis, were added during the course of this study. (Appendix 1 contains a complete list of my collections of the five Coastal Plain disjuncts and references to other collections.) It is now realized that the Midwest range of the five species is much greater than it was thought to be in the 1930's.

Certain distributional features of the five species should be indicated (cf. Figures 1 - 5): (1) With certain exceptions the

eastern range of all five species is restricted to the Coastal Plain or areas immediately adjacent to it. (2) Exceptions are the Oswego County, New York, record of *Fuirena pumila*, the Maine stations for *Rhynchospora macrostachya*, and the Augusta County, Virginia, locations for *Eleocharis melanocarpa* and *Scleria reticularis*. (3) There is an anomalous concentration of the species on the glaciated northern part of the Coastal Plain in New England and New York. (4) The midwestern stations, with the exception of the Cass County, Illinois, station for *Scleria reticularis*, are all north of the southern advance of Wisconsin glaciation. (5) There is a concentration of the five species in southwestern Michigan and northwestern Indiana.

RESULTS AND DISCUSSION

Observations made at approximately 50 lakes visited indicate that those with Coastal Plain species are similar in many respects to one another but significantly different from lakes without those species. In addition, there was observed a possible successional relationship among the 31 lakes which could account for some of the differences observed. This hypothesized succession is similar to that discussed by Wilson (1939) for soft water seepage lakes.

In the following discussion critical differences and similarities among the lakes with Coastal Plain plants are considered. These include characteristics mentioned by Peattie (1922), McLaughlin (1932), and Voss (1972). Successional relationships among the lakes are discussed in order to emphasize some of the basic similarities among apparently different habitats at which the five species were collected.

Surface Geology

The geologic formations, elevations, and geographic dispersion of the 31 locations where the Coastal Plain disjuncts have been collected in Michigan indicate significant differences among the communities. These differences show that the plants are not associated with post-glacial drainage channels as was suggested by Peattie (1922). Table 3 lists glacial surface features and altitudes at the sites. Eleven of them are on moraines at elevations to 950 feet, approximately 250 feet above the 700-foot contour marking the

maximum extent of the shore of the Glacial Great Lakes at the latitude of Allegan County (Martin, 1955). Fourteen locations are on outwash plains and six are on the bed of Glacial Lake Algonquin. In addition to being on three different glacial surface features not closely related to drainage features of the postglacial period some of the lakes are at considerable distances from those drainage features. Examples are Island Lake in Washtenaw County, Stony Lake in Kalamazoo County, Mud Lake in Barry County, and all of the locations in Newaygo County.

Habitat

Uniformity of features at Coastal Plain disjunct sites

Observations on the habitat in which Coastal Plain disjuncts are found confirm its basic uniformity. Three significant characteristics indicating this habitat uniformity are (1) regional substrate characteristics, (2) soil and water characteristics, and (3) fluctuating water levels. Two lakes which combine nearly optimal conditions are Keeler Lake in Van Buren County and Crooked Lake in Allegan County. Although the situation has been modified at Keeler Lake by the construction of a canal and dam to control the water level both lakes may be described as follows: The surrounding soil is noncalcareous sand and at least some of the shore is pure sand of the same type. Other portions of the shore consist of a surface layer of peat composed of decaying vascular plants rather than *Sphagnum*; this peat grades

into the sandy shore line. The peat and the sand both give a neutral to moderately acid reaction which results in soft water with a similar acidity. Neither lake has an inlet or a permanent outlet, and lake levels fluctuate greatly from season to season and from year to year.

Departures from this optimal set of conditions may reflect an earlier or later stage of succession and explain the lower diversity of Coastal Plain plants seen at many Michigan lakes. Lakes of the type just described are not, however, restricted to Michigan. Literature reports discussed below indicate that some of these characteristics are present at locations for Coastal Plain disjunct species outside Michigan, both in the Midwest and on the east coast.

Salient features of Coastal Plain disjunct locations

Water Level -

The single most obvious factor, both in its occurrence and its effect on the presence of the Coastal Plain disjuncts, is a fluctuating water level. Most of the lakes on which the species are found have neither inlet nor outlet. Some exceptions such as Austin Lake in Kalamazoo County and Keeler Lake in Van Buren County have only outlets, and these cease functioning during periods of low water. Such lakes, called seepage lakes (Wilson, 1939), often have a fluctuating water level and a gently sloping shore, thus a fluctuating shore line. At several Michigan locations a dual cycle of seasonal fluctuations superimposed over

yearly fluctuations is evident.

The effects of seasonal fluctuations are not marked, if present at all. In several locations observed recessions of water from mid summer to autumn were not followed by an increase in Coastal Plain species. Crooked Lake in Allegan County, an unnamed depression in Merrill Township of Newaygo County, Mud Lake in Barry County, and Pine Island Lake in Muskegon County all showed a significant drop of water level from mid to late summer in 1970. None, however, exhibited an increase in kind or quantity of Coastal Plain species. The relatively small drop in water level on many lakes from 1970 to 1971 resulted, by contrast, in marked changes in the abundance of Coastal Plain disjuncts.

Several workers have indicated changes in abundance of species from year to year at a single location. Deam (1940) says that this is not an uncommon occurrence and he gives some examples of species showing this phenomenon. Pepoon (1927) mentioned this change on Goose Lake in Indiana where several Coastal Plain plants were known before it was obliterated. Voss (1957b) commented on the possibility of finding Psilocarya scirpoides again in Emmett County, Michigan, where it was collected in a very low water year, and mentioned this factor in relation to several other Coastal Plain species in Michigan (Voss, 1972). Hanes (1947), and Hanes and Hanes (1947) mentioned an abundance of Rhynchospora macrostachya in "Island Pond" west of Schoolcraft in Kalamazoo County when the pond was nearly empty. In a high water year he was unable to find the same species. Sinnott (1912:30) says of Rhynchospora

macrostachya and some of its associates on Cape Cod, "They must of necessity be able to adapt themselves to the migrating shoreline." Fernald (1947) commented on the effect of pond level in the quality of collecting for several rare Virginia Coastal Plain species.

Field observations over a two-year period and data taken from herbarium labels also indicate the importance of fluctuations of water level for growth of Coastal Plain disjuncts. Psilocarya scirpoides was collected by Voss and by Stuckey in a dry, peaty depression southeast of Whitecloud, Michigan. Voss (personal communication) indicated that this location is Fry Lake. In 1964 when they collected this location the population of Psilocarya covered two to three acres in a pure stand. When I visited the site in 1970 and 1971 it was a pond with water up to one meter deep. A long search yielded no specimen of Psilocarya in either of these wet years. Both Voss and Stuckey have collected Fuirena pumila and Psilocarya scirpoides at Island Lake in Washtenaw County, and labels on specimens at MICH indicate that the species were more abundant when the water level was low. At Bankson Lake in Van Buren County Fuirena pumila was common in the fall of 1969. A year later only a few specimens were located. In 1971 increases over the wetter year of 1970 were noted at several lakes for each of the Coastal Plain disjuncts, except Eleocharis melanocarpa; e.g., Mud Lake in Barry County showed an increase of Fuirena pumila; Psilocarya scirpoides and Scleria reticularis increased at Crooked Lake, while Rhynchospora macrostachya showed a marked increase at Crooked Lake and at the Merrill Township site in

Newaygo County.

From the wetter year, 1970, to the drier year, 1971, no change in size of any population of Eleocharis melanocarpa was noticed. Specimens of E. melanocarpa were never seen as young plants; they were always found in large clones where young individuals were either not seen or not identified as such. Since Eleocharis melanocarpa produces plump, apparently viable seed it is assumed that it does reproduce by seed and that young plants were not recognized, although no attempts to germinate them were made. In light of these observations it is difficult to conclude whether or not E. melanocarpa responds to water level changes as do the other four Coastal Plain disjuncts.

Regional Substrate -

Soils in a region where a seepage lake is located may have a significant effect on the chemistry of the lake and subsequently on its floristic composition (Wilson, 1939; Veatch, 1933). United States Department of Agriculture soil surveys were consulted to determine the validity of the field observation that Coastal Plain disjunct sites are normally in regions of relatively infertile, non-calcareous, sandy soils. Table 4 gives the results of this search indicating soil types on which the sites are found in eight counties and characterizing the carbonate content if any was given in the surveys. The table shows that most of the sites are on acidic (noncalcareous) sand or sandy loam.

Calcareous soils are indicated in four counties and these surround only six of the lakes studied. In Kalamazoo County the

Table 4. Soil classification of substrates on which Coastal Plain disjunct sites in Michigan are located, listed according to the counties in which the sites are located.

County	Soil types *	Presence of carbonates
Allegan	Allegan sand	not given
	Clyde sand	not given
Barry	Coloma loamy fine sand	noncalcareous
	Bellafontane sandy loam	#
Cass	Miami sand	not given
Kalamazoo	Bellafontane sandy loam	#
	Coloma loamy sand	noncalcareous
	Coloma sandy loam	noncalcareous
	Fox loam	calcareous
	Fox sandy loam	calcareous
	Plainfield sandy loam	noncalcareous
Kent	Coloma sand	noncalcareous - strongly acid
	Plainfield sand	noncalcareous - strongly acid
Muskegon	Plainfield loamy sand	noncalcareous
Washtenaw	Bellafontane sandy loam	#
Van Buren	Bellafontane sandy loam	#
	Coloma loamy sand	noncalcareous
	Fox loam	calcareous
	Fox sandy loam	calcareous
	Plainfield sand	noncalcareous - strongly acid

* Soil classification terminology of the original survey is used.
# Bellafontane sandy loam is said to be noncalcareous and acid in the upper two to three feet but calcareous with a neutral to slightly basic pH below that.

Sources: Allegan Co.: Fippin and Rice, 1902. Barry Co.: Deeter, 1928. Cass Co.: Geib, 1908. Kalamazoo Co.: Perkins and Tyson, 1928. Kent Co.: Wildermuth, 1926. Muskegon Co.: Pregitzer, 1968; Wheeting, 1929. Van Buren Co.: Wildermuth, 1928. Washtenaw Co.: Veatch, 1930.

southeast shore of Austin Lake, where *Fuirena pumila* is found, is on the calcareous Fox series (Perkins, 1928). Keeler Lake in Van Buren County, which has four of five Coastal Plain disjuncts is also on Fox soils (Wildermuth, 1928). Bellafontane sandy loam, which is characterized by having the upper two to three feet free of carbonates and the lower levels moderately calcareous (Veatch, 1930), is the substrate for four other lakes in Barry, Kalamazoo, Van Buren, and Washtenaw Counties. All other sites are on sterile sandy soil or on sandy loam lacking carbonates.

In his discussion of the sandy loams of Van Buren County Wildermuth (1928) indicates that the porous nature of some of these, e.g., Fox and Bellafontane, may have resulted in considerable leaching. He says that these soils are frequently noncalcareous near the surface.

Shoreline Substrate -

The soils on which the Coastal Plain disjuncts are found are of three types including pure sand with essentially no organic content, pure humus with no inorganic content, and mixtures of the two. The pure sand is usually a better substrate for *Fuirena pumila* and *Eleocharis melanocarpa* while the other three species are usually on soil with some organic content or on pure humus. Literature reports and herbarium labels often call the humus soil type "peat" however, its singular lack of *Sphagnum* makes Pepoon's (1927) description of "sedge peat" a more accurate term. Although a few lakes with Coastal Plain disjuncts have *Sphagnum* on some portion of the shore, at no Michigan location were any of these

species associated with Sphagnum or growing on soil that contained recognized Sphagnum debris.

Some of the smaller lakes visited were ponds or simply sedge peat depressions characterized by the presence of Rhynchospora macrostachya and usually by Psilocarya scirpoides. These include the site in Merrill Township, Newaygo County (Fig. 6); "East Beltline Pond" in Kent County (Fig. 7); and the drying lakebed in Holton Township, Muskegon County (Fig. 8). These sites are occasionally dry and, in terms of succession, are probably older lakes (Wilson, 1939).

At the other edaphic extreme are lakes with sandy shores characterized by soils like those of the region but with most of the finer particles and carbonates, if any were originally present, removed by wave action. Sinnott (1912) attributed the sandy shores of Cape Cod ponds to two factors. Either the shores are steep enough to allow waves to strike unabated, or the ponds are big enough to allow large waves to form. In either case wave action removed lighter particles leaving only sand. The sandy lakes are younger in terms of succession and have sedge peat only in areas protected from wave action. They are likely to have Fuirena pumila and Eleocharis melanocarpa on wet sand of abandoned beaches. Burns Lake and Pine Island Lake in Muskegon County, Daggett Lake (Fig. 9) and Mud Lake (Fig. 10) in Barry County, Bankson Lake in Van Buren County, and Island Lake in Washtenaw County are examples of younger, sandy lakes.

Voss (1972) has commented that marl shores are a suitable

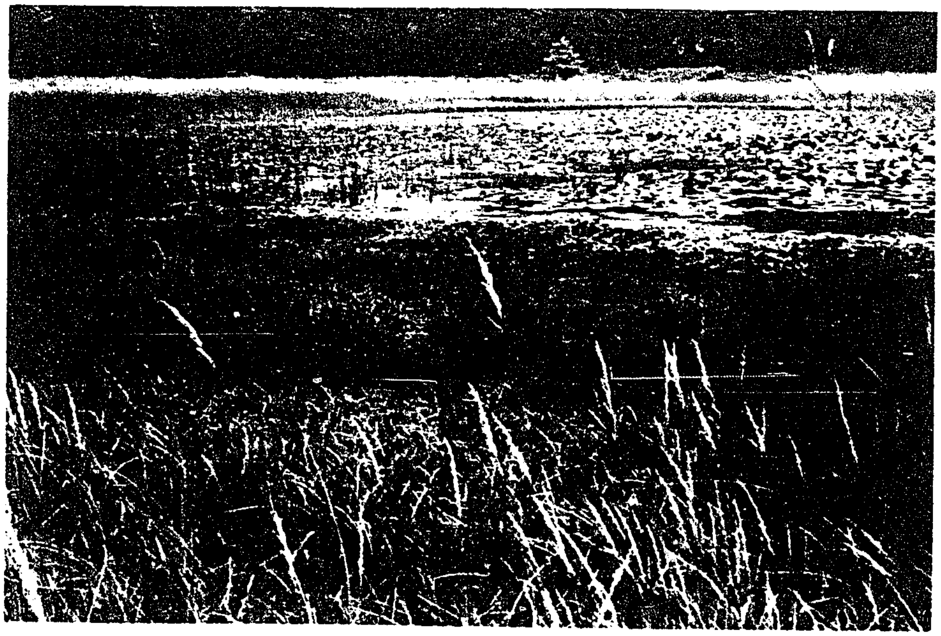


Figure 6. Peaty shore of the unnamed lake in Merrill Township, Newaygo County. The black dots in the middle foreground are a solid stand of Rhynchospora macrostachya. At its maximum the water reaches to the near foreground.

