2001. Proceedings of the Indiana Academy of Science 110:51–78

THE STRUCTURE AND COMPOSITION OF VEGETATION IN THE LAKE-FILL PEATLANDS OF INDIANA

Anthony L. Swinehart[1] and **George R. Parker:** Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907

Daniel E. Wujek: Department of Biology, Central Michigan University, Mount Pleasant, Michigan 48859

ABSTRACT. The vegetation of 16 lake-fill peatlands in northern Indiana was systematically sampled. Peatland types included fens, tall shrub bogs, leatherleaf bogs and forested peatlands. No significant difference in species richness among the four peatland types was identified from the systematic sampling. Vegetation composition and structure, along with water chemistry variables, was analyzed using multivariate statistical analysis. Alkalinity and woody plant cover accounted for much of the variability in the herbaceous and ground layers of the peatlands, and a successional gradient separating the peatlands was evident. A multivariate statistical comparison of leatherleaf bogs from Indiana, Michigan, Ohio, New York, New Jersey and New Hampshire was made on the basis of vegetation composition and frequency and five climatic variables. The vascular vegetation communities of Indiana peatlands and other peatlands in the southern Great Lakes region are distinct from those in the northeastern U.S., Ohio and the northern Great Lakes. Some of these distinctions are attributed to climatic factors, while others are related to biogeographic history of the respective regions.

Keywords: Peatlands, leatherleaf bogs, fens, ecological succession, phytogeography

Within midwestern North America, the northern counties of Illinois, Indiana and Ohio represent the southern extent of peatland communities containing characteristic plant species of northern or boreal affinity. Here, peatlands are restricted to favorable microclimates such as small, water-filled kettles; and they never occur in great expanses as they do in the northern Lake States, the northeast and Canada, where regional topography and climate are more favorable for peat production. Peatland plant communities that occur at their range limits are important because they enhance the biological richness of these areas and potentially increase the genetic diversity of the plant species (Lesica & Allendorf 1995) due to their responses to heightened environmental stress. The occurrence of peatland communities with boreal affinities in marginal environments may amplify factors that favor their formation, and therefore provide excellent opportunities to study phytogeography and glacial relics.

While characteristically northern species such as *Chamaedaphne calyculata, Andromeda glaucophylla,* and *Carex oligosperma* often make "southern outlier peatlands" conspicuous to botanists, studies of such peatlands in New York, New Jersey and southern Michigan have shown a flora exhibiting mixed geographic affinity (Crow 1969; Lynn & Karlin 1985; Karlin & Lynn 1988). Although many studies have characterized the peatland flora of Canada (Jeglum et al. 1974; Slack et al. 1980; Sims et al. 1982; Glaser 1992), the northern Great Lakes region (Gates 1942; Vitt & Slack 1975; Glaser 1987; Glaser et al. 1992), and the northeastern United States (Worley & Sullivan 1980; Worley 1981; Lynn & Karlin 1985; Sorenson 1986; Damman & French 1987; Dunlop 1987; Karlin & Lynn 1988; Fahey & Crow 1995), relatively few have characterized the peatland plant communities in the southern Great Lakes region.

While extra-local and regional accounts of peatland plant communities in the region have been presented by Transeau (1905; 1906) (southern Michigan) and Waterman (1926) (northern Illinois), Ohio is the only state in the area that is represented by thorough treat-

[1]*Current address:* Department of Biology, Hillsdale College, Hillsdale, Michigan 49242

ments of its peatland plant communities (see Jones 1941; Aldrich 1943; Andreas 1989; Andreas & Bryan 1990; Andreas & Knoop 1992). Local or individual accounts of peatlands in the region include sites in southern Michigan (Crow 1969a,b; Sytsma & Pippen 1981, 1982; Glime et al. 1980, 1982; Keough & Pippen 1981, 1984), northern Illinois (Reichle & Doyle 1965; Sheviak & Haney 1973), Ohio (Aughanbaugh & Diller 1968; McQueen & Giesy 1975; Collins et al. 1982; Knoop 1987; Lauschman 1991), and Indiana (Hessler 1896; Markle 1916; Cain 1928; Lindsey 1932; Potzger 1934; Hull 1937; Friesner & Potzger 1946; Starcs 1961; Welch 1963; Lindsey et al. 1969; Wilcox 1982; Wilcox et al. 1986; Swinehart 1994; and Swinehart & Starks 1994). Few of the investigations of Indiana peatlands were quantitative in nature, and many were conducted on the same peatlands, such as Cabin Creek Raised Bog, due to greater public familiarity with their location.

The relative dearth of scientific attention to the peatlands in Indiana is not a function of insufficient study areas. Over 90 notable sites are known (Swinehart 1997) and, doubtless, many others remain to be found by scientists. *Sphagnum*-dominated communities in the state have been documented as far south as the city of Indianapolis (Cain 1928), and brown-moss-dominated peatlands reach well into the southern half of Indiana (Friesner & Potzger 1946; Welch 1962). A conservative estimate of historic peatland coverage in the state (based on true peat soils rather than mucks) is 62,000 ha, the main concentration being in northcentral Indiana (see Swinehart 1997). Considering the average surface area of individual peatlands in Indiana (approximately 20 ha (Swinehart 1997)), it becomes apparent that peatlands were extremely frequent in the northern part of the state during pre-settlement times. Unfortunately, as much as 87% of Indiana's wetlands has been destroyed (Dahl 1990), mostly as a result of agricultural development of the landscape.

The objectives of the present paper are to: 1) characterize lake-fill peatlands in Indiana based on the composition and structure of the vegetation of 16 bogs, fens and forested peatlands, 2) investigate the floral, hydrological and seral relationships of the peatlands using canonical correspondence analysis, and 3) compare the peatland flora of Indiana to other peatlands in the southern Great Lakes region as well as to peatlands in the North and Northeast.

STUDY AREA

The 16 peatlands described in this paper are located within the northern three tiers of counties in Indiana (Fig. 1). The entire area is blanketed with glacial deposits, the most recent being of Wisconsin age (Fig. 1). The glacial drifts cover bedrock composed chiefly of Devonian and Mississippian shales. In some areas of northeast Indiana, this bedrock is separated from the surface by over 150 m of glacial deposits. The elevations of the peatlands range from 155–320 m, with a mean of 262 m (SD = 35) (Swinehart 1997). The glacial drifts are rich in limestone originating from the Michigan basin that, along with the presence of lime-rich bedrock, imparts a strongly alkaline reaction in the ground and surface waters of the region.

Northeast and north-central Indiana is characterized by hundreds of lakes, and a distinct lake district stretches from the Huron River Valley of Michigan (see Transeau 1905–6) through the northeast corner of Indiana to a point nearly 160 km southwest. These lake basins consist mostly of kettles, created in the interlobate area of the former Saginaw and Erie Lobes of Wisconsin age. The lakes occurring west of the interlobate area (north-central Indiana) are a result of the stagnation and downmelting of the Saginaw Lobe *circa* 15,000 years BP. All of the peatlands in the present paper are the result of in-filling of lake basins (Swinehart 1997; Swinehart & Parker 2000).

The climate of northern Indiana is summarized in Table 1. In relation to the more northern latitudes of Canada, the northern Great Lakes region, and the northeastern United States (with the exception of New Jersey), the mean annual temperature in northern Indiana is warmer on average (Table 1). Mean annual precipitation is similar to other regions. However, mean annual snowfall in northern Indiana is generally less, and the number of frost-free days is generally more with the exception of northern New Jersey which varies from 130–180 frost-free days (Lynn & Karlin 1985) (Table 1). Climatic conditions in Indiana most closely resemble those governing the