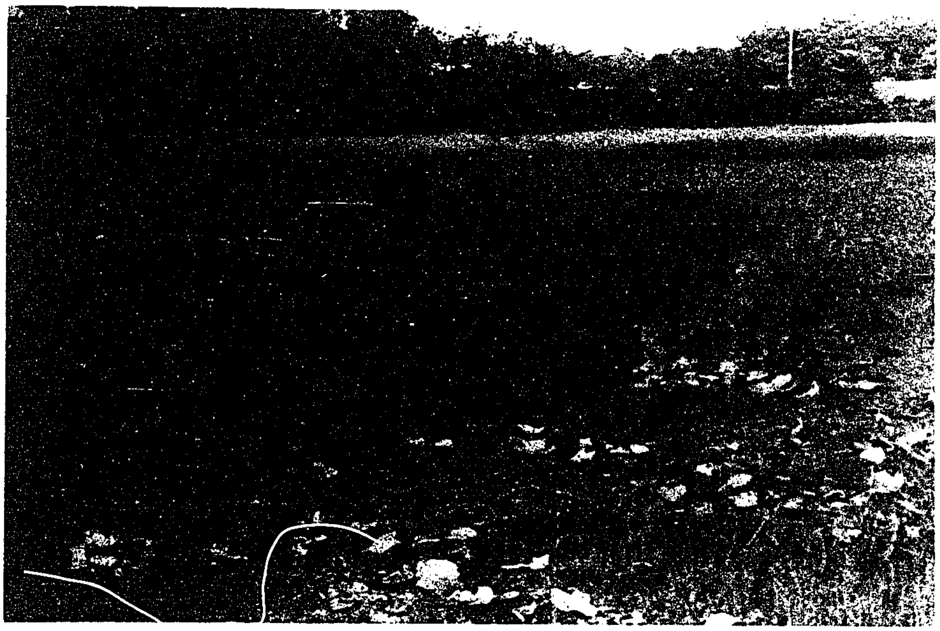


Figure 7. The peaty bottom of "East Beltline Pond" in 1971. In the midground is a nearly solid stand of *Rhynchospora macrostachya* ca. three feet tall. This area is submerged only during the wettest years.

Figure 8. Drying lakebed, Holton Township, Allegan County showing the peaty bottom, nearground, and the sedge shore, background, where *Rhynchospora macrostachya* is found.

Figure 9. Daggett Lake showing a sandy shore on which *Eleocharis melanocarpa* grows. The maximum extent of the water level is in the middle left foreground. The patch of vegetation in the right foreground is one of three known Michigan locations of *Juncus scirpoides*.

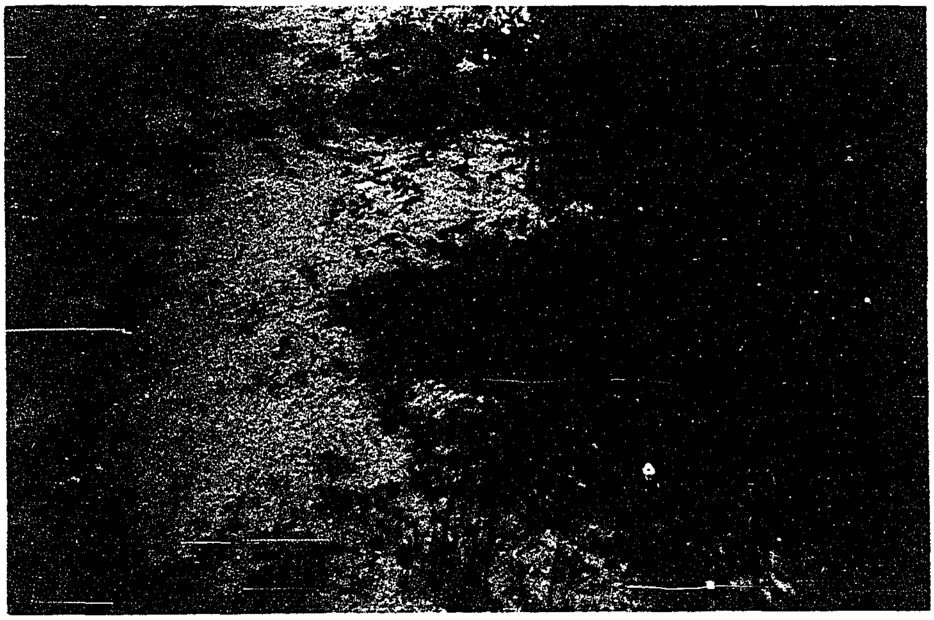


Figure 10. The sandy beach of Mud Lake where Fuirena pumila grows. The maximum extent of the water level is on the left margin of the dense band of vegetation.

habitat for *Rhynchospora macrostachya* and *Psilocarya scirpoides*. He mentions Arbutus Lake in Muskegon County where *P. scirpoides* and *R. macrostachya* have been collected as an example of this habitat type. There is, on the contrary, no evidence of marl as a substrate for Coastal Plain disjuncts at this site. Arbutus Lake (Fig. 11) is on noncalcareous dune sands (Pregitzer, 1968; Wheeting, 1929) and the shore is of three types: (1) Along the east edge there is sand mixed with some sedge peat. (2) On the west and northeast sedge peat is well developed. (3) At the extreme north end is a small *Sphagnum* bog with ericaceous species, as well as *Menyanthes trifoliata*, *Rhynchospora alba*, and *Eriophorum* sp. At Arbutus Lake I collected *Rhynchospora macrostachya* on deep sedge peat on the northeast shore where there was no evidence of marl. Whether lower levels in the soil profile are marl is unknown and possibly irrelevant.

Two anomalous lakes were, however, visited. At Augustine Lake in Lake County Voss collected *Rhynchospora macrostachya* on the north shore in *Chara* filled marly pools, and at Round Lake, in Allegan County, Bazuin collected the same species in shallow water where *Chara* is abundant. No explanation for these anomalies is available.

Soil and Water Chemistry -

As indicated above the soil on which Coastal Plain disjunct sites are found in Michigan is usually noncalcareous and sandy. This type of soil is often acid, and seepage lakes in such areas have soft moderately acid water (Hutchinson, 1957; Wilson, 1939).

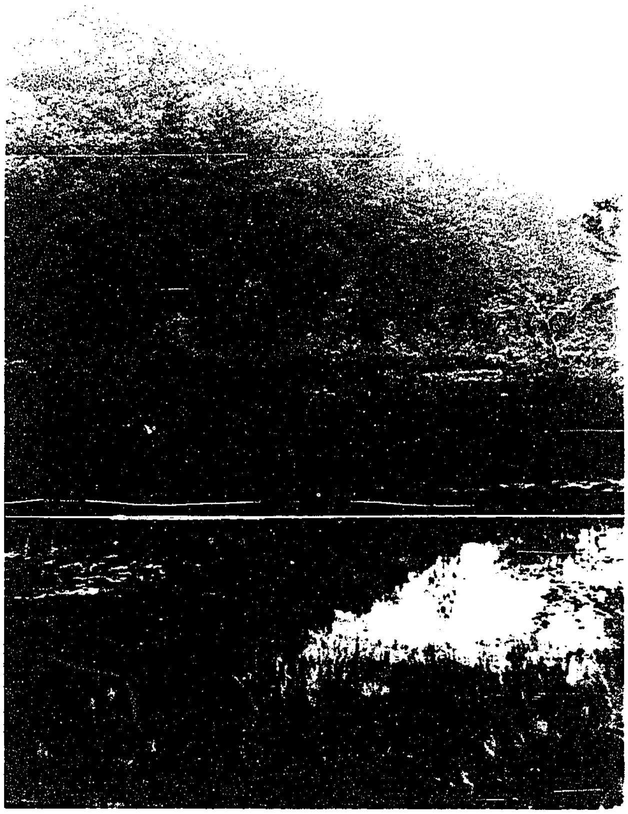


Figure 11. "Arbutus Lake" showing, in the background, a stable dune. The islands in the midground support a Chamaedaphne bog.

This and data given below confirms the nearly neutral to acid, softwater conditions of Michigan locations for these species.

Actual measurements of soil pH (Table 5) indicate a range from 7.0 at Mud Lake in Barry County to 4.4 at Crooked Lake in Allegan County. The measurements show no significant difference in acidity between sand and sedge peat. Water hardness measured at Crooked Lake was fewer than five parts per million of magnesium and calcium combined. In addition to direct measurements of soil pH and water hardness Veatch (1933:412) in a study of these factors and their relation to vegetation said that plant species may be good indicators of soil and water conditions. Eriocaulon septangulare, in Michigan, is "a very reliable indicator of soft, and nearly neutral or slightly acid water" found on noncalcareous sand and peat. This indicator species was collected on eight lake shores with Coastal Plain disjuncts: Ely Lake in Allegan County; Daggett Lake, Mud Lake, and Otis Lake in Barry County; and Burns Lake, Carr Lake, one of the "Five Lakes", and Pine Island Lake in Muskegon County.

Climate -

Cain (1944) emphasized the role of climate in plant distribution and discussed the complementary role that climatic factors play in determining plant distribution. Specific factors that might influence the distribution of any of the Coastal Plain species and indicate the uniformity of their locations will not be discussed here. However, a few general comments are relevant to the role of climate in controlling their distributional limits. Elliott

Table 5. pH values for soils collected at nine Michigan stations for Coastal Plain disjunct species.

Location	pH		
	sand	mixed sand and peat	peat
unnamed Lake, Merrill Twp.			4.9
Pine Island Lake		6.5	
drying lakebed, Holton Twp.		5.4	
"East Beltline Pond"			5.4
Daggett Lake	4.8 & 5.6*		
Mud Lake	5.7 & 7.0		
Ely Lake	5.0	4.9 & 5.2	
Crooked Lake	4.6		4.4, 5.2, & 4.6
Pretty Lake	6.5		

* When more than one sample was collected readings from each are given.

(1953), Livingston (1903), and Potzger (1948) have discussed the tension zone in Michigan, and Curtis (1959) has mapped it for Wisconsin. This zone in Michigan is approximately 50 miles wide and lies along a line between Muskegon and Midland (Potzger, 1948). Only one collection of five Coastal Plain disjuncts, Psilocarya scirpoides from Emmet County, is north of this tension zone.

Curtis (1959) found a good correlation between the tension zone in Wisconsin and several climatic factors including precipitation, summer temperature, and summer evaporation. Similar correlations could probably be made in Michigan. If the limit of northward expansion of Coastal Plain disjuncts is climatic, as is implied by these considerations; then, the several anomalous stations in New England might not be very closely related to the presence or absence of the Coastal Plain. It may be that climatic factors are of primary importance.

In order to determine whether some climatic factors might act in New England as they appear to in the Midwest, an effort was made to determine if the tension zone between a northern and southern vegetation type similar to that in Michigan and Wisconsin might exist. Tree species mapped by Little (1971) and reaching their northern or southern limit in New England and in the region of the tension zone of the Midwest are listed in table 6. Based on these limits, there is reason to believe that the tension zone may be rather discrete in New England and lie from Long Island to southern or central Maine. Eighteen of the species mapped by Little reach their limit in this area and in the Midwestern tension zone. All

Table 6. Species reaching their northern or southern limit in the tension zone of Michigan or Wisconsin and in New England.

Reaching northern limit*	Reaching southern limit
Juniperus virginiana	Abies balsamea
Acer negundo	Picea mariana
Carya glabra	Pinus resinosa
Carya ovata	Thuja occidentalis
Celtis occidentalis	Betula papyrifera
Cornus florida	
Juglans nigra	
Liriodendron tulipifera	
Morus rubra	
Platanus occidentalis	
Quercus bicolor	
Quercus velutina	
Sasafrass albidum	

* Species presented in the same order as in Little (1971).

five Coastal Plain disjuncts reach their northern limit on the east coast in this area.

Discussion of specific Coastal Plain disjunct sites

Crooked Lake in Allegan County is in two respects an ideal locale for the southwestern Michigan occurrence of Coastal Plain species. First, it shows a greater diversity of habitats than is found at most other sites. Second, Crooked Lake is the only place in the state from which all five of the species defined as Coastal Plain disjuncts are found. Partly as a result of its habitat diversity, some of the specific differences and similarities among the 31 communities surveyed can be determined best by examination of specific communities and by comparison with Crooked Lake. Thus the standard of comparison is the most diverse and in some sense the best site for these species in Michigan.

Crooked Lake -

Crooked Lake in Clyde Township of Allegan County is on sandy deposits of the bed of Glacial Lake Algonquin at an elevation of 670 feet. By the presence of an abandoned shore line three or four meters above the present lake level, it can be seen that at one time Crooked Lake was a part of a much larger lake including several of the nearby lakes that also have Coastal Plain species on their shores. Figure 12 is a sketch map of the lake indicating several distinct vegetation zones surrounding the south, east, and west shores.

The vegetation on Crooked Lake shows considerable diversity

Figure 12. Sketch map of Crooked Lake showing 1970-1971 water levels and the vegetation zones described in the text.

Key:

= two track road

= maximum extent of lake at approximately the 670 foot contour

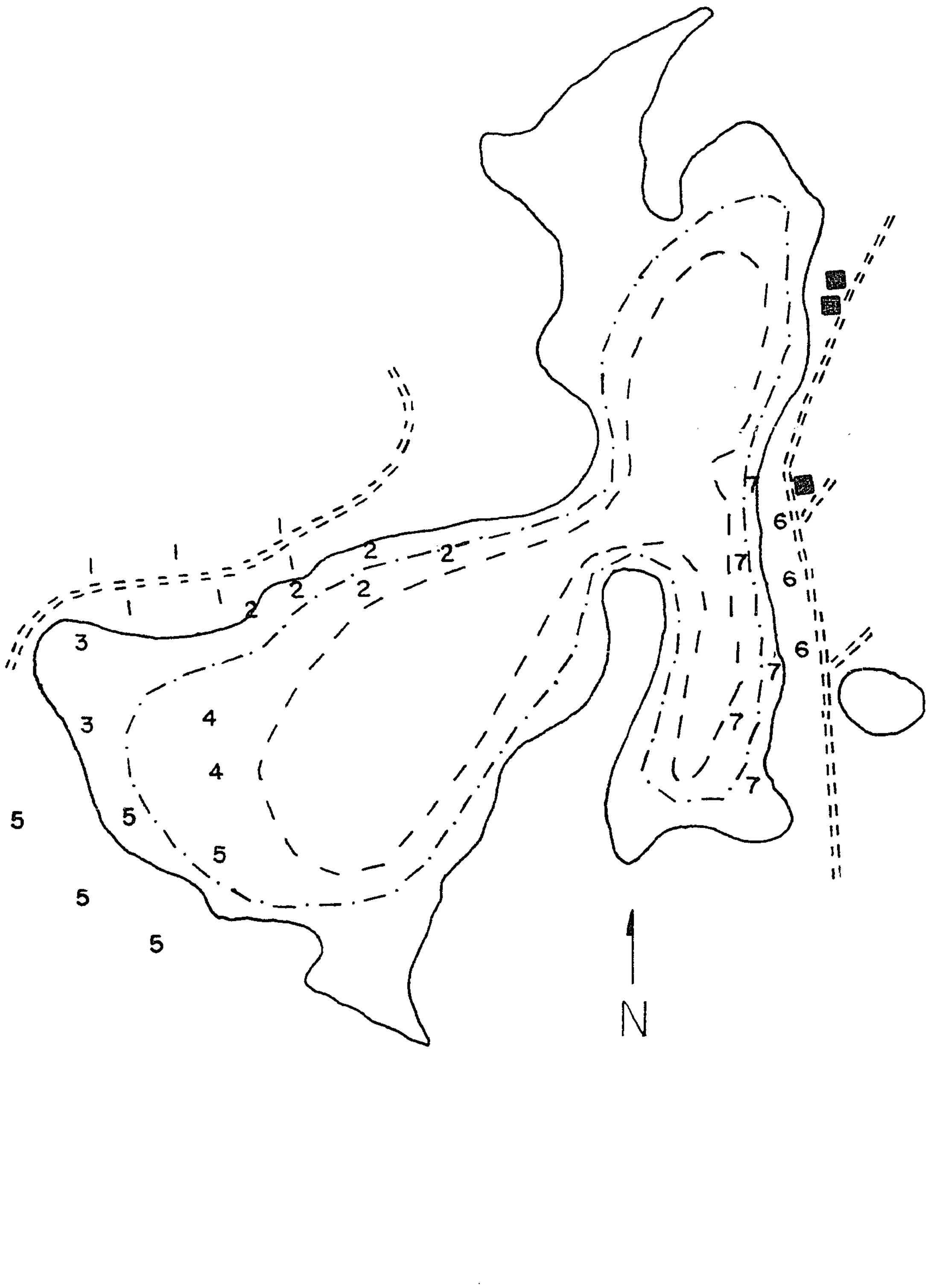
= shore line in 1970

= shore line in 1971

= cottage

1 - 7 = vegetation zones

Scale: 1 inch = approximately .13 miles
1 mile = approximately 7.5 inches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due, in part, to the diversity of the soil substrate. This substrate varies from pure sedge peat on the exposed lake bottom (zones 3 and 4, Fig. 12) to pure sand above the high water line (zones 1 and 6, Fig. 12) between these areas can be found various mixtures of sand and sedge peat (zones 2 and 7, Fig. 12). This soil and vegetation diversity is nearly unique for Coastal Plain disjunct sites in Michigan and provides a unique opportunity to compare the relationships among the five Coastal Plain disjunct species and their habitats.

A second factor contributing to the exceptional growth of Coastal Plain species on Crooked Lake is the considerable fluctuations in water level. These changes are large and result in a shore line which may fluctuate as much as 100 meters from year to year and changes nearly as great from season to season (Figs. 13 and 14). Seasonal movement in the shore line, during two years of observation had little effect on plant growth, however. Bottom exposed as the shore line gradually receeded through the growing season did not support vascular vegetation (Fig. 14). Year-to-year changes in water level are, on the other hand, remarkable in their effect (Fig. 13). Zones 2, 3, and 7 were submerged in the spring of 1970 and that fall were exposed and without vegetation. During 1971 these areas remained uncovered and by August supported a luxuriant growth dominated by Rhynchospora macrostachya and Psilocarya scirpoides with Fimbristylis autumnalis, Rotala ramosior, and several other species (Figs. 13 and 15). Even larger changes in water level appear to have occurred in past years. Zone 5 is a

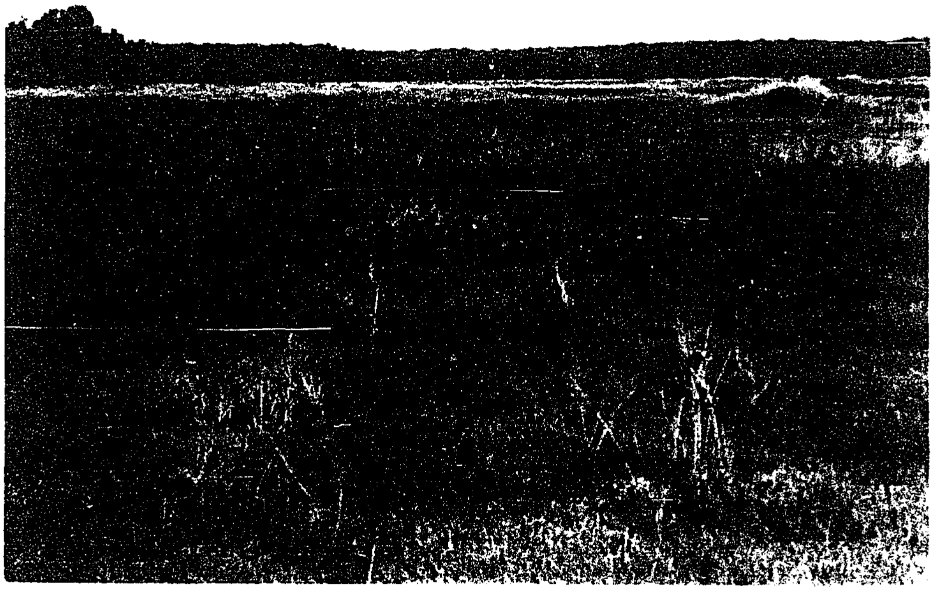

Figure 13. Sedge peat flat on Crooked Lake (zone 3 in Fig. 12) showing development of vegetation after water has receeded for two seasons. When the lake is full this area is completely submerged. Psilocarya scirpoides and Rhynchospora macrostachya are abundant on this flat.

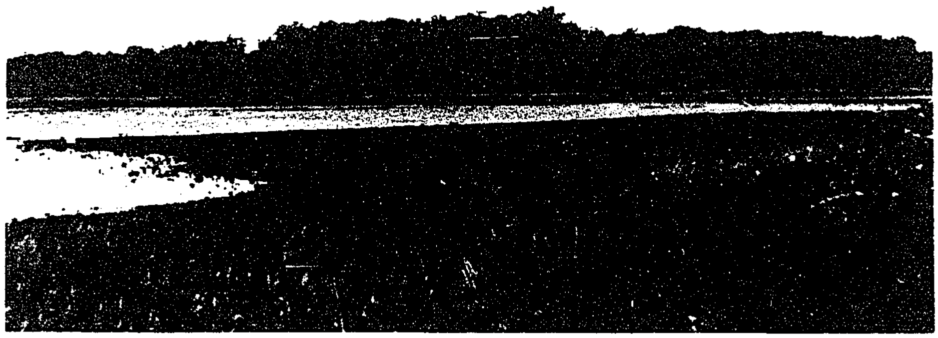

Figure 14. A peaty flat on the east shore of Crooked Lake. The area is bare of vegetation after one season's emergence.

Figure 15. A close view of the peaty flat shown in Figure 6 showing the dense cover after two seasons emergence. Compare with Figure 14: At left center is a specimen of Psilocarya scirpoides ca. 3 dm tall.

large blueberry field in which about half of the bushes are dead from drowning following a rise in water level. This field was probably planted at a time when the lake was very nearly dry. Along the eastern shore are abandoned pleasure boats now useless because of the low water level but apparently brought to the lake when it was at a much higher level, possibly that indicated as the high water mark in Figure 12.

On the wide zone of mud surrounding the lake in low water periods and on the shore above this zone there can be seen differences in species composition that indicate differences in ecological tolerances of the five Coastal Plain disjuncts. During periods of higher water, as in 1970, Psilocarya scirpoides, Rhynchospora macrostachya, and Scleria reticularis were confined to an area of mixed sand and peat between zones 1 and 2 (Fig. 16). During 1971, however, when a wide band of vegetation began to develop around the lake on the abandoned shore, differences in habitats occupied by the five species were noticed. Eleocharis melanocarpa was on drier sandy areas in zones 1 and 6 where it grew in large clones of several square meters in both years. In 1971 zones 2, 3, and 7 were peaty areas where both Rhynchospora macrostachya and Psilocarya scirpoides were exceedingly abundant (Fig. 17). The former species often formed large clones of a few square meters along the previous years high water mark (Figs. 18 and 19); it is thought that this is due to either wave wash concentrating achenes or a large number of fruits all having fallen to the ground from a single parent plant in the previous fall.

Figure 16. The sandy east shore of Crooked Lake. At the far right is zone 6 and at the far left zone 7. During high water years Psilocarya scirpoides, Rhynchospora macrostachya, and Scleria reticularis may be restricted to sporadic occurrence in the sandy strip. Extreme high water is at the right foreground.

Figure 17. Sedge peat flat (zone 3) on Crooked Lake. The numerous black dots in the midground are inflorescences of Rhynchospora macrostachya and Psilocarya scirpoides.

Figure 18. A solid stand of Rhynchospora macrostachya at the previous years high water line. Photo taken on the east shore of Crooked Lake in 1971.

Figure 19. A close view of the stand of Rhynchospora macrostachya shown in figure 18. Note the large amount of bare ground between the plants.

Psilocarya scirpoides was scattered but common in these areas. In zone 3 well above wave wash the two species were scattered and both were abundant on a large sedge peat flat (Figs. 13, 15 and 17). Scleria reticularis formed a pure stand of several square meters in zone 4 during the lower water year. It was the only vascular plant common in this area. Fuirena pumila was not seen in 1971. Only two specimens were seen in 1970 on a small, bare, shallow, peaty pocket in the area where pure sand of zone 6 and pure peat of zone 7 mixed.

The different ecological requirements of the species expressed by their sorting into zones during a low water year at Crooked Lake indicate that a less diverse site with fewer zones might have fewer Coastal Plain disjuncts. A further indication is that younger sandy lakes might have a different assemblage than older peaty lakes.

Unnamed Lake, Merrill Township -

A nameless lake in Merrill Township, Newaygo County located at an elevation of 950 feet on outwash sands from the Saginaw and Lake Michigan Lobes of the retreating Wisconsin glacier is the home for two Coastal Plain disjuncts, Rhynchospora macrostachya and Eleocharis melanocarpa. This location with its fluctuating water level, lower in 1971 than in 1970 and much lower in both years than the apparent maximum, has a typical assemblage of species for Coastal Plain disjunct sites that are less sandy than Crooked Lake. It lacks several species present on Crooked Lake including Fuirena pumila, which is usually found on sandier lakes, and several

species commonly on sandy beaches with Fuirena; e.g., Stachys hyssopifolia, Lycopus uniflorus, and Xyris difformis. Species present at this location and also at Crooked Lake include, Polygala cruciata, Solidago remota, and Rhexia virginica, on relatively dry sandy soil, and Panicum meridionale and Rhynchospora capitellata on areas with more organic material and closer to the center of the pond.

Eleocharis melanocarpa forms a large clone on sandy soil well above the high water level of the pond. The situation is very similar to those in zones 1 and 6 on Crooked Lake where Eleocharis melanocarpa is also abundant. The mucky area immediately below the high water level is like zones 2 and 7 at Crooked Lake. Here in 1971 Rhynchospora macrostachya formed large pure stands at or near the previous years high water line, and these were apparently established from the scattered plants above high water in 1970 (Figs. 20 and 21).

The absence of Psilocarya scirpoides in an apparently ideal location may have been due to the water level not receeding far enough for it to become prevalent, lack of dispersal to this location, or unsuitable microclimate on the northern edge of the tension zone.

"East Beltline Pond" -

An unnamed depression in Grand Rapids Township, Kent County, is in terms of succession the oldest lake of the 31 that I visited. (Bazuin called this location "East Beltline Pond" on collection labels.) It is in a kettle hole in a sandy moraine just south of

Figure 20. A solid stand of Rhynchospora macrostachya at the previous years high water line. Photo taken on the unnamed lake in Merrill Township, Newaygo County. Compare to figure 18 showing a similar situation on Crooked Lake. A 3" by 5" card is shown for scale.

Figure 21. A closer view of the stand of Rhynchospora macrostachya shown in Figure 20. Note the bare ground between plants and compare to Figure 19. A 3" by 5" card is shown for scale.

the Grand River drainage channel at an elevation of 750 feet.

Bazuin and Voss collected *Rhynchospora macrostachya* at this location in 1955, but they apparently did not see *Psilocarya scirpoides*; the water level was higher then and the location was a pond. In 1970 and 1971 when the pond was empty of water both *Psilocarya scirpoides* and *Rhynchospora macrostachya* were present with *Hypericum boreale*, *Eleocharis obtusa*, *E. robbinsii*, and *Fimbristylis autumnalis*. The species present and the general aspect of the pond were very similar to zone 3 at Crooked Lake as it appeared in 1971 (Figs. 7 and 22, cf. Figs. 15 and 17).