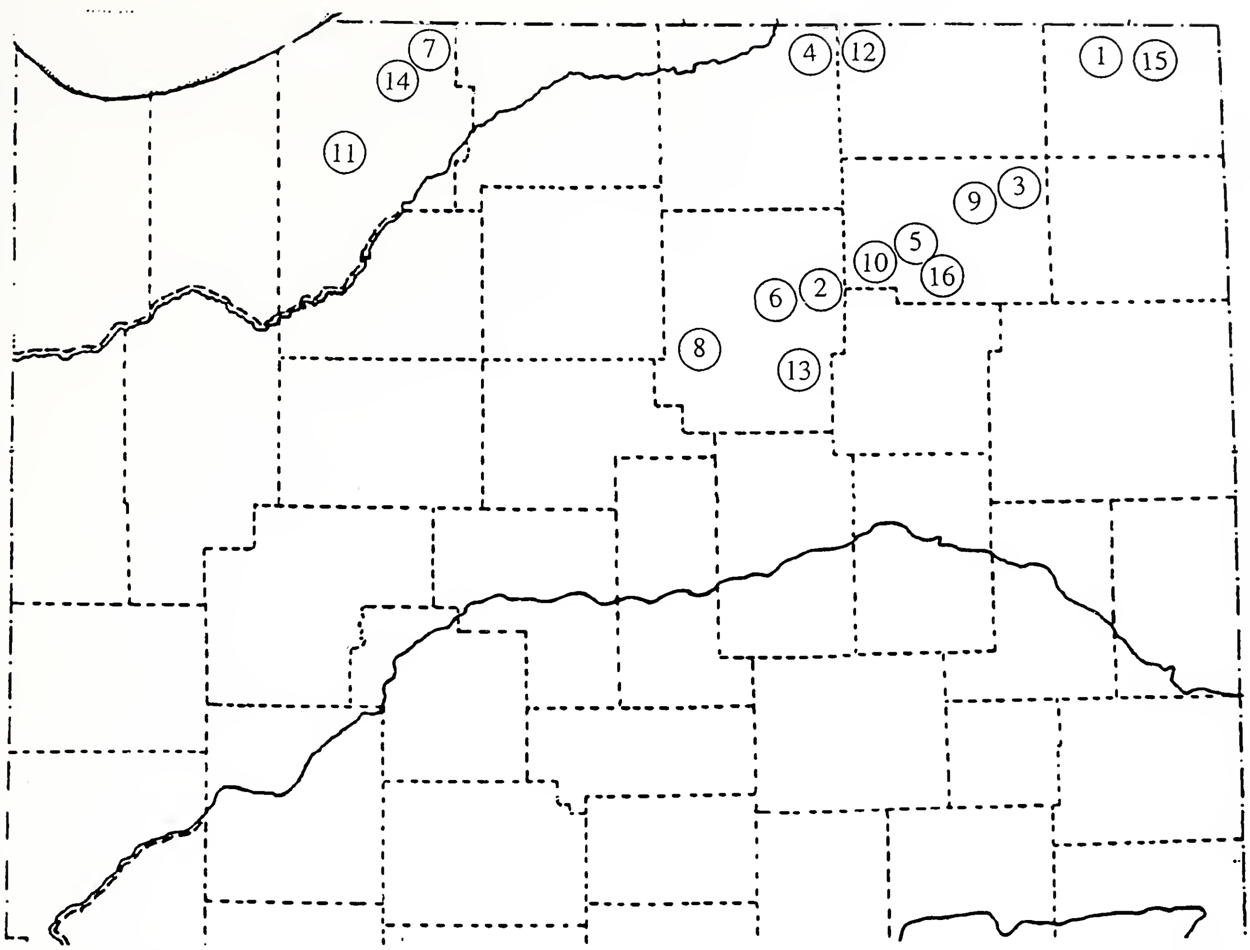

Figure 1.—Map of northern Indiana showing the location of study areas. 1) Binkley Fen, 2) Kiser Lake Fen, 2) Svoboda Fen, 4) Blueberry Bog, 5) Hickory Bog, 6) Little Chapman Bog, 7) Thompson Bog, 8) Burket Bog, 9) Dutch Street Bog, 10) Leatherleaf Bog, 11) Shoemaker Bog, 12) Yost Bog, 13) Little Arethusa Bog, 14) Mount Pleasant Bog, 15) Ropchan Memorial Bog, 16) Tamarack Bog.

peatland communities of northern Ohio (Table 1).

Most of the peatlands in the present study are located within the *Quercus-Carya* (oak-hickory) forest type (see Lindsey et al. 1965). Thompson Bog, Mt. Pleasant Bog, Dutch Street Bog, and Svoboda Fen are within the *Fagus-Acer* (beech-maple) association. Shoemaker Bog occurs within the dry-prairie region of northwest Indiana.

All of the peatlands are presently surrounded by agricultural fields. While Mt. Pleasant Bog (18 ha), Ropchan Memorial Bog (14 ha), Tamarack Bog (14 ha), Thompson Bog (6 ha), Blueberry Bog (10 ha), Hickory Bog (0.6 ha) and Kiser Lake Fen (2 ha) have a limited terrestrial forest buffer, Little Chapman Bog (9 ha), Burket Bog (25 ha), Dutch Street Bog (16 ha), Leatherleaf Bog (4 ha), Shoemaker Bog (15 ha), Yost Bog (8 ha), Little Arethusa Bog (15 ha), Svoboda Fen (25 ha) and Binkley Fen (31 ha) are buffered only by a narrow margin of wet or mesic forest associated with the lagg.

The individual basins range in maximum depth from 4.5–17 m with a mean maximum depth of 14.7 m (Swinehart 1997). The surface peat is classified as Houghton Muck and ranges from 1–7 m in depth (Swinehart & Parker 2000). Only two leatherleaf bogs and one fen exhibit a central pond of open water. The remainder have their entire surface area covered with peat, although below the surface, the peat is mostly unconsolidated and often contains large, open pockets (Swinehart & Parker 2000).

METHODS

Definitions.—In some parts of Europe and in Canada, the term bog is usually confined to any peatland where nutrient input is strictly ombrotrophic, designating all other peatlands, acid or alkaline, strongly or weakly minerotrophic, as fens. Authors studying New Eng-

Table 1.—Climate variables for several regions of eastern North America, including northwest and northeast Indiana. * Data from Schaal (1966). ** Data from NOAA (1974) for Charlottburg.

	Ontario (Sims et al. 1982)	Northern New York (Andrus et al. 1983)	New Hampshire (Fahey & Crow 1995)	Northern lower Michigan (Gates 1942)	Northern New Jersey (Lynn & Karlin 1985)	Southwest Michigan (Crow 1969a)	Northeast Ohio (Andreas & Bryan 1990)	Northwest Indiana (LaPorte) (NOAA 1974)	Northeast Indiana (Albion) (NOAA 1974)
Mean annual precip. (cm)	75	100	116.9	70.6	110	83.8	103.8	127	83
Mean annual snowfall (cm)	—	190	287.8	157	—	101	154.7	75–125*	75–100*
Mean annual temp. (°C)	−1	—	6.3	5.7	9.8**	9.2	9.6	9.9	9.6
Mean January temp. (°C)	−20	−9.3	−8.8	−7.2	−2	−11.4	−3.5	−3.4	−3.4
Mean July temp. (°C)	15	18.4	19.7	20	22	29.5	21.6	23.6	22.9
Avg. frost-free days	±90	105	105–130	±138	±140–170	150	165	±150*	±150*

Table 2.—Mean values ($n = 3$) for pH, conductivity, alkalinity, and hardness from interstitial waters of 16 Indiana peatlands. Acronyms in parentheses correspond with Tables 3, 4, 5, and 6. * Exact locations available from the Indiana Department of Natural Resources, Division of Nature Preserves.

Name of peatland*	County	Township/ Range*	pH	Conductivity (μMHOS)	Total alkalinity (ppm)	Calcium hardness (ppm)	Magnesium hardness (ppm)
Binkley Fen (BF)	Steuben	T38N, R13E	6.5	238	120	128	12
Kaiser Lake Fen (KLF)	Kosciusko	T33N, R7E	6.9	606	340	280	48
Svoboda Fen (SVF)	Noble	T35N, R11E	6.5	371	180	160	40
Blueberry Bog (BLB)	Elkhart	T38N, R7E	3.5	68	20	8	0
Hickory Bog (HB)	Noble	T33N, R8E	4.7	27	30	8	0
Little Chapman Bog (LCB)	Kosciusko	T33N, R6E	6.0	95	80	60	0
Thompson Bog (THB)	LaPorte	T38N, R1W	3.4	60	20	8	0
Burket Bog (BUR)	Kosciusko	T32N, R5E	3.9	44	12	8	0
Dutch Street Bog (DSB)	Noble	T35N, R10E	3.7	79	12	20	0
Leatherleaf Bog (LB)	Noble	T33N, R8E	4.7	48	20	8	0
Shoemaker Bog (SHB)	LaPorte	T36N, R3W	3.7	51	20	8	0
Yost Bog (YB)	Lagrange	T38N, R8E	3.2	96	12	8	0
Little Arethusa Bog (LAB)	Kosciusko	T31N, R7E	6.2	146	64	56	0
Mount Pleasant Bog (MPB)	LaPorte	T38N, R2W	3.9	75	12	8	0
Ropchan Memorial Bog (RMB)	Steuben	T38N, R12E	4.4	84	20	8	0
Tamarack Bog (TAM)	Noble	T33N, R9E	3.9	63	12	8	0

land bogs (Worley (1981), Johnson (1985), and Davis & Anderson (1991)) agree that a "true bog" refers to ombrotrophic peatlands. Crum (1988), though sparingly, also uses this definition. The problem with using nutrient source as a defining character arises in the difficulty encountered when trying to separate a bog from a fen, because the outward characteristics (i.e., vegetation) of a minerotrophic *Sphagnum*-dominated peatland and an "ombrotrophic" *Sphagnum*-dominated peatland are sometimes patchy or even indistinguishable.