This site is particularly interesting as it gives insight into the ecological relationships between *Rhynchospora macrostachya* and *Psilocarya scirpoides*. In 1970 both species were abundant on the sedge peat. Since *Psilocarya* occupied the wetter center of the site and *Rhynchospora* a drier zone surrounding it in 1970, it was assumed that moisture represented the limiting factor in their growth. However, in 1971, when the pond was somewhat drier, *Rhynchospora* had spread to the middle of the pond and formed a large nearly pure stand. *Psilocarya* was found only infrequently on bare pockets of peat among the *Rhynchospora* (Fig. 23). This relationship suggests that, although excess moisture limits both species, *Psilocarya scirpoides* is also limited by competition when in the presence of *R. macrostachya*.

Eleocharis melanocarpa has also been found at this location, probably on the sandy margin of the pond. Bazuin collected it in 1939, but I was unable to find it in either 1970 or 1971.

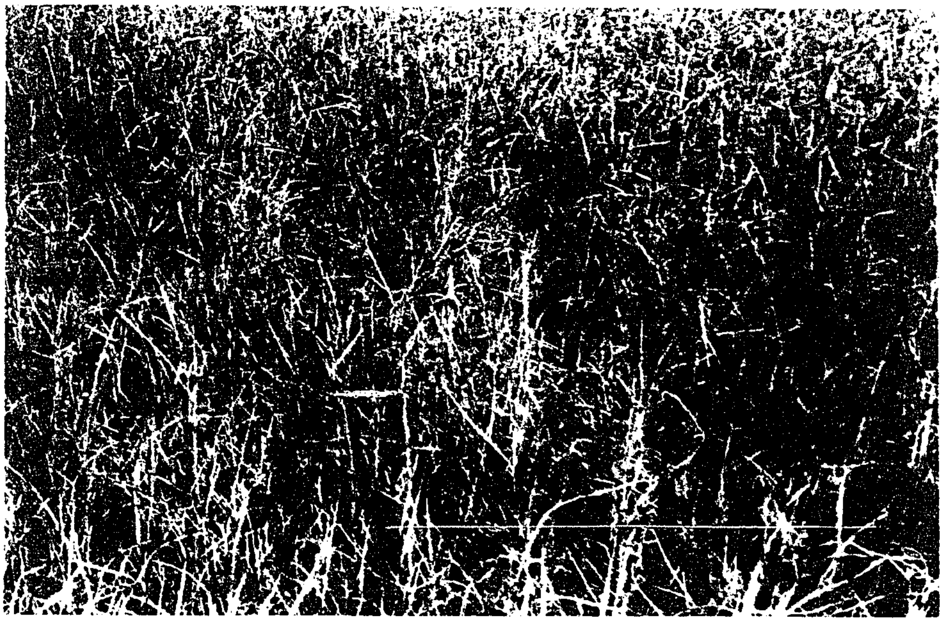

Figure 22. A nearly solid stand of Rhynchospora macrostachya growing in an area that is submerged only when the water level is at its highest on "East Beltline Pond". Compare with Figures 18 and 20 showing similar habitats on Crooked Lake and on the unnamed lake in Merrill Township.

Figure 23. A closer view of the habitat shown in Figure 22. Note the bare pockets of peat between the plants, and compare to Figures 19 and 21.

One of the "Five Lakes", East of Carr Lake -

Departure from Crooked Lake toward younger, sandier locations is shown by the nameless lake east of Carr Lake in Muskegon County. Older maps call this site, Carr Lake, and several nearby ponds and depressions "Five Lakes". It is located at an elevation of 657 feet on deposits left by Glacial Lake Algonquin. Voss (1967, 1972) has indicated that the five lakes are usually nearly dry, and they presumably have sedge peat bottoms. However, in 1970 this location was a nearly full, sandy-shored lake with relatively little peaty shore. The peaty bottom and sandy shore certainly represent a stage of succession earlier than that at Crooked Lake.

Psilocarya scirpoides and Fuirena pumila were on the wet sandy shore with Fimbristylis autumnalis, Cyperus rivularis, and Stachys hyssopifolia. Rhynchospora macrostachya was in a protected area where some organic material had accumulated, and Eleocharis melanocarpa was on drier sand with Rhexia virginica. Rhynchospora macrostachya, Psilocarya scirpoides, and Eleocharis melanocarpa again appear in situations like those on Crooked Lake; and the appearance of the first two on the wet predominantly sandy shore is analogous to their sporadic occurrence on Crooked Lake in 1970 when they were in sandier, drier areas between zones 1 and 2 and zones 6 and 7 (Figs. 12 and 16).

Pretty Lake -

Pretty Lake in Kalamazoo County is a kettle lake in the lateral moraine of the Lake Michigan lobe of the Wisconsin ice sheet at an elevation of 901 feet. On the northwest edge of the lake is a

small island on which Coastal Plain disjuncts may be found (Fig. 24). The island is sandy and has very little relief but is, according to a local resident, nearly connected to the mainland during periods of low water level. Significant plants on the island include: Panicum meridionale, Eleocharis melanocarpa, Fimbristylis autumnalis, Fuirena pumila, Scirpus smithii, Stachys hyssopifolia, and Solidago remota. All are typical of sandy lake shores having Coastal Plain disjuncts. Such a floral composition compares favorably with several other sites including Carr Lake in Muskegon County and Bankson and Keeler Lakes in Van Buren County which are predominantly sandy.

Since there is not a distinct wet, sandy shore flora on Crooked Lake it is difficult to make a direct comparison with young sandy lakes like Pretty Lake where Fuirena abounds. However, through transition types such as those described above for the "Five Lakes" location it can be seen that these young lakes are at the beginning of a progression of stages leading from sandy lakes to peaty depressions.

Indiana Lakes –

Peattie (1922) and McLaughlin (1932) considered Indiana to be the midwestern center of distribution for the Coastal Plain element and particularly the Coastal Plain disjuncts. McLaughlin thought Indiana was also a center of dispersal from which the Coastal Plain element in Wisconsin had originated. The sloughs; i.e., "water channels between the dunes" (Deam, 1940:1128) and lakes in the area of Lake and Porter Counties were described in a

Figure 24. The island at Pretty Lake. In the open areas _Eleocharis melanocarpa_ and _Fuirena pumila_ are common. The island may be nearly submerged during periods of highwater levels.

general way by Pepoon (1927) and were, according to him, sandy bottomed with a large quantity of sedge peat. He indicated that they were periodically nearly empty of water due to natural fluctuations in their water levels. Various authors have discussed either directly or indirectly the flora of these lakes (Peattie, 1930; Pepoon, 1927; Swink, 1969; Deam, 1940) and it is not difficult to discern their ecologic and floristic similarity to Crooked Lake and Keeler Lake in Michigan. Swink in discussing plants found on Goose Lake in Porter County, Indiana listed some of the associates of Psilocarya scirpoides and Fuirena pumila as Drosera intermedia, Eleocharis olivacea, Fimbristylis autumnalis, and Hypericum boreale all of which also are found on Crooked Lake.

Apparently the midwestern lakes on which the five Coastal Plain disjuncts are located are similar ecologically at least in such respects as are mentioned in the preceeding pages and this similarity is reflected in the presence of not only the Coastal Plain element but many associated species.

Cape Cod Ponds -

Several eastern locations for the five Coastal Plain disjuncts appear, from descriptions in the literature, to be essentially similar to the midwestern localities. In a discussion of the Cape Cod pond flora sinnott (1912) mentioned the northern extension of the Coastal Plain flora on the Cape, and discussed several of the environmental conditions associated with its occurrence there. Most notable of these characteristics is the large number of ponds occurring on glacial sand, with no drainage and a subsequent

fluctuation in water level. On these ponds, where wave action is intense, there is a sandy shore, while on protected shores there is muck and a more luxuriant vegetation. This intermittently submerged bottom and wet shore harbors an element including the Coastal Plain disjuncts. Although, as in Michigan, some species are found more commonly in sandy situations and others are more closely associated with an accumulation of organic material, they are all associated with the fluctuating shoreline.

Some of the Michigan locations most like Sinnott's description of Cape Cod ponds are Daggett and Otis Lakes in Barry County, Austin and Pretty Lakes in Kalamazoon County, Ely and Crooked Lakes in Allegan County, Carr Lake in Muskegon County, and Keeler Lake in Van Buren County. The flora of the Cape Cod ponds is also much like that of the ponds and lakes in Michigan and Indiana on which the Coastal Plain disjuncts are found. In both areas there are several Coastal Plain species which are near or at their northern limit on the Cape, present in southwestern Michigan and adjacent Indiana, but rare or absent elsewhere off the Coastal Plain. Many other species, less restricted in their distribution, are found in both locations. Table 8 lists some of these. Such floristic similarity emphasizes the ecologic similarity between the two areas.

Table 7. Coastal Plain species and their associates appearing on Cape Cod ponds and on certain midwestern lake shores.

A. Present in both locations but rare or absent elsewhere off the Coastal Plain.

Eleocharis melanocarpa	Carex albolutescens
Eleocharis robbinsii	Polygala cruciata
Psilocarya scirpoides	Rhexia virginica
Fuirena pumila	Stachys hyssopifolia
Rhynchospora macrostachya	Lycopus amplectens
Scleria reticularis	(Solidago tenuifolia, S. remota)*

B. Commonly associated with the above in both locations but not primarily restricted to the Midwest and to the Coastal Plain.

Dulichium arundinaceum	(Drosera longifolia, D. intermedia)
(Fimbristylis frankii, F. autumnalis)	Hypericum canadense
Hemicarpha micrantha	(Lycopus rubellus, L. americanus)
Cladium mariscoides	Gerardia purpurea
(Xyris caroliniana, X. difformis)	Utricularia spp.

* Species in parentheses are closely related "ecologic equivalents" the former appearing on Cape Cod the latter in the Midwest.

DISPERSAL POTENTIAL OF COASTAL PLAIN DISJUNCTS

The possibilities of vectors for the dispersal of Coastal Plain disjuncts into the Midwest have been discussed by both Peattie (1922) and McLaughlin (1932). Both concluded that the vector was water and that dispersal was along a continuous shoreline. One fact militates against water dispersal of the five species considered here. They do not occur on continuous or flowing bodies of water, but, nearly without exception, they are found on isolated seepage lakes.

Many workers, accept bird dispersal and consider it to be of great significance in the movement of littoral and marsh plants (Gleason and Cronquist, 1964; Good, 1964; Kerner, 1896; Pilj, 1969; Polunin, 1960; Ridley, 1930; Wulff, 1943). These authorities discuss two methods of bird dispersal: ingestion and later ejection of viable seeds and transport of seeds adhering to birds. Ridley (1930) in a thorough review of the topic cites species of Eleocharis, Rhynchospora, and Scleria as having been transported by these means, and further cites the Cyperaceae as particularly well suited to bird dispersal.

It is true that none of the five species have achenes which appear to be particularly suited to dispersal by mechanical adherence to birds. However all of the Coastal Plain disjuncts except Scleria reticularis do have barbed bristles that could serve in this capacity. Rhynchospora macrostachya has achenes

approximately 10 mm long and 5 mm wide. These achenes are possibly too large to normally adhere to birds in particles of mud; however, the other four species have much smaller fruits. There appears to be no evidence either from the literature or from observations that any of the five species except *Rhynchospora macrostachya* are food for waterfowl. At several locations plants of *Rhynchospora* were missing inflorescences. This was apparently due to the feeding activities of waterfowl, and at one location ducks were observed feeding on a large stand of the species. The role of bird dispersal is difficult to measure empirically due to the difficulty of marking specific propagules and observing their movement. It is reasonable to suggest, however, that dispersal by birds may be effective in the case of the Coastal Plain disjuncts.

Several species of water birds are known to migrate along a route leading from the East coast to the Midwest. Cooke (1915) and Lincoln (1939, 1950) discuss the east-west migration of certain water birds and Lincoln's discussion of Redheads, *Aythya americana* Eyton, and Coots, *Fulica americana* Gmelin, show them to be potential vectors for transportation of seeds to the Midwest during their spring migrations. Redheads banded at their breeding grounds in Utah have been recovered in Lyon County, Minnesota; Port Clinton, Ohio; and Cambridge, Maryland (Lincoln, 1939). Two Coots banded in Wisconsin were recovered in Maine and Connecticut respectively (Lincoln, 1939). Spring return flights along the same route as fall migrations would make these birds ideal for the movement of Coastal Plain species to their midwestern locations. Other

possible vectors include species such as Canvasbacks, Aythya valisineria Wilson, returning to the pothole country of the Canadian Prairies from winter grounds in Maryland, Virginia, and the Carolinas (Lincoln, 1950). In the absence of fossil evidence, however, no absolute answer can be available to the question of time of dispersal. The mere presence of potential vectors for transport of seeds at the present time neither precludes dispersal at an earlier postglacial time nor provides convincing evidence for a more recent arrival in the Midwest.

AN ORDINATION OF COMMUNITIES WITH COASTAL PLAIN DISJUNCTS

In order to make an objective comparison among the communities studied, an ordination of 21 of them was constructed (Fig. 25; Appendix 2). Correlation between a community's position on the ordination and environmental and floristic characteristics may indicate a cause and effect relationship (Bray and Curtis, 1957). Several relationships were noticed and the most striking of these shows that communities with _Fuirena pumila_ have sandy shores. In addition the correlations lend evidence for other environmental relationships discussed in the preceeding sections.

The techniques described by Bray and Curtis (1957), Cox (1972), and Greig-Smith (1964) were used and resulted in the ordination shown in Figure 25. Although Cox suggested that a correlation coefficient of .90 indicates a good fit of position on the ordination with dissimilarity indices, the value obtained from this ordination is only .79. However this is considered to be sufficiently high to show meaningful relationships. A three-dimensional ordination could have resulted in a higher correlation. However, it could account for an additional 21 percent of the variance at most. Also three-dimensional relationships are more complex and less readily interpreted, therefore no attempt was made to construct a three-dimensional ordination.

Figures 26, 27, 28, and 29 each show the position on the ordination of communities with one of the Coastal Plain disjuncts.