Several authors continue to use a more traditional definition of bog where domination by *Sphagnum* mosses is a delimiting criterion. This is because the differences between a *Sphagnum*-dominated peatland and a peatland not dominated by *Sphagnum* are quite obvious, and the relative rapidity by which a non-*Sphagnum*-dominated peatland becomes *Sphagnum*-dominated (see Vitt & Kuhry 1992; Kuhry et al. 1993) denotes drastic ecological changes during and subsequent to the transition. This abrupt, ecological transition should be reflected more definitively in the nomenclature that is used to describe these systems. Andreas (1985), Dunlop (1987), Karlin & Lynn (1988) and Andreas & Bryan (1990) have all used the term bog to refer to peatlands dominated by *Sphagnum* regardless of the source of nutrient inputs.

In the present paper, peatlands with a bryoflora dominated by *Sphagnum* are termed bogs, peatlands with a bryoflora dominated by mosses of the family Amblystegiaceae are termed fens, and peatlands that have developed a canopy of forest vegetation are termed forested peatlands—regardless of source of water/nutrients. Bogs, fens and forested peatlands are distinguished from marshes, swamps and sloughs by the presence of significant deposits of peat (partially decayed organic material) rather than muck, and the absence of long periods of standing water (water table is at or slightly below the surface). Differences in mineral richness among bogs are qualified with the terms "mineral-rich" or "mineral-poor."

Selection of sites.—Two main criteria were used in the selection of the peatlands for this investigation: 1) peatlands occurring in defined basins (rather than those associated with rivers and streams), and 2) peatlands exhibiting a characteristic flora that distinguished them from typical marshes, swamps and sloughs. Characteristic plants included *Andromeda glaucophylla, Betula pumila, Carex oligosperma, Carex trisperma, Chamaedaphne calyculata, Coptis trifolia, Drosera* spp., *Larix laricina, Menyanthes trifoliata, Potentilla fruticosa, Sarracenia purpurea, Sphagnum* spp., *Vaccinium macrocarpon,* and *V. oxycoccos.* Selection of individual sites was contingent upon authorization by landowners.

Vegetation sampling.—The 16 peatlands selected included three fens (Binkley, Kiser and Svoboda), four tall-shrub bogs (Blueberry, Hickory, Little Chapman and Thompson), five leatherleaf bogs (Burket, Dutch Street, Leatherleaf, Shoemaker and Yost), and four forested peatlands (Little Arethusa, Mt. Pleasant, Ropchan Memorial and Tamarack). Vegetation in open peatlands was sampled by establishing a baseline along the long axis of each peatland. Transects spaced at 25 m or 50 m intervals (depending on the size of the peatland), and stretching across the predominant vegetation of each peatland [i.e., exclusive of lagg (the nutrient-rich, swampy margins of a peatland)], were established perpendicular to the baseline. Nested quadrats were placed at 25 m or 50 m intervals along each transect. In tall-shrub bogs and some forested peatlands, terrain hindered systematic spacing of sampling plots. In such cases, a single line transect was established through the predominant vegetation in the respective peatland.

Vegetation was stratified on the basis of height or stem diameter at breast height (DBH): The tree layer included living stems $>$ 4 cm DBH, the shrub layer included living stems $\leq$ 4 cm DBH and greater than 1 m in height, the herbaceous layer was vegetation less than 1 m in height, the ground layer was restricted to bryophytes, and the aquatic layer comprised submerged or floating plants (e.g., *Potamogeton* (pondweeds) and *Lemna* spp. (duckweeds)). The tree layer was sampled with 400 m^2 quadrats, the shrub layer with 100 m^2 quadrats, and all other layers with 1 m^2 quadrats.

Total percent frequency, total percent cover (density and basal area for trees), and importance values were calculated for each species in each peatland. Percent frequency was calculated by dividing the number of quadrats in which a species was found in a given peatland

Table 3.—Tree layer vegetation in 16 Indiana peatlands. The first number in each cell is the percent frequency, the second number is the density per hectare, the third number is the basal area per hectare, and the fourth number is the importance value for each species in the respective peatlands. Peatland acronyms correspond with those listed in Table 2. A "P" means the species was present as trees, but occurred outside of the sampling quadrats. "ND" means the species was present, but no numerical data is available. * Data from Swinehart (1994).

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Acer rubrum	—	—	—	—	—	100, 125, 0.41, 33	P
Acer saccharinum	—	—	—	—	—	—	—
Amelanchier laevis	—	—	—	—	—	—	—
Aronia melanocarpa	—	—	—	—	—	—	—
Betula alleghaniensis	—	P	—	—	—	33, 8.3, 0.08, 6	—
Fagus grandifolia	—	—	—	—	—	—	—
Fraxinus pennsylvanica	—	—	—	—	—	—	—
Juniperus communis	3, 0.83, 0.004, 8	—	—	—	—	—	—
Larix laricina	—	14, 5.5, 0.02, 100	4, 0.9, 0.003, 50	—	—	100, 141.7, 1.8, 55	—
Liriodendron tulipifera	—	—	—	—	—	—	—
Nyssa sylvatica	—	—	—	—	—	—	—
Pinus strobus	—	—	—	—	—	—	—
Populus tremuloides	3, 0.83, 0.002, 8	—	4, 0.9, 0.003, 50	26, 13, 0.11, 63	—	33, 8.3, 0.04, 6	—
Prunus serotina	6, 1.7, 0.004, 16	—	—	—	—	—	—
Quercus palustris	—	—	—	17, 6.5, 0.02, 27	—	—	—
Salix pedicellaris	3, 1.7, 0.007, 12	—	—	—	—	—	—
Salix sp.	3, 1.7, 0.07, 23	—	—	—	—	—	—
Sassafras albidum	—	—	—	—	—	—	—
Toxicodendron vernix	6, 1.7, 0.007, 16	—	—	—	—	—	—
Ulmus americana	—	—	—	—	—	—	—

by the total number of quadrats sampled in each peatland. Percent cover was calculated by dividing the sum of observed cover values (determined visually) for each species in each peatland by the total number of quadrats in each peatland. Importance values for herbs and bryophytes represent the sum of the relative frequency and relative cover, divided by two and multiplied by 100.

Species that were not recorded in the quadrats, but were noted elsewhere in the peatland, were included in the species lists (Tables 3–7) as "present." However, no attempt was made to locate rare plants or to compile a complete flora for the sites. The Indiana Department of Natural Resources, Division of Nature Preserves maintains qualitative lists for many of the peatlands.

Vouchers for all bryophytes were placed in the private herbarium of the first author at Hillsdale College and in the Kriebel Herbarium of Purdue University (PUL). In addition, duplicate voucher specimens of *Sphagnum* spp. from Hickory, Leatherleaf and Tamarack Bogs were placed in the University of Michigan Herbarium (MICH). All other duplicate Sphagna were placed in the Herbarium of Binghamton University (BING). Nomenclature of *Sphagnum* follows Andrus (1980, 1987). Nomenclature of all other mosses follows Crum & Anderson (1981). Nomenclature of hepatics follows Crum (1991), and nomenclature of vascular plants follows Swink & Wilhelm (1994), with the exception of plants of the genus *Toxicodendron.*

Water chemistry.—Water was sampled at three locations in the area containing the predominant vegetation (e.g., open mat rather than lagg). All water samples were collected within a one-week period in late July (1995), after the rainy season had passed. Water was collected from pools of standing water or interstitial waters of the peat depending on conditions. Interstitial waters were obtained by pushing a glass jar into the peat and allowing water to enter the mouth of the jar. Titration of samples for total alkalinity, calcium hardness, and magnesium hardness was conducted within two hours of collection. Values for pH and specific conductance were taken on site with a Cole-Parmer digital pH meter, and an Orion Conductivity/TDS meter, respectively.

Table 3.—Extended.