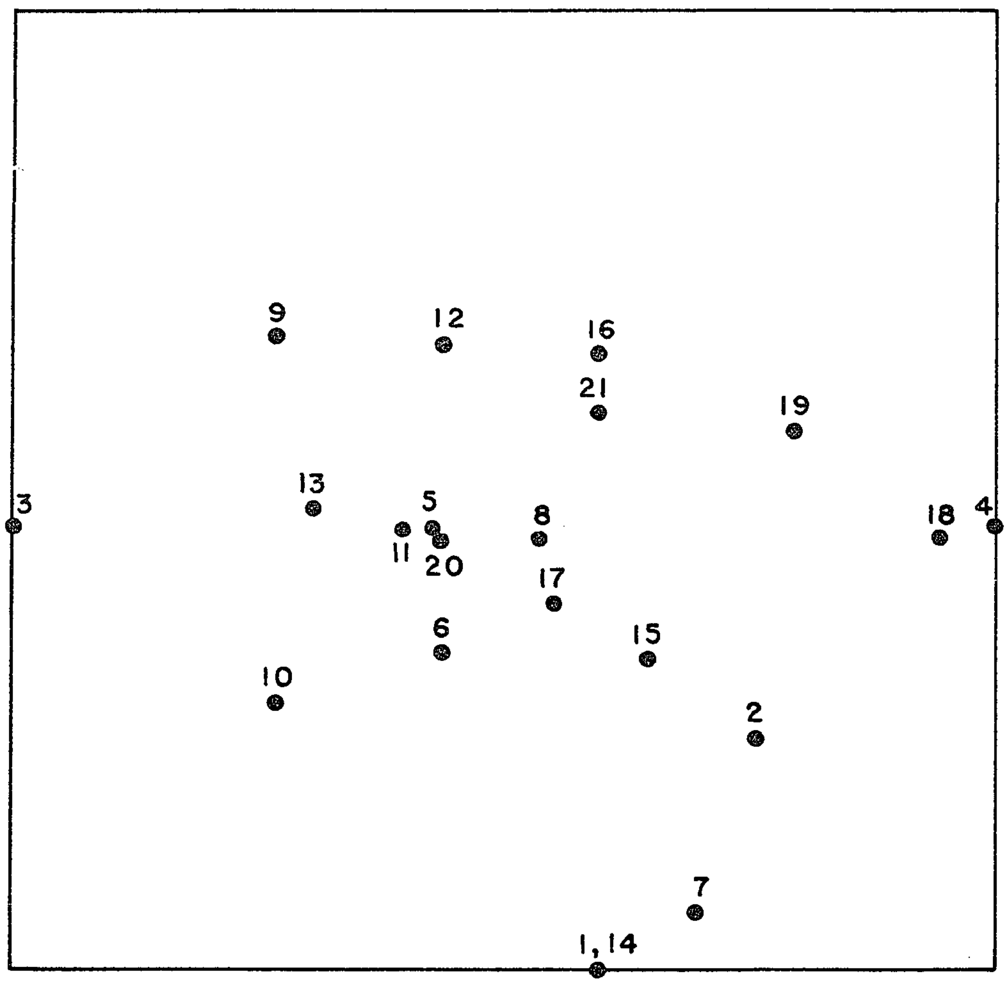

Figure 25. Two dimensional ordination of 21 Michigan communities on which Coastal Plain disjuncts are present. See Appendix 2 and Table 3 for the names and locations of the communities.

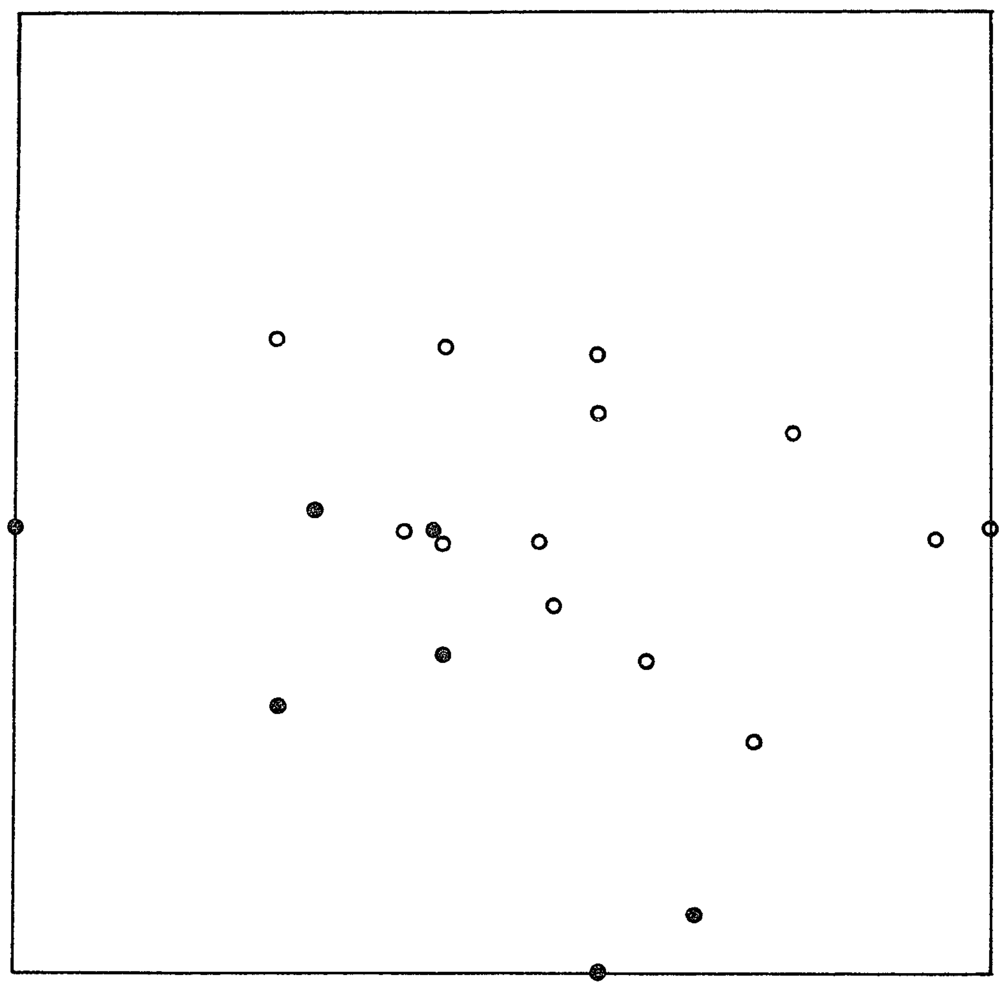

Figure 26. Distribution on the ordination of communities with Fuirena pumila o.

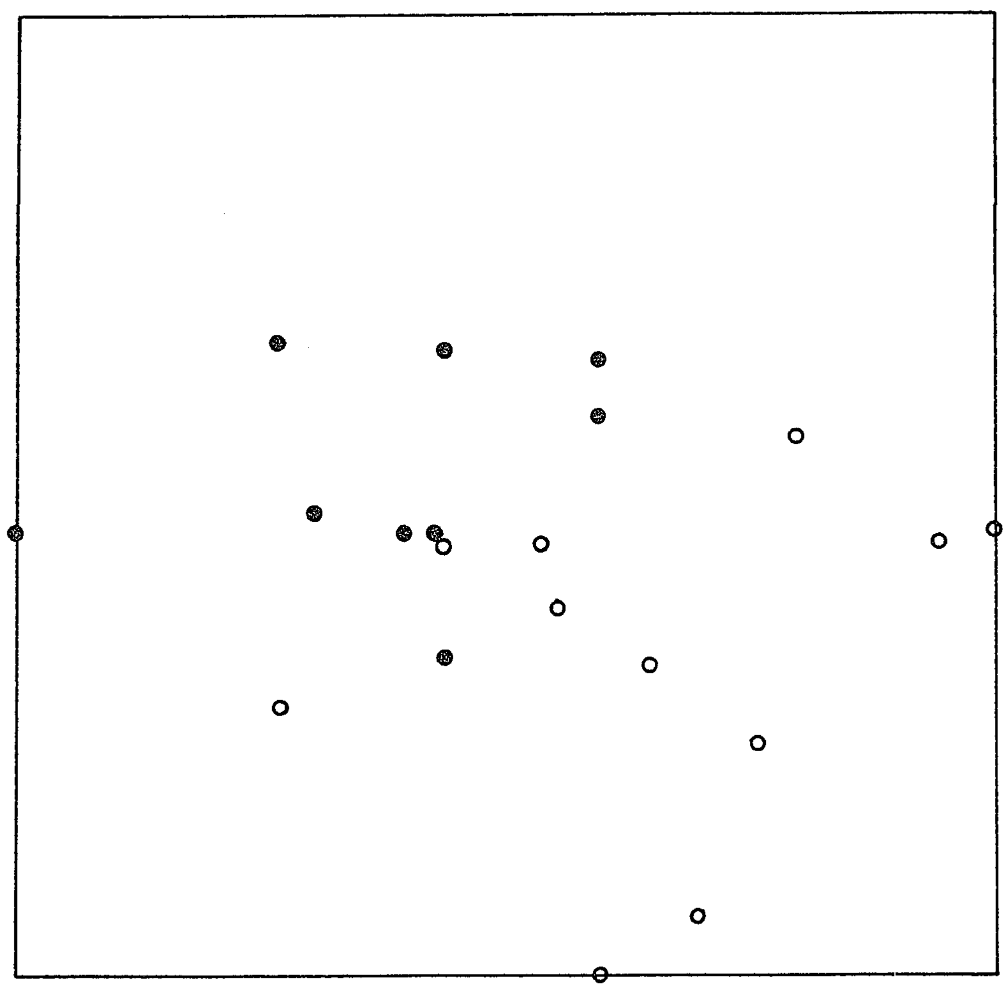

Figure 27. Distribution on the ordination of communities with Eleocharis melanocarpa o.

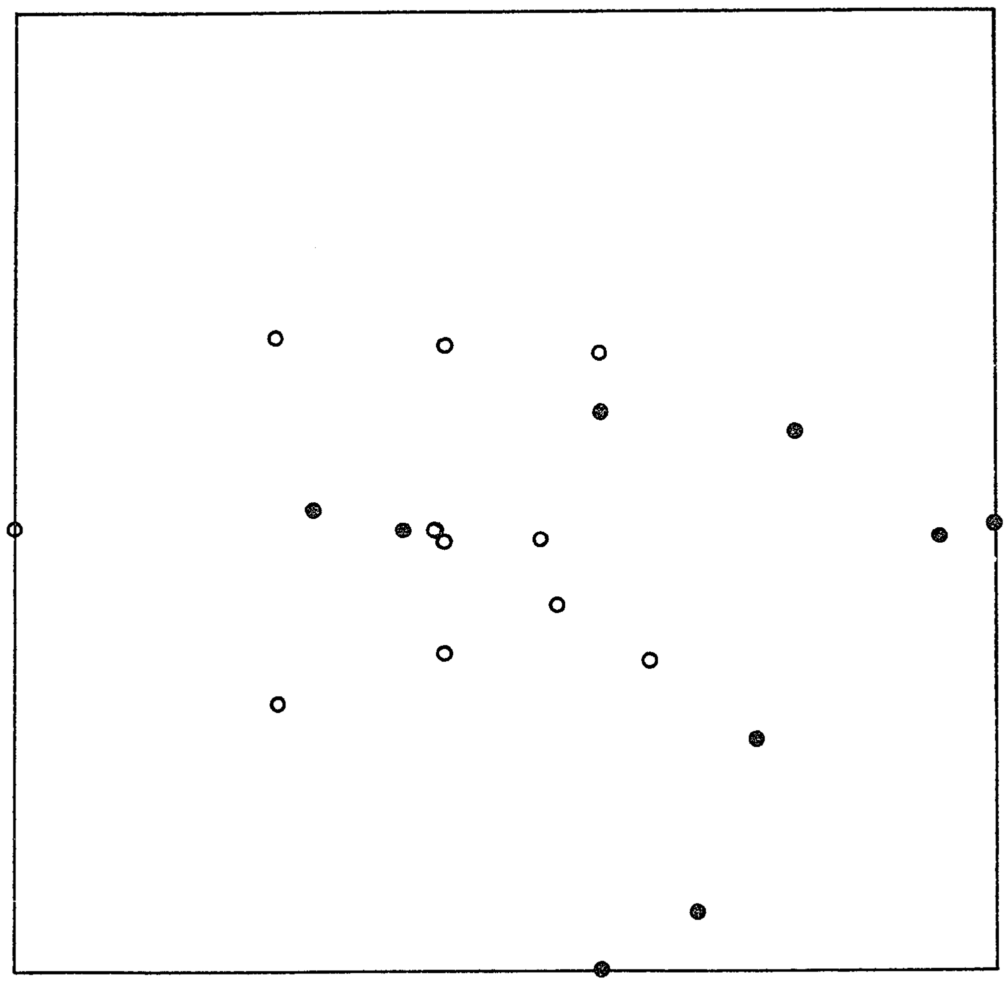

Figure 28. Distribution on the ordination of communities with Psilocarya scirpoides o.