Leatherleaf bogs					Forested peatlands			
DSB	YB	BUR	SH	LB	LAB	MPB	TAM*	RMB
64, 122, 1.5, 98	55, 72.5, 0.54, 83	26, 24, 0.14, 84	3, 0.78, 0.002, 50	—	100, 245, 7.8, 36	86, 277, 8.3, 50	ND	100, 485, 4, 45
—	—	4, 3.7, 0.04, 16	3, 0.78, 0.002, 50	—	64, 63.6, 1.7, 11	36, 19.6, 1.1, 12	ND	17, 8.3, 0.09, 2
—	—	—	—	—	27, 6.8, 0.05, 2	—	ND	—
—	—	—	—	—	9, 2.3, 0.004, <1	—	—	—
—	—	—	—	—	—	—	—	100, 171, 1.3, 21
—	—	—	—	—	—	P	—	—
—	9, 1.1, 0.01, 8	—	—	—	27, 6.8, 0.24, 3	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	91, 313, 1.4, 22	64, 41.1, 0.4, 11	P	75, 135, 2.3, 22
—	—	—	—	—	9, 2.3, 0.02, <1	—	—	—
2, 0.5, 0.002, 1	—	—	—	—	—	14, 3.6, 0.1, 2	—	—
—	—	—	—	—	—	57, 76.8, 4.9, 18	—	P
—	—	—	—	—	—	—	—	—
—	—	—	—	—	9, 2.3, 0.02, <1	—	ND	—
—	10, 8.7, 0.09, 17	—	—	—	—	7, 1.8, 1.1, 1	ND	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	18, 9.1, 0.05, 4	—	—	8, 2.1, 0.14, 1
—	—	—	—	—	—	—	ND	—
—	—	—	—	—	45, 18.2, 0.05, 4	—	—	33, 10.4, 0.02, 4
—	—	—	—	—	100, 156, 1.7, 17	14, 3.6, 0.1, 2	ND	25, 18.7, 0.12, 4

Statistical analyses.—Canonical Correspondence Analysis (CCA) of the vegetation and environmental variables was conducted with PC-ORD Version 2.0 (McCune & Mefford 1995). Data used in the vegetation matrix include the percent cover for each herbaceous and aquatic layer species in each peatland. Data used in the environmental variable matrix include values for total alkalinity, pH, total percent shrub cover, and total tree basal area in each peatland.

In the regional comparison of vegetation in leatherleaf bogs, data were taken from several published studies. A data-type that was common to all of the papers was percent frequency for each species. To reduce bias caused by differences in sampling design, frequencies were converted to a scale of 1 to 5, where 1 = 1–19%, 2 = 20–39%, 3 = 40–59%, 4 = 60–79%, and 5 = 80–100%. Detrended Correspondence Analysis (DCA) was used to determine the variability in the vegetation. A second matrix that included mean annual precipitation, mean annual temperature, mean July temperature, mean January temperature, and mean number of frost-free days was incorporated with the vegetation data in a CCA ordination.

RESULTS AND DISCUSSION

Species richness.—A total of 131 vascular plants, 49 bryophytes, and one alga was recorded from the 16 peatlands (Tables 3–7). The mean number of vascular plants, calculated from species found in quadrats only, was determined for leatherleaf bogs, fens, tall-shrub bogs and forested peatlands. Although the mean number of species from the leatherleaf bogs appeared comparatively small, no significant differences in species richness among the four peatland types were identified. An analysis of species richness as a function of alkalinity (indicative of the degree of minerotrophy) showed no significant relationship ($p = 0.107$, $R^2 = 0.175$). Although peatlands at extremes of the gradient harbor characteristic, dominant plants that are adapted for specific pH and mineral conditions, data suggest that both ends of the gradient may reduce species richness because of common factors such as substrate inundation and anoxia. While mineral-rich peatlands and fens are generally

Table 4.—Shrub layer vegetation in 16 peatlands in Indiana. The first number in each cell is the percent frequency for each species, the second number is the percent cover, and the third number is the importance value for each species in the respective peatlands. Peatland acronyms correspond with Table 2. A "P" means the species was present as shrubs, but occurred outside of the sampling quadrats. * Data from Swinehart (1994).

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Acer rubrum	—	7, 0.11, 2	22, 1, 13	17, 0.74, 4	P	100, 15, 17	—
Amelanchier laevis	—	—	—	—	—	—	—
Aronia melanocarpa	—	—	—	4, 0.04, 1	—	100, 15, 17	80, 14, 20
Betula alleghenienesis	3, 0.03, 1	—	—	—	—	33, 0.3, 3	—
Betula pumila	10, 0.23, 3	17, 3.3, 13	4, 0.11, 2	—	—	—	—
Carpinus caroliniana	—	—	—	—	—	—	—
Cephalanthus occidentalis	—	—	—	—	29, 3, 4	33, 1.7, 4	40, 19, 16
Chamaedaphne calyculata	—	—	—	—	—	—	20, 1, 4
Cornus foemina	20, 4.3, 11	—	4, 0.37, 3	9, 0.48, 2	—	—	—
Cornus stolonifera	93, 23.8, 58	34, 3.2, 18	—	4, 0.22, 1	—	—	—
Decodon verticillatus	—	—	—	—	—	P	—
Gaylussacia baccata	—	—	—	—	—	—	20, 1, 4
Ilex verticillata	—	—	11, 0.85, 8	—	14, 5, 3	—	40, 12, 12
Larix laricina	—	7, 0.34, 3	48, 3.4, 34	—	—	—	—
Lindera benzion	—	—	—	—	—	—	—
Nemopanthus mucronatus	—	—	—	—	—	67, 16.7, 15	20, 2, 4
Nyssa sylvatica	—	—	—	—	—	—	—
Parthenocissu quinqnefolia	—	—	—	—	—	—	—
Pinus strobus	—	—	—	—	—	—	—
Populus tremuloides	13, 1.2, 5	—	—	13, 0.30, 3	—	33, 1.7, 4	—
Potentilla fruticosa	3, 0.33, 1	—	—	—	—	—	—
Prunus serotina	—	—	—	—	—	—	—
Quercus palustris	—	—	—	26, 2.7, 8	—	—	—
Rosa palustris	7, 0.33, 2	7, 0.38, 3	4, 0.04, 1	13, 0.69, 3	P	P	—
Salix candida	—	—	—	43, 3.1, 11	—	—	—
Salix discolor	—	3, 0.17, 1	—	—	—	—	—
Salix lucida	—	—	4, 0.11, 2	—	—	—	—
Salix pedicellaris	20, 1.9, 8	3, 0.17, 1	—	26, 1.3, 6	—	—	—
Salix sericiea	7, 0.83, 3	—	—	—	—	—	—
Salix serrissima	—	38, 2.3, 16	—	—	—	—	—
Salix sp.	—	—	—	—	P	—	—
Spirea tomentosa	—	10, 0.55, 4	11, 0.18, 5	4, 0.04, 1	—	P	—
Toxicodendron vernix	23, 0.93, 7	58, 8.3, 38	48, 3, 32	100, 38.7, 58	P	33, 3.3, 5	—
Toxicodendron radicans	—	—	—	—	—	—	—
Ulmus americana	—	—	—	—	—	—	—
Vaccinium corymbosum	—	—	—	9, 0.65, 2	—	100, 46.7, 33	100, 51, 41
Viburnum lentago	—	—	P	—	—	—	—
Vitis riparia	3, 0.33, 1	—	—	—	—	—	—

characterized as having a richer flora, most of the species that contribute to the greater richness are probably infrequent or rare members of the community, and may result from greater habitat heterogeneity rather than an overall more optimal growth environment.

Structure and composition of the plant communities.—*Extremely mineral-rich fen:* Extremely mineral-rich fens, represented in this study by Kiser Lake Fen, have strong groundwater influence that is often artesian in nature. Because the water is under pressure, these "raised fens" exhibit peat that accumulates far above the average water table of the surroundings. In Kiser Lake Fen, peat deposits are slowly sprawling up nearby hillsides. The substrate, though quaking, is not treacherous. A similar raised peatland occurs in Randolph County (Friesner & Potzger 1946). Peat that accumulates in this type of wetland is often underlain by significant deposits of marl (Friesner & Potzger 1946; Swinehart & Parker 2000) or a peaty tufa (Stewart et al. 1994). Extremely mineral-rich fens in Indiana are characterized by a dense, low growth of *Potentilla fruticosa,* the fen

Table 4.—Extended.