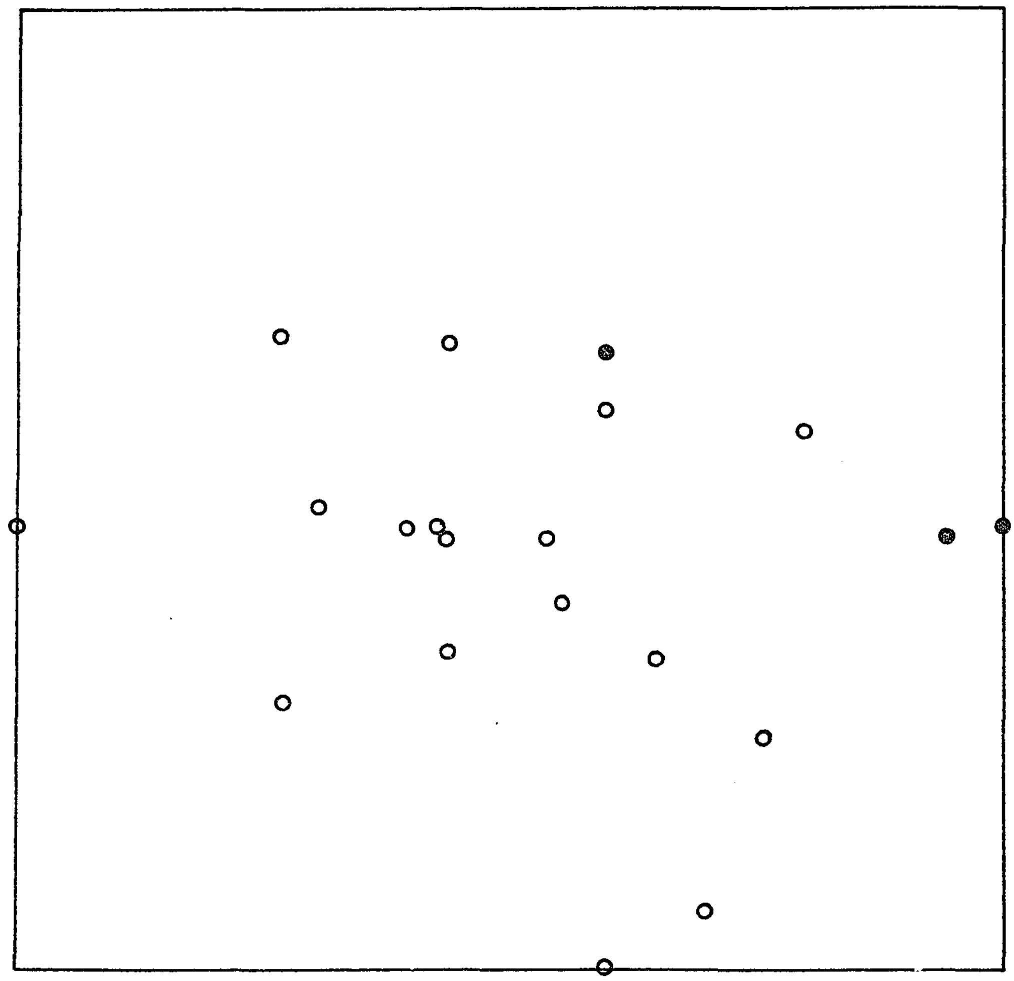

Figure 29. Distribution on the ordination of communities with Rhynchospora macrostachya o.

Of these, communities with Fuirena pumila form a coherent group on the right side of the ordination, and communities with Psilocarya scirpoides, Rhynchospora macrostachya, and Eleocharis melanocarpa are more widespread but do occupy specific areas. The indication from these data, assuming that the X and Y axes represent environmental gradients (Greig-Smith, 1964; Bray and Curtis, 1957), is that there are differences in habitat requirements of the four species. But it must be kept in mind that these differences are within the framework of the common characteritics of the communities outlined in the preceeding discussion.

Correlation of the communities with environmental conditions shows that the abscissa can be taken to represent soil types (Fig. 30), but there is not a clear relationship of either ordinate or abscissa with any other feature tested, including glacial topography, geography, and altitude. No meaningful quantitative measurements of water level fluctuation could be made in the two summers spent in the field, and this factor was not plotted on the ordination. The relationship between soil type and species composition is shown by a comparison of Figures 26, 27, 28, and 29, with figure 30. As soils become less sandy there is an evident change from an abundance of Fuirena pumila and Eleocharis melanocarpa to communities with Psilocarya scirpoides and Rhynchospora macrostachya.

According to Margalef (1963) and Odum (1971) there is often lower diversity in communities in early and late stages of succession while an intermediate stage may show a higher diversity.

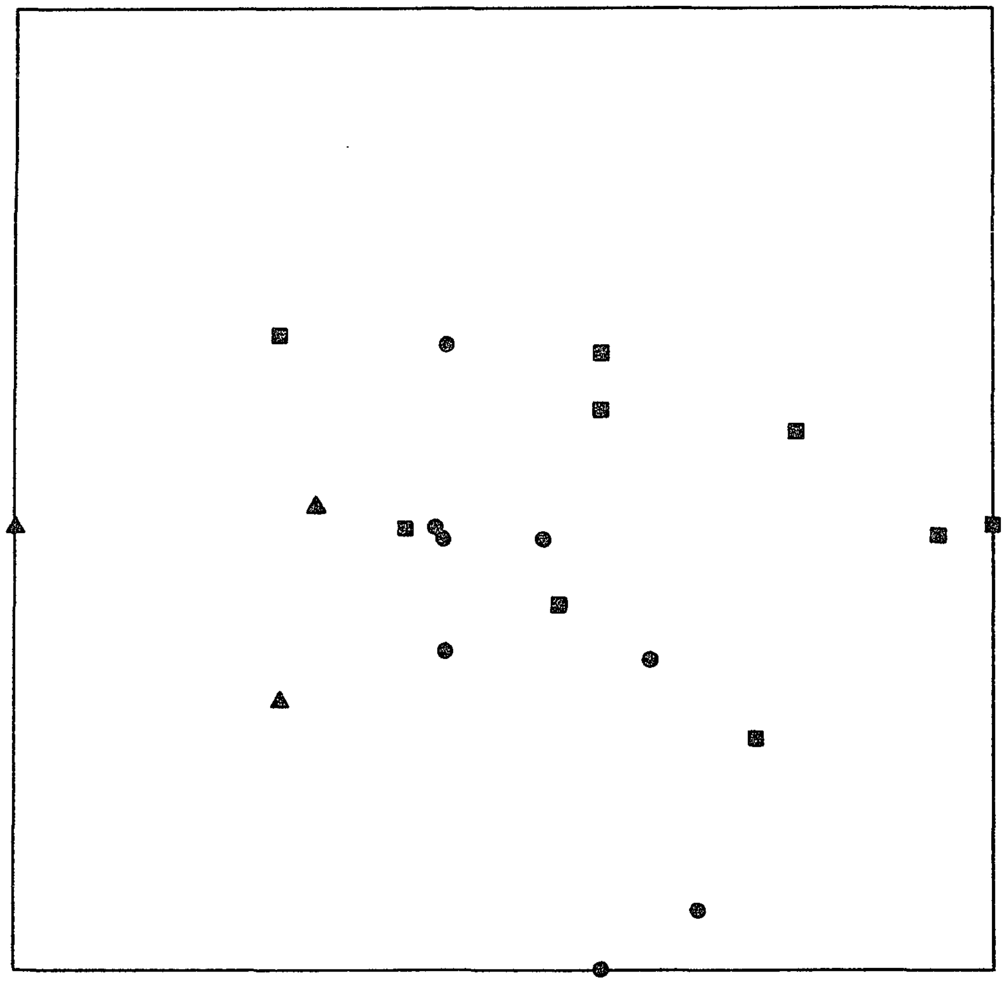

Figure 30. Distribution on the ordination of communities where Coastal Plain species occur on sandy (■), peaty (▲), and both sandy and peaty shores (●).

In Figure 31 the number of species used in constructing the ordination that appears in each community is plotted (cf. Appendix 2). This measure of diversity shows a slight trend for less diverse communities to appear at the ends of the X axis; i.e., the peaty and sandy ends of the abscissa. This evidence lends support to the earlier contention that these two soil types are represented in late and early stages of succession respectively.

Three factors contribute possible sources of error to conclusions based on the ordination. (1) The correlation coefficient is low. (2) Quantitative data is lacking on critical environmental factors such as microclimate and water level fluctuation. (3) Only 21 communities are ordinated rather than all 31 visited. An attempt to ordinate all 31 communities resulted in correlation coefficients varying from .02 to $\cong$ .30 depending on the end points chosen. In order to give a higher correlation coefficient ten communities were eliminated. These were chosen because they frequently had a dissimilarity index of 1 when compared with several other communities. Interestingly, they are also communities for which collection data are inadequate. High dissimilarity values may then reflect a dearth of information rather than actual dissimilarity. On this basis, that they are not well collected, the exclusion of ten communities seems justified.

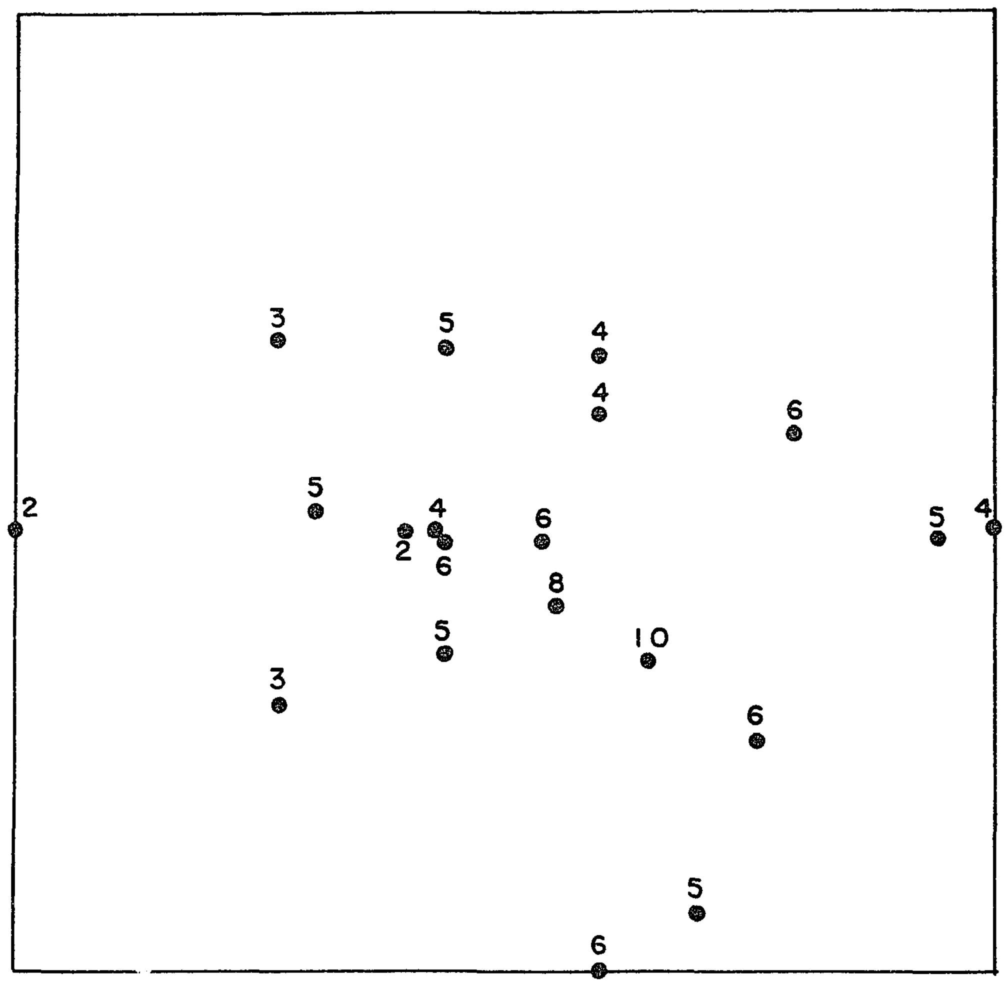

Figure 31. Distribution on the ordination of communities with varying degrees of diversity (10 is high diversity and 2 is low.).

CONCLUSIONS

The observations and data in the previous sections support a hypothesis to explain the arrival and persistence of certain Coastal Plain species in the Midwest. This hypothesis is unlike any presented heretofore, but it is consistent with observations made by previous workers and with data on these species in Michigan. In summary this hypothesis states that Coastal Plain species were disbtibuted, probably by birds, from the northern part of the Coastal Plain. They persist in the Midwest because of a unique combination of ecological conditions suitable for their growth. Finally, their distribution in the Midwest is related not so closely to geologic history as to the present distribution of a suitable habitat.

Ecological Relations

Many data presented support the contention that five Coastal Plain disjuncts are found in ecological situations that are very similar. The salient features of this habitat in Michigan and the Midwest include a lake or pond with (1) a fluctuating water level, (2) no inlet or permanent outlet, and (3) shores of noncalcareous sand or sedge peat. These lakes are located north of the southern advance of glacial ice and south of the northern reaches of the tension zone.

Where a suitable lake is present the fluctuating shoreline

frequently presents bare ground which early in succession is a sandy strand, but later is more likely to be a peaty flat. On this bare ground the Coastal Plain species may become established. Species like Fuirena pumila and Eleocharis melanocarpa readily colonize sandy beaches whereas Rhynchospora macrostachya, Psilocarya scirpoides, and Scleria reticularis may become established as succession proceeds.

Some factors seem to have no significance in the presence of the Coastal Plain species. These include proximity to the Lake Michigan shore, topographic features related to glaciation, and altitude.

Origin in the Midwest

The origin of the Coastal Plain element in the Midwest must take into account mode of dispersal, the route by which the species arrived, and the time of arrival. Of these there is evidence presented above only for bird dispersal and for the place of origin, but on the route and time only little evidence exists, and theories such as those given by Fernald (1931, 1937) or Gleason and Cronquist (1964) must suffice.

The Coastal Plain disjuncts studied all inhabit land-locked lakes and are reasonably well adapted to dispersal by water birds but not by wind. These facts support the idea that they were probably dispersed by birds and possibly, but not necessarily, over great distances at a single jump.

The point of origin on the Coastal Plain is almost certainly in

the east on the Atlantic Coastal Plain. The evidence for this is in the relative scarcity of Coastal Plain disjuncts in the Mississippi Embayment and on the Gulf Coastal Plain. Further evidence for origin on the northern part of the Coastal Plain in New England is the similarity between certain Cape Cod ponds and midwestern lake shores on which some of the Coastal Plain disjuncts appear. This may simply mean, however, that the plants were preadapted to a certain type of habitat within glaciated territory.

Persistence in the Midwest

The most significant problem in a consideration of Coastal Plain plants in the Midwest is why they persist. Peattie (1922) and McLaughlin (1932) agreed that they persist as relict colonies on Glacial Great Lakes shores and on Glacial Great Lakes' drainage features. Voss (personal communication) in his 1955 address at the American Institute of Biological Science meetings agreed but postulated a subsequent inland migration along river channels. The present distribution of the species discussed in this paper does not support this hypothesis. The following is considered to be in keeping with the facts presented. The Coastal Plain disjuncts can now be found wherever suitable habitat exists: on the Coastal Plain, in a few isolated relict stations in the piedmont and mountains of the southern states, and within the boundaries of glaciation and south of the northern boundary of the tension zone. The last mentioned area is primarily in New England and the Midwest around the southern end of Lake Michigan. In the eastern United

States wherever glaciation left noncalcareous sand and lakes with fluctuating water levels and wherever climate permits, the Coastal Plain disjuncts and their associates may be found.