Leatherleaf bogs					Forested peatlands			
DSB	LB	YB	BUR	SH	LAB	MPB	TAM*	RMB
42, 2	P	65, 4.5, 15	55, 2.8, 23	3, 0.03, 2	45, 3.6, 6	36, 3.8, 11	3, 1, 6	83, 18.2, 23
—	—	—	—	—	18, 0.91, 2	—	P	—
53, 14, 22	—	35, 2.9, 8	33, 1.7, 14	3, 0.47, 5	—	14, 0.43, 3	11, 1, 10	P
—	—	—	—	—	—	—	—	42, 4.6, 9
—	—	—	—	—	—	—	—	—
—	—	—	—	—	9, 0.09, 1	—	—	—
42, 17, 22	1, 1, <1	25, 6.4, 11	37, 1.5, 14	37, 3.3, 42	—	7, 0.21, 2	—	—
—	—	5, 0.5, 1	—	—	—	—	—	—
—	—	—	—	—	9, 0.27, 1	—	—	—
—	—	—	—	—	P	—	—	—
—	—	—	—	16, 2.9, 27	—	—	—	—
—	—	—	4, 0.74, 4	—	—	—	—	17, 1.7, 3
—	—	45, 4, 11	11, 1.8, 9	9, 0.78, 10	82, 17.3, 18	7, 0.07, 2	16, 3, 21	100, 28.3, 32
—	—	—	—	—	27, 3.6, 5	—	—	—
—	—	—	—	—	54, 5.9, 8	—	13, 2, 15	—
24, 3, 8	—	5, 0.5, 1	22, 1.5, 11	—	9, 0.91, 1	—	P	33, 5, 8
—	—	—	—	—	—	86, 40.7, 52	—	—
—	—	—	—	—	18, 0.73, 2	—	—	—
—	—	—	—	—	—	21, 0.64, 5	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	18, 0.91, 2	—	11, 1, 10	—
—	—	10, 0.3, 2	—	—	—	—	—	—
—	P	5, 0.05, 1	11, 0.18, 3	—	45, 2.4, 5	P	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	3, <1, 1	5, 0.05, 1	—	—	—	P	—	—
11, 0.3, 2	—	100, 18.2, 36	37, 2.5, 18	16, 0.84, 14	100, 15.9, 19	7, 2.9, 4	5, <1, 6	33, 4.2, 7
—	—	—	—	—	9, 0.45, 1	—	—	—
—	—	—	—	—	54, 4.1, 7	—	—	—
80, 21, 34	P	50, 4.7, 13	7, 0.55, 4	—	100, 18.6, 21	64, 10.4, 22	21, 5, 31	75, 12.1, 18
—	—	—	—	—	—	—	—	—
—	—	—	—	—	9, 0.09, 1	—	—	—

counterpart of *Chamaedaphne calyculata.* The herbaceous flora is dominated by grasses, sedges, and plants common to prairies, such as *Solidago* and *Rudbeckia. Parnassia glauca* and *Selaginella* are frequently present and indicate extremely calcium-rich conditions. Common shrubs include *Betula pumila, Cornus foemina, C. stolonifera, Salix pedicellaris,* and *Toxicodendron vernix.* The bryophyte community is characterized by calcicolous species such as *Amblystegium riparium* and *Fissidens adianthoides.* A few isolated hummocks support *Sphagnum fimbriatum* and *S. magellanicum. Chara* (an alga) is common in pools of standing water.

Mineral-rich fen: This type of peatland, like the previous, has a strong groundwater influence and a low shrub component occupied by *Potentilla fruticosa.* It differs in that its substrate is more treacherous (usually floating), the groundwater is not under pressure, no marl is present in the sediment profiles, and extremely calcicolous species such as *Parnassia glauca* and *Selaginella* are absent. *Scirpus acutus* is a significant component of the herbaceous flora, and *Typha* is a common asso-

Table 5.—Herbaceous layer vegetation in 16 peatlands in northern Indiana. The first number in each cell is the percent frequency for each species, the second number is the percent cover, and the third number is the importance value for each species in the respective peatlands. Peatland acronyms correspond with Table 2. A "P" means the species was present in the herbaceous layer, but occurred outside of the sampling quadrats. * Data from Swinehart (1994).

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Acer rubrum	—	3, 0.03, <1	7, 0.07, <1	17, 0.17, 2	P	33, 0.3, 5	20, 0.2, 4
Alisma subcordata	—	—	—	—	—	—	—
Andromeda glaucophylla	—	—	P	—	—	—	—
Aronia melanocarpa	—	—	—	—	—	33, 1, 6	40, 1.2, 9
Betula allegheniensis	—	—	—	—	—	—	—
Betula pumila	3, 0.17, 1	—	7, 0.3, 1	—	—	—	—
Bidens sp.	3, 0.17, 1	—	11, 0.11, 1	—	28, 1, 3	—	20, 8, 15
Calla palustris	—	—	—	—	—	—	—
Calopogon pulchellus	—	—	—	P	—	—	—
Caltha palustris	—	P	—	—	—	—	—
Cardamine bulbosa	P	—	—	—	—	—	—
Cardamine pratensis	—	31, 0.45, 4	—	—	—	—	—
Carex crinita	—	—	—	—	7, <1, 1	—	—
Carex lasiocarpa	—	3, 0.34, 1	—	—	—	—	—
Carex oligosperma	—	—	—	—	—	—	—
Carex rostrata	—	—	—	—	—	—	—
Carex sp.	80, 53, 45	—	—	17, 3, 4	7, <1, 1	—	—
Carex trisperma	—	—	—	—	—	—	—
Cephalanthus occidentalis	—	—	—	—	29, 3, 4	—	—
Chamaedaphne calyculata	—	—	—	—	—	P	20, 1, 5
Coptis trifolia	—	—	—	—	—	—	—
Cornus foemina	7, 0.33, 1	—	4, 0.04, <1	—	—	—	—
Cornus stolonifera	13, 0.57, 3	7, 0.86, 1	7, 0.22, 1	—	—	—	—
Cuscuta sp.	—	—	—	—	—	—	—
Cypripedium acaule	—	—	—	—	—	—	—
Decodon verticillatus	—	—	P	—	—	—	—
Drosera intermedia	—	—	—	—	—	—	—
Drosera rotundifolia	—	17, 0.17, 2	P	69, 0.69, 6	—	33, 0.3, 5	—
Dryopteris spinulosa	—	—	—	—	—	—	—
Dulichium arundinaceum	—	—	—	—	64, 34, 18	P	20, 2, 7
Eleocharis sp.	—	10, 1.2, 2	78, 13.2, 16	—	—	—	—
Equisetum fluviatile	—	—	—	4, 0.04, <1	—	—	—
Equisetum palustris	13, 0.27, 2	—	—	—	—	—	—
Eriophorum virginicum	—	—	P	—	—	—	—
Eupatorium maculatum	—	P	P	—	—	—	—
Eupatorium perfoliatum	—	—	—	—	7, <1, 1	—	—
Galium sp.	—	—	—	—	P	—	21, 1, 5
Gaylussacia baccata	—	—	—	—	—	—	—
Hypericum virginicum	—	—	33, 0.85, 3	22, 0.87, 3	36, 4, 5	—	60, 12, 28
Ilex verticillata	—	—	4, 0.11, <1	17, 0.17, 2	—	—	—
Impatiens capensis	17, 1.6, 4	14, 0.59, 2	—	—	64, 6, 8	—	—
Iris versicolor	—	—	—	4, 0.22, 1	—	—	—
Isotria verticillata	—	—	—	—	—	—	—
Juncus sp.	—	—	11, 0.18, 1	—	7, <1, 1	—	—
Leersia oryzoides	—	—	—	—	50, 5, 6	—	—
Lindera benzoin	—	—	—	—	—	—	—
Liparis loesellii	—	—	—	—	—	—	—
Liriodendron tulipifera	—	—	—	—	—	—	—
Lycopodium lucidulum	—	—	—	—	—	—	—
Lycopodium obscurum	—	—	—	—	—	—	—
Lysimachia terrestris	—	—	—	—	—	—	—
Lysimachia thrysiflora	—	—	—	17, 0.52, 2	—	—	—

Table 5.—Extended.