APPENDIX 1:
SOURCES FOR DISTRIBUTION DATA OF COASTAL PLAIN DISJUNCTS

Eleocharis melanocarpa

Representative specimens[1]

MICHIGAN: Allegan Co.: Crooked Lake, Bazuin 8865 (MICH), Pierce 1456 (MICH!, RM!, WMU!); Ely Lake, Bazuin 1156 (MSU!), Pierce 1403 (WMU!), 1407 (WMU!); Clyde Twp. S ½ sect. 24, Pierce 1445 (MICH!, RM!, WMU!), 1727A (MICH!, RM!, WMU!). Barry Co.: Daggett Lake, Voss 8205 (MSU!), Pierce 1436 (MICH!, RM!, WMU!). Cass Co.: Dewey Lake, Pierce 1469 (MICH!, RM!, WMU!), Pepoon 1302 (MICH), Voss 8810 (MICH); Dowagiac Swamp, Pepoon 69 (MSU). Kalamazoo Co.: Austin Lake, Rapp 5158 (WMU!), Hanes 1644 (MSU!); Eagle Lake, Hermann 9040 (MSU!), Pierce 1510 (MICH!, RM!, WMU!); Pretty Lake, Hanes and Hanes 4426 (WMU!), Pierce 1522 (MICH!, RM!, WMU!). Kent Co.: "East Beltline Pond", Grand Rapids Twp. sect. 2, Bazuin 1533 (MSU!); Little Bostwick Lake, Bazuin 574 (MSU!), 1503 (MSU!), Pierce 1650 (MICH!, RM!, WMU!); Pine Lake, Bazuin 1692 (MSU), 1715 (MSU!); Reeds Lake, Bazuin 3 (AQC). Muskegon Co.: Burns Lake, Pierce 1617 (WMU!); Carr Lake, Voss 9153 (MICH), Pierce 1626 (MICH!, RM!, WMU!); Eggleston Twp. N ½ sect. 32 near Carr Lake, Pierce 1637 (MICH!, RM!, WMU!); Pine Island Lake, Pierce 1606 (MICH!, RM!, WMU!); Twin Lakes, Pierce 1560 (MICH!, RM!, WMU!), McLouth s.n. June 26, 1900 (MSU!), Wheeler

[1]Specimens I have examined are indicated by an exclamation point (!).

s.n. June 26, 1900 (MSU!). Newaygo Co.: Houseman Lake, Pierce 789 (MICH!, RM!, WMU!), Voss 11801 (MSU!); Merrill Twp. sect. 36, Pierce 1570 (MICH!, RM!, WMU!). Van Buren Co.: Keeler Lake, Hyypio and Schuyler 1034 (MICH), Pierce 1484 (MICH!, RM!, WMU!), 1490 (MICH!, RM!, WMU!); Keeler, Pepoon 896 (MSU!).

INDIANA: Porter Co.: Dune Park, Umbach 432 (MICH!), 3817 (COLO!, RM!), Moffatt 334 (MICH!).

MASSACHUSETTS: Barnstable Co.: Harwich, Fernald (Plantae Exsiccatae Grayanae) 327 (COLO!, RM!).

NEW JERSEY: Cape May Co.: Cold Spring, Witte s.n. June 1, 1931 (RM 126843!).

SOUTH CAROLINA: Bamberg Co.: 3.5 mi. north of Salkehatchie River on U.S. 301, Ahles 54353 (COLO!).

FLORIDA: Duval Co.: near Jacksonville, Curtiss 5668 (RM!).

Literature sources

INDIANA: Jasper Co.: Deam, 1940; Swink, 1969. LaPorte Co.: Hill, 1898; Swink, 1969. Porter Co.: Deam, 1940; Hill, 1898; Swink, 1969.

MASSACHUSETTS: Barnstable Co.: Fogg, 1930; Seymour, 1969; Sinnott, 1912; Svenson, 1937. Plymouth Co.: Seymour, 1969; Svenson, 1937.

RHODE ISLAND: Providence Co.: Seymour, 1969; Svenson, 1937. Washington Co.: Seymour, 1969.

NEW YORK: Richmond Co.: Hollick and Britton, 1882. Suffolk

Co.: Britton, 1880; Ferguson, 1922; Fernald, 1908; Leggett, 1874; Miller, 1871; Svenson, 1937.

NEW JERSEY: Burlington Co.: Stone, 1911; Svenson, 1937. Cape May Co.: Stone, 1911; Svenson, 1937. Cumberland Co.: Stone, 1911. Monmouth Co.: Britton, 1889.

DELAWARE: Sussex Co.: Tatnall, 1946.

VIRGINIA: Augusta Co.: Carr, 1940; Massey, 1961; Svenson, 1957. Isle of Wight Co.: Fernald, 1938; Massey, 1961. Rockingham Co.: Svenson, 1957.

NORTH CAROLINA: [All North Carolina records are from Radford et. al. (1968).] Brunswick Co.: Johnston Co.: New Hanover Co.: Richmond Co.: Wayne Co.

SOUTH CAROLINA: [All South Carolina records are from Radford et. at. (1968).] Bamberg Co.: Barnwell Co.: Berkeley Co.: Clarendon Co.: Darlington Co.: Williamsburg Co.

GEORGIA: [All Georgia records are from Svenson (1937).] Bullock Co.: Decatur Co.: Tift Co.

FLORIDA: [All Florida records are from Svenson (1937).] Duval Co.: Gadsden Co.: Leon Co.: Walton Co.

TEXAS: Leon Co.: Correll and Johnston, 1970; Svenson, 1937. Upshur Co.: Correll and Johnston, 1970.

Fuirena pumila

Representative specimens

MICHIGAN: Allegan Co.: Crooked Lake, Pierce 1720 (WMU!). Barry Co.: Mud Lake near Delton, Pierce 1408 (WMU!), 1668 (MICH!, WMU!), Schuyler 3870 (NY); Otis Lake, Pippen 357 (WMU!). Cass Co.: [Edwardsburg], [John Wright] s. n. Aug. 23, 1838 (MICH). Kalamazoo Co.: Austin Lake, Pierce 1833 (MICH!, RM!, WMU!); Eagle Lake, Hanes and Hanes 1144 (WMU!), Pierce 1505 (MICH!, RM!, WMU!), Kenoyer s. n. Sept. 20, 1930 (MSU!); Pine Island Lake, Gilbert 54048 (ALBC); Pretty Lake, Pippen 430 (WMU!), Pierce 1511 (MICH!, RM!, WMU!); Stony Lake, Pierce 1670 (MICH!, RM!, WMU!). Kent Co.: Dean Lake, Bazuin 680 (MSU!), Pierce 1657 (MICH!; RM!, WMU!). Muskegon Co.: Eggleston Twp. N½ sect. 32 near Carr Lake, Voss 3228 (MICH), 9161 (MICH), Pierce 1631 (MICH!, RM!, WMU!); Burns Lake, Pierce 1612 (WMU!); Pine Island Lake, Voss 5295 (MICH), Pierce 1592 (MICH!, RM!, WMU!). Van Buren Co.: Bankson Lake, Pippen 423 (WMU!), Pierce 1678 (MICH!, RM!, WMU!); Keeler Lake, Hyypio and Schuyler 1032 (MSU!), Pierce 1472 (MICH!, RM!, WMU!), 1704 (MICH!, RM!, WMU!). Washtenaw Co.: Island Lake, Stuckey 2455 (OS).

MASSACHUSETTS: Barnstable Co.: Brewster, Fernald (Plantae Exsiccatae Grayanae 331) (RM!). Hampden Co.: Springfield, Andrews 94 (RM!).

SOUTH CAROLINA: Jasper Co.: Savanna River Swamp, Radford, Bozeman, and Leonard 11491 (COLO!).

Literature sources

MICHIGAN: Cass Co.: Wright, 1839; Voss, 1972. Macomb Co.: Wheeler and Smith, 1881 (This report is likely in error.) Washtenaw Co.: Voss, 1972.

INDIANA: Porter Co.: Bush, 1905; Deam, 1940; Swink, 1969.

MASSACHUSETTS: Barnstable Co.: Bush, 1905; Coville, 1890; Fogg, 1930; Sears, 1908; Seymour, 1969. Hampden Co.: Bush, 1905; Fernald, 1924; Seymour, 1969. Middlesex Co.: Coville, 1890; Knowlton et. at., 1911; Sears, 1908; Seymour, 1969.

RHODE ISLAND: Providence Co.: Bush, 1905; Coville, 1890; Seymour, 1969.

NEW YORK: Suffolk Co.: Long Island: Bush, 1905, Coville, 1890; Ferguson, 1922, 1928; Grahm and Henry, 1933; Leggett, 1874. Fishers Island: Hanmer, 1940.

NEW JERSEY: Atlantic Co.: Britton, 1889; Stone, 1911. Cape May Co.: Bush, 1905; Coville, 1890; Stone, 1911. Monmouth Co.: Britton, 1889; Coville, 1890; Stone, 1911. Ocean Co.: Stone, 1911.

DELEWARE: New Castle Co.: Coville, 1890. Sussex Co.: Tatnall, 1946.

MARYLAND: Wicomico Co.: Coville, 1890. Worcester Co.: Redmond, 1932.

VIRGINIA: Nansemond Co.: Massey, 1961. Princess Anne Co.: Bush, 1905; Fernald, 1940.

NORTH CAROLINA: [All North Carolina records except New Hanover Co. are from Radford et. al. (1968).] Bertie Co.: Bladen Co.:

Carteret Co.: Chowan Co.: Columbus Co.: Craven Co.: Dare Co.: Gates Co.: Greene Co.: Harnett Co.: Harford Co.: Hyde Co.: Johnston Co.: Jones Co.: New Hanover Co.: Bush, 1905; Coville, 1890. Palmico Co.: Pender Co.: Scotland Co.: Wake Co.: Washington Co.: Wayne Co.: Wilson Co.

FLORIDA: Alachua Co.: Coville, 1890. Columbia Co.: Bush, 1905. Duval Co.: Coville, 1890. Lake Co.: Bush, 1905.

LOUISIANA: No county given: Coville, 1890 (This is a doubtful record.).

Psilocarya scirpoides

Representative specimens

MICHIGAN: Allegan Co.: Clyde Twp. S½ sect. 24, *Voss 8170* (MICH); Crooked Lake, *Pierce 1721* (MICH!, RM!, WMU!), *1812* (MICH!, RM!, WMU!). Barry Co.: Mud Lake near Delton, *Schuyler 3912* (NY). Emmett Co: Little Traverse Bay, Fallass *s.n.* [1914] (ALBC). Kalamazoo Co.: Mud Lake, *Hanes s.n.* Aug. 26, 1935 (MICH); Portage Bog, *Kenoyer s.n.* Sept. 1931 (MSU!); Stony Lake, *Hanes 3337* (MSU!); near West Lake, *Hanes s.n.* Sept. 12, 1935 (MICH). Texas Twp. sect. 34, *Hanes* and *Hanes 1154* (WMU!). Kent Co.: Dean Lake, *Bazuin 3999* (MSU!), 4203 (MSU!), Cole s.n. Oct. 8, 1898 (BLH); Grand Rapids Twp. NW¼ SW¼ sect. 2, *Pierce 1654* (MICH!, RM!, WMU!). Muskegon Co.: "Arbutus Lake" Laketon Twp. SW¼ sect. 16, *Voss 9168* (MICH); Eggleston Twp. N½ sect. 32 near Carr Lake, *Pierce 1629* (MICH!, RM!, WMU!), *Voss 9160* (MSU!); Little Blue Lake, *Bazuin 6737* (MICH, MSU!); Holton Twp. NW¼ sect. 30, *Voss 5287* (MICH). Newaygo Co.: Everett Twp. W½ sect. 23, *Voss 11796* (MSU!), *Stuckey 2444* (OS). Van Buren Co.: Keeler Lake, *Hyypio* and *Schuyler 1031* (MSU!). Washtenaw Co.: Island Lake, *Voss 11373* (MSU!), *Voss 12398* (MICH).

INDIANA: Porter Co.: Dune Park, *A. Chase 906* (MICH!, MSU!, RM!); Tamarack, *Lyon s.n.* Aug. 16, 1925 (MICH!).

MASSACHUSETTS: Barnstable Co.: Brewster, *Fernald* and *Long* (*Plantae Exsiccatae Grayanae*) *329* (RM!); Harwich, *Fernald* and *Long 16335* (RM!).

RHODE ISLAND: Providence Co.: Smithfield, Olney s.n. s.d. (RM 278064!).

CONNECTICUT: Hartford Co.: Hartford, Bissell 114 (3179) (RM!).

NORTH CAROLINA: Cumberland Co.: Fayetville, Biltmore Herbarium 4431[b] (RM!).

Literature sources

WISCONSIN: Marquette Co.: Greene, 1953. Waupaca Co.: Greene, 1953.

MICHIGAN: Emmett Co.: Voss, 1957a, 1957b, 1972. Washtenaw Co.: Voss, 1972.

INDIANA: La Grange Co.: Deam, 1940. La Porte Co.: Deam, 1970; Swink, 1969. Porter Co.: Deam, 1940; Swink, 1969. Starke Co.: Deam, 1940; Swink, 1969.

MASSACHUSETTS: Barnstable Co.: Bean et. al., 1963; Fernald and Griscom, 1935, Fogg, 1930; Seymour, 1969; Sinnott, 1912. Hampden Co.: Bean et. al., 1963; Fernald, 1908, 1924; Seymour, 1927, 1969.

RHODE ISLAND: Bristol Co.: Bean et. al., 1963, Providence Co.: Seymour, 1969.

DELAWARE: Sussex Co.: Smith, 1939; Tatnall, 1946.

MARYLAND: Nicomico Co.: Smith, 1939.

VIRGINIA: Nansemond Co.: Fernald, 1940, 1947; Massey, 1961. Norfolk Co.: Fernald, 1947; Fernald and Griscom, 1935. Princess Anne Co.: Fernald, 1947; Fernald and Griscom, 1935; Massey, 1961.

Southampton Co.: Fernald, 1947.

NORTH CAROLINA: [All North Carolina records are from Radford et. al. (1968).] Columbus Co.: Harnett Co.: New Hanover Co.

SOUTH CAROLINA: [All South Carolina records are from Radford et. al. (1968).] Kershaw Co.: Lee Co.: Williamsburg Co.