Leatherleaf bogs					Forested peatlands			
DSB	LB	YB	BUR	SH	LAB	MPB	TAM*	RMB
—	3, <1, <1	15, 0.25, 2	4, 0.11, 1	—	82, 2.1, 7	50, 0.78, 7	86, 3, 10	83, 1.3, 12
—	P	—	—	—	—	—	—	—
P	11, 4, 3	P	P	—	—	—	—	—
15, 0.35, 4	—	—	7, 0.3, 1	3, 0.94, 2	—	14, 0.36, 2	3, <1, 1	—
—	—	—	—	—	—	—	—	17, 0.17, 2
—	—	—	—	—	—	—	—	—
—	—	—	—	—	54, 2.3, 6	14, 2.9, 5	5, <1, 1	8, 0.25, 1
—	—	—	—	—	—	7, 3.6, 5	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	18, 2.7, 4	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	P	—	—	—	—	14, 0.43, 2	—	—
—	—	—	—	—	—	—	—	—
—	14, 5, 4	20, 1.7, 4	74, 15.8, 22	—	—	—	—	—
—	78, 24, 18	15, 1.7, 3	11, 0.41, 2	P	—	—	—	8, 1.7, 4
—	—	—	—	—	18, 1.8, 3	—	—	—
—	—	—	—	—	—	—	P	33, 2.2, 8
6, 1.8, 3	11, 2, 2	30, 4, 7	—	3, 0.47, 1	—	—	—	—
42, 24, 31	71, 19, 15	55, 14.2, 17	85, 46.5, 43	94, 69, 72	—	P	—	—
—	—	—	—	—	P	—	—	8, 0.42, 2
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	14, 0.14, 2	—	—
—	—	—	—	—	—	7, 0.21, 1	P	—
—	P	40, 4.2, 8	7, 0.73, 2	—	—	—	—	—
P	—	—	4, 0.04, 1	—	—	—	—	—
P	—	P	—	—	—	—	—	—
—	—	—	—	—	45, 1.4, 4	—	27, 1, 3	—
2, 0.02, 1	3, <1, <1	5, 0.05, 1	4, 0.37, 1	—	—	7, 2.1, 4	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
4, 0.33, 1	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	3, <1, <1	—	—	—	18, 0.36, 2	—	—	—
—	—	—	4, 0.55, 1	—	P	—	—	—
—	14, <1, 2	20, 1.4, 4	11, 0.33, 2	3, 0.31, 1	—	7, 1.4, 3	—	—
—	—	—	—	—	9, 0.27, 1	7, 0.21, 1	8, <1, 1	75, 3.8, 16
—	7, <1, 1	—	—	—	81, 7.1, 13	7, 0.07, 1	—	17, 1.7, 5
2, 0.02, 1	P	—	P	—	—	—	—	—
—	—	—	—	—	P	—	—	—
—	P	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	11, 1, 2	—
—	—	—	—	—	P	—	—	—
—	—	—	—	—	—	14, 0.14, 2	—	—
—	—	—	—	—	P	—	P	—
—	—	—	—	—	—	—	P	—
—	—	—	—	—	—	—	—	—
—	3, <1, <1	P	—	—	P	7, 0.71, 2	—	—

Table 5.—Continued.

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Maianthemum canadense	—	—	—	—	—	—	—
Menyanthes trifoliata	—	—	4, 0.92, 1	22, 5.6, 7	—	—	—
Mitchella repens	—	—	—	—	—	—	—
Nuphar advena	—	P	4, 0.37, 1	P	—	P	—
Nymphaea odorata	—	—	—	—	—	—	—
Nyssa sylvatica	—	—	—	—	—	—	—
Onoclea sensibilis	—	—	—	P	7, <1, 1	—	—
Osmunda cinnamomea	—	—	—	—	—	—	—
Osmunda regalis	—	7, 1.7, 2	44, 13, 13	26, 7.4, 9	—	33, 30, 29	—
Parnassia glauca	P	—	—	—	—	—	—
Parthenocissus quinquefolia	3, 0.03, 1	—	—	—	—	—	—
Pinus strobus	—	—	—	—	—	—	—
Poaceae (unidentified)	10, 1.8, 3	—	4, 0.37, 1	—	—	—	60, 10.6, 26
Polygonum sp.	—	—	—	—	—	—	—
Populus tremuloides	—	—	—	4, 0.13, <1	—	—	—
Potentilla anserina	—	—	—	4, 0.04, <1	—	—	—
Potentilla fruticosa	60, 20, 22	27, 7.8, 9	48, 4.4, 7	—	—	—	—
Potentilla palustris	—	—	15, 0.59, 2	35, 0.75, 3	—	—	—
Prunus serotina	—	—	—	—	—	—	—
Quercus palustris	—	—	—	—	P	—	—
Quercus rubra	—	—	—	—	—	—	—
Ranunculus sp.	3, 0.17, 1	—	—	—	—	—	—
Rosa palustris	3, 0.33, 1	—	18, 1, 2	13, 0.3, 1	—	—	—
Rubus allegheniensis	3, 0.17, 1	—	—	—	—	—	—
Rubus hispidus	—	10, 0.9, 2	—	—	—	—	—
Rudbeckia sp.	10, 0.10, 2	—	—	—	—	—	—
Rumex sp.	—	P	—	—	—	—	—
Saggitaria latifolia	—	—	4, 0.04, <1	—	—	—	—
Salix candida	—	—	—	—	—	—	—
Salix pedicellaris	—	7, 0.72, 1	4, 0.04, <1	39, 1.3, 4	—	—	—
Salix serrissima	—	7, 0.38, 1	—	—	—	—	—
Sarracenia purpurea	—	—	18, 1.7, 3	35, 1.6, 4	—	—	—
Scirpus acutus	7, 1, 2	34, 19, 17	74, 19.5, 20	4, 0.22, 1	—	—	—
Scirpus americanus	3, 0.33, 1	—	—	—	—	—	—
Scirpus cyperinus	—	—	—	—	P	—	—
Selaginella sp.	P	—	—	—	—	—	—
Solanum dulcamara	—	—	—	—	—	—	P
Solidago sp.	37, 0.93, 7	—	—	—	—	—	—
Spiraea tomentosa	—	7, 0.21, 1	7, 0.37, 1	—	—	—	—
Symplocarpus foetidus	3, 0.17, 1	—	—	—	—	—	—
Thelypteris palustris	13, 0.57, 3	45, 6, 10	81, 8, 12	78, 5.3, 11	7, <1, 1	—	—
Toxicodendron radicans	—	—	4, 0.04, <1	—	—	—	—
Toxicodendron vernix	—	—	—	26, 1.7, 4	—	33, 1.7, 7	—
Trientalis borealis	—	—	—	—	—	—	—
Triglochin maritima	—	—	—	4, 0.22, 1	—	—	—
Typha sp(p).	—	90, 34, 34	26, 1.2, 3	61, 3.8, 8	P	—	—
Ulmus americana	—	—	—	—	—	—	—
Urtica procera	—	—	7, 0.22, 1	—	14, <1, 2	—	—
Vaccinium corymbosum	—	—	P	—	—	67, 2.7, 13	—
Vaccinium macrocarpon	—	—	52, 2.5, 6	52, 14.6, 18	—	—	—
Vaccinium oxycoccos	—	—	—	—	—	—	—
Viola blanda	—	24, 0.83, 4	—	P	—	—	—
Viola cucullata	3, 0.17, 1	P	—	35, 0.35, 3	—	—	—
Viola pallens	—	—	—	—	—	—	—
Viola sp.	—	—	44, 0.81, 4	—	—	—	—
Woodwardia virginica	—	—	—	—	—	100, 15, 33	P
Unidentified sedges	—	—	—	34, 0.91, 5	35, 1, 4	—	—

Table 5.—Continued - Extended.

Leatherleaf bogs					Forested peatlands			
DSB	LB	YB	BUR	SH	LAB	MPB	TAM*	RMB
—	—	—	—	—	45, 3.5, 7	71, 13.2, 25	97, 24, 29	58, 2.5, 12
—	—	—	—	—	9, 0.91, 2	—	—	—
—	—	—	—	—	P	—	—	—
P	—	5, 1, 1	4, 0.18, 1	—	—	7, 1.4, 3	—	—
—	—	P	—	—	—	—	—	—
—	—	—	—	—	—	57, 6.2, 15	—	—
—	—	—	—	—	P	—	—	8, 0.25, 1
—	—	—	—	—	45, 6.8, 10	14, 1.3, 3	73, 6, 11	42, 3.8, 13
—	—	—	—	—	P	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	54, 2.4, 6	—	13, 1, 2	—
—	—	—	—	—	—	7, 0.21, 1	—	—
4, 2, 3	—	5, 1, 1	—	—	—	—	—	8, 0.83, 3
—	P	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	P	—	P	—	—	—	—	—
—	—	—	—	—	—	—	22, 1, 3	—
—	—	5, 0.15, 1	—	—	—	—	13, 1, 2	—
—	—	—	—	—	—	7, 0.07, 1	—	—
—	—	—	—	—	—	—	—	—
—	18, 4, 3	—	—	—	18, 0.54, 2	—	—	8, 0.25, 1
—	—	—	—	—	—	—	16, 1, 2	—
44, 3, 14	—	20, 1.3, 3	—	3, 0.16, 1	18, 0.73, 2	—	57, 6, 10	8, 0.25, 1
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	11, <1, 1	—	P	—	—	—	—	—
—	—	—	—	—	P	—	—	—
—	—	—	P	—	P	—	—	—
—	—	—	—	—	—	—	—	—
P	P	15, 1.4, 3	P	—	9, 0.27, 1	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
27, 11, 16	P	10, 0.2, 1	P	P	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	15, 3.7, 5	—	—	—	—	—	—
—	—	—	—	—	54, 7.7, 12	—	—	—
—	—	—	—	—	—	—	—	8, 0.83, 3
—	—	—	—	—	36, 0.73, 3	—	—	—
—	—	30, 0.8, 4	4, 0.18, 1	—	—	—	—	—
—	—	—	—	—	18, 0.36, 2	43, 1.3, 7	89, 7, 13	25, 0.75, 4
—	—	—	—	—	—	—	—	—
—	29, 5, 4	—	7, 0.3, 1	—	P	—	—	—
—	—	—	—	—	27, 0.27, 2	—	—	—
—	—	—	—	—	—	21, 0.5, 3	P	8, 1.7, 4
24, 2.7, 8	—	20, 3.5, 5	—	—	36, 2.7, 5	21, 1.5, 4	11, 1, 2	25, 1.5, 6
—	10, 2, 2	30, 7.7, 9	7, 1.8, 2	—	9, 0.27, 1	—	—	—
9, 3, 5	—	10, 2, 3	22, 3.2, 6	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	64, 2.2, 6	—	—	—
—	—	—	—	—	—	—	—	—
29, 7, 14	36, 15, 10	35, 17.6, 18	48, 8.8, 13	34, 16.7, 22	—	7, 0.21, 1	—	—
—	14, 1, 1	—	—	—	—	—	—	—

Table 6.—Bryophytes from 16 peatlands in northern Indiana. The first number in each cell is the percent frequency for each species, the second number is the percent cover, and the third number is the importance value for each species in the respective peatlands. Peatland acronyms correspond with Table 2. A "P" means the species was present in the ground layer, but occurred outside of the sampling quadrats.

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Amblystegium riparium	4, 11.9, 55	—	—	—	7, <1, 1	—	—
Aulacomnium palustre	P	7, 1, 2	—	56, 7.7, 22	7, <1, 1	33, 6.7, 14	20, 0.02, 7
Bryum pseudotriquetrum	—	3, 0.03, 1	—	—	—	—	—
Callicladium haldanianum	—	—	—	—	—	—	—
Calliergon cordifolium	—	—	—	—	—	—	—
Calliergon giganteum	—	—	—	—	28, 1, 3	—	—
Calliergonella cuspidata	—	59, 5.8, 35	44, 5.1, 29	4, 0.04, 1	—	—	—
Campylium polygamum	—	17, 2.7, 13	7, 0.92, 5	—	—	—	—
Campylium stellatum	—	7, 0.45, 3	74, 15.7, 65	—	—	—	—
Climacium americanum	—	—	—	—	P	—	—
Drepanocladus fluitans	—	14, 1.5, 9	—	—	—	—	—
Drepanocladus sp.	—	—	—	—	—	—	20, 6, 10
Eurhynchium hians	23, 6, 30	—	—	—	—	—	—
Fissidens adianthoides	3, 0.03, 2	21, 1.4, 11	—	—	—	—	—
Helodium paludosum	—	—	—	—	—	—	—
Hypnum pratense	—	—	—	—	—	—	—
Isopterygium elegans	—	P	—	—	—	—	—
Leucobryum albidum	—	—	—	—	—	—	P
Lophocolea heterophylla	—	3, 0.3, 1	—	9, 0.09, 3	—	—	—
Mnium affine var. *ciliare*	3, 2.7, 8	—	—	—	—	—	—
Mnium affine var. *rugicum*	—	3, 0.69, 3	—	—	—	—	—
Mnium cuspidatum	—	—	—	—	—	—	—
Pallavicinia lyellii	—	—	—	—	—	—	—
Philonotis fontana	—	—	—	—	—	—	—
Plagiothecium denticulatum	—	—	—	—	—	—	—
Polytrichum strictum	—	—	—	—	—	—	—
Rhynchostegium serrulatum	—	—	—	—	—	—	—
Riccia fluitans	—	P	—	—	P	—	—
Sphagnum affine	—	—	—	—	—	33, 1.7, 5	—
Sphagnum bartlettianum	—	—	—	P	—	—	—
Sphagnum capillifolium	—	—	—	—	—	—	—
Sphagnum centrale	—	—	—	13, 7, 9	—	—	—
Sphagnum cuspidatum	—	—	—	—	—	—	40, 26, 28
Sphagnum fallax	—	—	—	—	—	—	—
Sphagnum fimbriatum	P	10, 7, 21	—	39, 25.7, 29	28, 25, 11	—	—
Sphagnum fuscum	—	—	P	—	—	—	—
Sphagnum isoviitae	—	—	—	—	—	—	—
Sphagnum magellanicum	3, 1, 5	—	—	—	—	—	P
Sphagnum palustre	—	—	P	26, 19.1, 21	—	100, 71.7, 75	—
Sphagnum papillosum	—	—	—	—	—	—	—
Sphagnum recurvum	—	—	—	—	—	33, 1.7, 5	60, 59.8, 54
Sphagnum russowii	—	—	—	—	P	—	—
Sphagnum sp.	—	—	—	—	—	—	—
Sphagnum squarrosum	—	—	—	—	—	—	—
Sphagnum teres	—	P	P	17, 12.6, 14	—	—	—
Sphagnum warnstorfii	—	—	P	4, 0.43, 2	—	—	—
Tetraphis pellucida	—	—	—	—	—	—	—
Thuidium allenii	—	—	—	—	—	—	—
Thuidium delicatulum	—	—	—	—	—	—	—

ciate. Other typical herbaceous species include *Drosera rotundifolia, Eleocharis* spp., *Osmunda regalis, Thelypteris palustris* and *Viola blanda. Menyanthes trifoliata, Sarracenia purpurea* and *Vaccinium macrocarpon* are often present locally. Shrubs are occasional on these open fens. *Toxicodendron vernix* is by far the most abundant. *Betula pumila,*

Table 6.—Extended.

Leatherleaf bogs					Forested peatlands			
DSB	LB	YB	BUR	SH	LAB	MPB	TAM*	RMB
—	—	—	—	—	18, 1.4, 5	—	—	17, 2.9, 7
84, 16, 29	12, <1, 1	25, 3.2, 7	18, 3.7, 7	6, 0.47, 3	P	21, 1.7, 13	40, 1, 11	67, 12.1, 27
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	24, 1, 8	—
—	—	—	—	—	—	—	—	8, 0.83, 3
—	—	—	—	—	—	—	—	—
—	—	—	—	—	9, 0.91, 3	—	—	—
—	—	—	—	—	—	7, 0.71, 5	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	7, 2.1, 10	—	—
—	—	—	—	—	—	21, 2.5, 16	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	9, 3.6, 6	—	—	—
—	—	—	—	—	—	36, 1.3, 15	27, <1, 8	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	13, <1, 5	—
—	—	—	—	—	36, 5.3, 14	57, 3.8, 31	76, 5, 30	42, 3, 12
—	—	P	—	—	—	—	—	—
—	—	—	—	—	—	—	13, <1, 5	—
9, 0.88, 2	—	35, 2.1, 9	7, 1.7, 3	—	—	—	—	—
—	—	—	—	—	—	—	5, 1, 4	8, 0.08, 2
—	P	—	—	—	P	—	—	P
—	—	—	—	—	54, 14.4, 29	7, 0.36, 3	—	42, 11.3, 21
13, 4.7, 6	—	10, 2.2, 3	37, 8.5, 15	—	—	—	—	—
6, 4.1, 4	—	—	—	—	—	—	—	—
—	—	20, 7.5, 9	—	—	—	—	—	—
—	25, 12, 8	—	30, 25.2, 23	84, 66.5, 69	—	—	—	—
53, 23, 27	—	—	—	—	—	—	—	50, 17.9, 29
2, 0.22, 1	—	15, 9, 8	7, 0.48, 2	—	—	7, 0.36, 3	—	—
—	—	—	—	—	—	—	—	—
—	—	—	11, 2.2, 4	—	—	—	—	—
38, 7.8, 13	4, <1, 1	60, 26.5, 28	4, 0.37, 1	41, 23.9, 29	—	—	—	—
—	4, 3, 2	—	—	—	—	—	<1, <1, 3	—
—	—	—	67, 36.7, 40	—	—	—	—	—
31, 16.6, 18	4, 2, 1	60, 37.1, 34	7, 2.2, 3	—	—	—	3, 2, 6	—
—	—	—	—	—	—	—	—	—
—	4, <1, 1	—	—	—	—	—	—	—
—	4, <1, 1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	18, 0.36, 4	7, 0.36, 3	30, 2, 12	—
—	—	—	—	—	18, 0.91, 5	—	—	—
—	—	—	—	—	54, 13, 27	—	5, <1, 4	—

Cornus foemina, C. stolonifera, Rosa palustris, Salix pedicellaris and *Spiraea tomentosa* are also common. *Larix laricina* is present locally and usually is found around the periphery of the mat where the substrate is more stable. Closer to the upland, where the peat is grounded, trees of *Acer rubrum, Betula alleghaniensis* and *Populus tremuloides* are

Table 7.—Aquatic layer vegetation from 16 peatlands in northern Indiana. The first number in each cell is the percent frequency for each species, the second number is the percent cover, and the third number is the importance value for each species in the respective peatlands. Peatland acronyms correspond with Table 2. A "P" means the species was present in the ground layer, but occurred outside of the sampling quadrats.