Rhynchospora macrostachya

Representative specimens

MICHIGAN: Allegan Co.: Crooked Lake, Pierce 1457 (MICH!, RM!, WMU!), 1815 (MICH!, RM!, WMU!); Ely Lake, Searles 87 (WMU!), Bazuin 9624 (MICH), Pierce 1389 (MICH!, RM!, WMU!); Clyde Twp. S½ sect. 24, Voss 8169, (MICH), Pierce 1443 (MICH!, RM!, WMU!); Perch Lake, Voss 9141 (MICH); Round Lake, Bazuin 4984 (MSU!), Allen s.n. Aug. 18, 1937 (MSU!). Barry Co.: Otis Lake, Luteyn 439 (WMU!), Pierce 1425 (MICH!, RM!, WMU!). Cass Co.: no collector or location, Aug. 29, 1914 (AQC). Kalamazoo Co.: Austin Lake, Hanes s.n. Sept. 7, 1936 (WMU!); Eagle Lake, Pierce 1727 (MICH!, RM!, WMU!); Island Marsh, Hanes s.n. July 26, 1934 (MICH), Hanes and Hanes 953 (WMU!); Pine Island Lake, Hanes 6247 (MSU!); Portage Bog, Kenoyer s.n. Sept. 1931 (MSU!); Weeds Lake, Hanes 2219 (NY); West Lake, Hanes and Hanes 3348 (MICH). Kent Co.: Dean Lake, Cole KSM 50781 (AQC), Pierce 1662 (WMU!); Grand Rapids Twp. sect. 2, Bazuin 155 (MSU!), Voss 2824 (MICH), Pierce 1655 (MICH!, RM!, WMU!). Mason Co.: Augustine Lake, Voss 9217 (MICH). Muskegon Co.: "Arbutus Lake" Laketon Twp. SW¼ sect. 16, Voss 9167 (MICH), Pierce 1524 (MICH!, RM!, WMU!); Carr Lake, Voss 2839 (MICH), Pierce 1622 (MICH!, RM!, WMU!); Eggleston Twp. N½ sect. 32 near Carr Lake, Voss 2224 (MICH), Pierce 1634 (MICH!, RM!, WMU!); Deer Lake (Unger Lake), Pierce 1801 (WMU!); Little Blue Lake, Bazuin 6736 (MSU!); Little Goosegg Lake, Voss 3243 (MICH); Town Line Lake, McLouth s.n. Aug. 22, 1899 (MSU!);

Wood Lake, Voss 5284 (MICH); Holton Twp. N½ sect. 30, Voss 5286 (MICH), Pierce 1802 (MICH!, RM!, WMU!). Newaygo Co.: Bass Lake region, Bazuin 3637 (MSU!); Issac Lake, Voss 5280 (MICH); Merrill Twp. sect. 36, Pierce 1565 (MICH!, RM!, WMU!). Van Buren Co.: Bankson Lake, Pippen 414 (WMU!); Fox Lake Marsh, Pepoon 387 (MSU!); Keeler Lake, Hyypio and Schuyler 1036 (MSU!), Pierce 1494 (MICH!, RM!, WMU!); Pine Lake, Gates 1461 (MICH).

INDIANA: Porter Co.: Dune Park, A. Chase 910 (RM!), Miller's, Umbach s.n. Sept. 4, 1897 (MICH!, RM!); Tamarack, Lyon s.n. 1923-IX-9 (MICH!).

MASSACHUSETTS: Barstable Co.: South of Sparrow Young's Pond, Fernald and Long (Plantae Exsiccatae Grayanae) 332 (RM!).

CONNECTICUT: New London Co.: Groton, Jausson s.n. Sept. 10, 1933 (RM!).

NEW JERSEY: Cape May Co.: Marshville, Brown and Witte s.n. Sept. 5, 1936 (RM!); Bennett, Witte s.n. Oct. 1, 1927 (RM!), Walker 2298 (COLO!).

DELAWARE: Sussex Co.: Laurel, Woodams s.n. Sept. 6, 1920 (RM!).

NORTH CAROLINA: Dare Co.: Roanoke Island, Radford and Bozeman 45302 (COLO!).

TEXAS: Harris Co.: 4 mi. south of Hockley, Boon 327 (COLO!, RM!).

Literature sources

MICHIGAN: Berrien Co.: Swink, 1969. Cass Co.: Voss, 1972.

Mason Co.: Voss, 1972.

INDIANA: Cass Co.: Deam, 1940. Lake Co.: Deam, 1940; Swink, 1969. Porter Co.: Deam, 1940; Fassett, 1933; Swink, 1969. St. Joseph Co.: Swink, 1969. Steuben Co.: Deam, 1940.

ILLINOIS: Pulaski Co.: Mohlenbrock et. al., 1962.

MAINE: Cumberland Co.: Bean et. al., 1963. York Co.: Neal, 1940.

MASSACHUSETTS: Barnstable Co.: Fogg, 1930; Seymour, 1969; Sinnott, 1912. Bristol Co.: Schweinfurth, 1916; Seymour, 1969. Franklin Co.: Bean et. al., 1963; Fernald, 1908; Seymour, 1969. Hampshire Co.: Blake, 1913. Norfolk Co.: Blake, 1913; Seymour, 1969.

RHODE ISLAND: Kent Co.: Seymour, 1969. Providence Co.: Seymour, 1969. Washington Co.: Reynolds, 1907; Seymour, 1969.

CONNECTICUT: Fairfield Co.: Blake, 1913; Graves et. al., 1910. Litchfield Co.: Blake, 1913; Graves et. al., 1910; Harger, 1900; Seymour, 1969. New Haven Co.: Graves et. al., 1910; Seymour, 1969. New London Co.: Graves et. al., 1910; Seymour, 1969. Windham Co.: Harger et. al., 1922; Seymour, 1969.

NEW YORK: Oswego Co.: Wibbe, 1878. Suffolk Co.: Ferguson, 1924; Miller, 1872.

NEW JERSEY: Atlantic Co.: Stone, 1911. Camden Co.: Britton, 1889; Stone, 1911. Cape May Co.: Britton, 1889; Stone, 1911. Gloucester Co.: Britton, 1889; Stone, 1911. Ocean Co.: Britton, 1889; Stone, 1911.

MARYLAND: Charles Co.: Fernald, 1940. Somerset Co.: Beaven

and Oosting, 1939. Worcester Co.: Beaven and Oosting, 1939.

VIRGINIA: Arlington Co.: Massey, 1961. Caroline Co.: Fernald, 1942b; Massey, 1961. Charles City Co.: Fernald, 1940, 1942b; Massey, 1961. Essex Co.: Fernald, 1942b; Massey, 1961. Fairfax Co.: Fernald, 1940; Massey, 1961. James City Co.: Fernald, 1940. King and Queen Co.: Massey, 1961. King William Co.: Fernald, 1940; Massey, 1961. New Kent Co.: Fernald, 1940; Massey, 1961. Norfolk Co.: Fernald, 1942b; Massey, 1961. Prince George Co.: Fernald, 1940; Massey, 1961. Surry Co.: Massey, 1961.

NORTH CAROLINA: [All North Carolina records are from Radford et. al. (1968).] Beaufort Co.: Brunswick Co.: Camden Co.: Chowan Co.: Columbus Co.: Craven Co.: Cumberland Co.: Curituck Co.: Dare Co.: Jones Co.: Lenior Co.: Moore Co.: Onslow Co.: Perquimans Co.: Robeson Co.: Sampson Co.: Tyrell Co.: Washington Co.

SOUTH CAROLINA: [All South Carolina records are from Radford et. al. (1968).] Aiken Co.: Beaufort Co.: Berkeley Co.: Charleston Co.: Clarendon Co.: Colleton Co.: Darlington Co.: Dorchester Co.: Georgetown Co.: Lee Co.: Orangeburg Co.: Sumter Co.: Williamsburg Co.

MISSOURI: [All Missouri records are from Steyermark (1963).] Barton Co.: Bullinger Co.: Butler Co.: Howell Co.: Oregon Co.: Pemiscot Co.: Ripley Co.: Stoddard Co.

ARKANSAS: Clay Co.: Bucholz and Palmer, 1926.

OKLAHOMA: No county given: Fernald, 1937; Waterfall, 1952. (The dot in Figure 4 is in the same location as shown by Fernald.)

Scleria reticularis

Representative specimens

MICHIGAN: Allegan Co.: Crooked Lake, *Pierce 1811* (MICH!, RM!, WMU!), *Pierce* and *Pippen 1834* (MICH!, RM!, WMU!).

INDIANA: Porter Co.: Mineral Springs, *Nieuwland 10262* (US); Dune Park, *Umbach 4604* (MICH!, RM!), *2629* (RM!, COLO!).

MASSACHUSETTS: Middlesex Co.: Winchester, *Fernald* and *Weatherby* (*Plantae Exsiccatae Grayanae*) 147 (RM!).

CONNECTICUT: Hartford Co.: Hartford, *Bissell 113* (*3218*) (RM!).

NEW JERSEY: Atlantic Co.: Dorothy, *Brown s.n.* Aug. 12, 1927 (RM 126770!). Cape May Co.: Bennett, *Witte s.n.* Aug. 20, 1932 (RM 103181!).

Literature sources

WISCONSIN: Adams Co.: Hartley, 1966.

ILLINOIS: Cass Co.: Winterringer, 1958.

MICHIGAN: Berrien Co.: Hebert, 1934. (This is a doubtful report.)

INDIANA: Jasper Co.: Deam, 1940; Swink, 1969. Newton Co.: Deam, 1940; Swink, 1969. Porter Co.: Deam, 1940; Swink, 1969.

MASSACHUSETTS: Barnstable Co.: Core, 1936; Fogg, 1930; Sears, 1908; Seymour, 1969. Dukes Co.: Seymour, 1969. Hampden Co.: Core, 1936; Fernald, 1924; Seymour, 1969. Middlesex Co.: Core,

1936; Fernald, 1908; Knowlton et. al., 1911; Sears, 1908; Seymour, 1969. Plymouth Co.: Core, 1936.

RHODE ISLAND: Providence Co.: Core, 1936; Seymour, 1969. Washington Co.: Core, 1936; Seymour, 1969.

CONNECTICUT: Middlesex Co.: Seymour, 1969.

NEW YORK: Suffolk Co.: Leggett, 1874; Core, 1936; Ferguson, 1924, 1926.

PENNSYLVANIA: Lancaster Co.: Small and Carter, 1913.

NEW JERSEY: Atlantic Co.: Britton, 1889. Camden Co.: Core, 1936. Cape May Co.: Core, 1936; Stone, 1911. Cumberland Co.: Core, 1936. Ocean Co.: Britton, 1889.

DELAWARE: Kent Co.: Core, 1936. Sussex Co.: Core, 1936. Newcastle Co.: Core, 1936.

VIRGINIA: Arlington Co.: Massey, 1961. Augusta Co.: Massey, 1961.

SOUTH CAROLINA: Berkeley Co.: Core, 1936.

GEORGIA: Sumter Co.: Core, 1936.

FLORIDA: No county given: Core, 1936.[1]

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[1]*Scleria reticularis* is also known from Mexico (Core, 1936).

APPENDIX 2: DATA FOR ORDINATION

BASIC Computer Program for Finding Dissimilarity Matrix for the Ordination

```
1Ø DIM X(3Ø,3Ø), A(3Ø,3Ø)

2Ø INPUT R, C, N

3Ø MAT SIZE A(R,R)

4Ø REM READ AND SUM ROWS OF DATA

5Ø FOR I=1 TO R

6Ø FOR J=1 TO C

7Ø INPUT X(I,J)

8Ø S=S+X(I,J)

9Ø NEXT J

1ØØ X(I,C+1)=S

11Ø S=Ø

12Ø NEXT I

13Ø REM FIND SIMILARITY AND DISSIMILARITY INDEX

14Ø FOR I-1 TO R

15Ø FOR J=1 TO R

16Ø FOR K=1 TO C

17Ø IF (X(I,K)+X(J,K))=2 GO TO 25Ø

18Ø NEXT K

19Ø A(I,J)=T/(X(I,C+1)+X(J,C+1))

2ØØ PRINT A(I,J);",";TAB(Ø)

21Ø T=Ø
```

```
22Ø NEXT J
23Ø NEXT I
24Ø GO TO 28Ø
25Ø T=T+2
26Ø GO TO 18Ø
27Ø REM PRINT OUT MATRIX
28Ø GO TO 34Ø
29Ø PRINT "ANALYSIS COMPLETE"
3ØØ MAT PRINT A
31Ø STOP
```

Variables

R = Maximum possible number of species in the communities

C = Number of communities

N = Value from which 2W/(a+b) shall be subtracted to give dissimilarity values.

X(I,J) = Matrix of presence absence values where each row represents a community and each column a species (1 = presence of a species in a community; 0 = absence of the species)

N.B.: This program was written in BASIC for a SIGMA 7 computer, and use on other computers will require appropriate alterations. The program as written is suitable only with presence absence data.

Species List for Ordination

Community	# on figure 25	Eleocharis melanocarpa	Fuirena pumila	Juncus scirpoides	Panicum meridonale	Polygala cruciata	Psilocarya scirpoides	Rhexis virginica	Rhynchospora macrostachya	Scleria reticularis	Solidago remota	Stachys hyssopifolia
Unnamed lake, Merrill Twp.	1	X			X	X		X	X		X	
Pine Island Lake	2	X	X			X			X		X	X
Drying lakebed, Holton Twp.	3						X		X			
Burns Lake	4	X	X			X						X
Little Blue Lake	5					X	X		X			X
Arbutus Lake	6					X	X	X	X			X
Carr Lake	7	X				X			X		X	X
One of "Five Lakes"	8	X	X				X	X	X			X
Dean Lake	9		X				X		X			
"East Beltline Pond"	10	X					X		X			
Otis Lake	11		X						X			
Mud Lake	12		X		X		X		X			X
Drying lake bed, Clyde Twp.	13	X			X		X		X		X	
Ely Lake	14	X			X	X		X	X		X	
Crooked Lake	15	X	X		X	X	X	X	X	X	X	X
Stony Lake	16		X		X		X					X
Eagle Lake	17	X	X		X		X	X	X		X	X
Pretty Lake	18	X	X		X						X	X
Austin Lake	19	X	X	X	X				X			X
Keeler Lake	20	X	X	X	X		X		X			
Bankson Lake	21		X		X				X			X

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