	Fens			Tall-shrub bogs			
Species	KLF	SVF	BF	LCB	HB	THB	BLB
Chara sp.	P	—	P	—	—	—	—
Lemna minor	—	3, 0.17, 52	4, 0.04, 11	—	—	—	P
Lemna trisulca	—	P	—	—	—	—	—
Potamogeton sp.	—	—	7, 0.07, 22	P	—	—	—
Ranunculus longirostrus	—	—	—	—	—	—	—
Riccia fluitans	—	3, 0.03, 24	—	—	35, <1, 100	—	—
Utricularia intermedia	—	3, 0.03, 24	22, 0.22, 67	30, 1.39, 87	—	—	—
Utricularia vulgaris	P	P	—	4, 0.22, 13	—	P	—
Utricularia sp.	—	—	—	—	—	—	P
Wolffia sp.	—	—	—	—	—	—	—

common. The bryophyte community is characterized by *Calliergonella cuspidata, Campylium polygamum* and *C. stellatum.* Other common alkaliphilic bryophytes include *Bryum pseudotriquetrum, Drepanocladus fluitans, Fissidens adianthoides, Isoptergyium elegans,* and *Mnium affine* var. *rugicum. Sphagnum* forms isolated hummocks, and includes *S. fimbriatum, S. fuscum, S. palustre, S. teres* and *S. warnstorfii. Sphagnum warnstorfii,* recovered from Binkley Fen, is a new record for Indiana (Swinehart & Andrus 1998). Central ponds of open water are occupied by *Nuphar advena* and *Nymphaea tuberosa.* Submergent macrophytes include *Ceratophyllum demersum* and *Potamogeton* spp. Water-filled pools within the mat are frequented by *Chara* sp., *Lemna minor, L. trisulca, Riccia fluitans, Utricularia intermedia* and *U. vulgaris.*

Mineral-rich tall-shrub bog: Tall-shrub bogs of this type are relatively mineral-rich, and the substrate is extremely treacherous. They are distinguished from fens in that their surface has become dominated by *Sphagnum.* Where brown mosses once thrived, *Sphagnum fimbriatum* (characteristic), *S. palustre, S. teres,* and *Aulacomnium palustre* dominate. Many of the Sphagna form level carpets, while *S. fimbriatum* often forms hummocks around the stems of shrubs. *Toxicodendron vernix* forms dense stands and is nearly unavoidable when traversing these peatlands on foot, as it offers the only reliable support on the treacherous mat. Other common, characteristic shrubs include *Acer rubrum, Cephalanthus occidentalis, Rosa palustris* and *Salix pedicellaris. Cornus foemina, C. stolonifera, Ilex verticillata, Salix candida, Spiraea tomentosa,* and *Vaccinium corymbosum* are infrequent locally. The few trees that occur near the periphery of these bogs include *Acer rubrum, Populus tremuloides* and *Quercus palustris.* Herbaceous species are quite variable, but usually include *Dulichium arundinaceum, Hypericum virginicum* and *Thelypterus palustris. Calopogon pulchellus, Drosera rotundifolia, Menyanthes trifoliata, Osmunda regalis, Potentilla palustris, Sarracenia purpurea, Triglochin maritima* and *Vaccinium macrocarpon* are present locally. Pools of water in the mat are common. They are occupied by *Lemna minor, Potamogeton* spp., *Riccia fluitans, Utricularia intermedia* and *U. vulgaris.*

Leatherleaf bog: The vegetation assemblages of leatherleaf bogs vary relatively little among different peatlands. All leatherleaf bogs are characterized by a low shrub cover of *Chamaedaphne calyculata. Woodwardia virginica* is also characteristic of these peatlands, often forming a distinct zone in wetter areas. In most leatherleaf bogs, cranberries (*Vaccinium macrocarpon* and *V. oxycoccos*) are associated with both *Woodwardia* and *Chamaedaphne.* Other herbaceous layer species common to nearly all leatherleaf bogs in Indiana include *Andromeda glaucophylla,*

Table 7.—Extended.

Leatherleaf bogs					Forested peatlands			
DSB	LB	YB	BUR	SH	LAB	MPB	TAM*	RMB
—	—	—	—	—	—	—	—	—
—	<1, <1, 1	—	—	—	9, 0.09, 100	—	—	8, 0.08, 100
—	—	—	—	—	—	—	—	—
—	P	—	—	—	—	P	—	—
—	P	—	—	—	—	—	—	—
—	P	—	—	—	—	—	—	—
—	—	P	—	P	—	—	—	—
—	36, 3, 99	—	P	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	P	—	—	—	—	—	—	—

Carex oligosperma, C. rostrata, Decodon verticillatus, Drosera spp. (*D. rotundifolia* and/or *D. intermedia*), *Dulichium arundinaceum, Hypericum virginicum, Sarracenia purpurea, Scirpus cyperinus* and *Vaccinium corymbosum.* Shrubs are sparse on the mat, except for a few sites where dense "islands" of *Vaccinium corymbosum* are forming in dryer areas. Other characteristic shrubs found scattered on the mat include *Acer rubrum, Aronia melanocarpa, Nemopanthus mucronatus* and *Toxicodendron vernix. Cephalanthus occidentalis* always dominates the standing waters of the lagg. *Acer rubrum* and *Quercus palustris* are infrequent as trees on the mat. Curiously, *Larix laricina,* a common component of leatherleaf bogs in Michigan and other Great Lakes and northern localities, was absent from all of the leatherleaf bogs studied. It does, however, occur in abundance at Pinhook Bog, a leatherleaf bog in LaPorte County, Indiana (Wilcox 1982). The surface of the leatherleaf bogs is characteristically level; and complexes of clearly defined hummocks and hollows, common in northern peatlands (see Vitt et al. 1975), are essentially absent. The Sphagna, rather than occurring as a gradient of species according to the hydrology and chemistry of hummocks and hollows, are more often represented by only a few species common to the extreme conditions. In animal trails and other low, wet depressions and pools, *Sphagnum cuspidatum* dominates. In drier areas and raised "hummocks," more drought-tolerant species such as *S. magellanicum* and *S. papillosum* (and infrequently, *S. capillifolium*) dominate. These relatively dry areas usually harbor the xerophyte *Polytrichum strictum.* In more or less level "carpets," *S. recurvum* and *S. bartlettianum* are most common; and *S. fallax* and *S. isoviitae* are occasional. Near the more mineral-rich waters of the lagg, *S. centrale, S. fimbriatum, S. palustre* and *S. squarrosum* may be present. *Aulacomnium palustre* is ubiquitous in leatherleaf bogs, and it was also found in all of the other peatlands with the exception of Binkley Fen.

Mineral-poor tall-shrub bog: These peatlands are characterized by a nearly impenetrable cover of shrubs. *Vaccinium corymbosum* always dominates, and *Aronia melanocarpa* and *Nemopanthus mucronatus* are subdominant. The vegetation indicates that these tall-shrub communities developed from leatherleaf bogs. Both representatives in this study (Blueberry and Thompson Bogs), have remnant, depauperate specimens of *Chamaedaphne calyculata* surviving in the few patches where shrubs have not crowded them into extinction. *Woodwardia virginica,* another characteristic leatherleaf bog species, is also remnant in these tall-shrub bogs. Other understory flora is variable and relatively scarce due to the dense shrub layer. The lagg waters, like leatherleaf bogs, are occupied almost exclusively by *Cephalanthus occidentalis.* The bryophyte flora, like some of the vascular plants, suggests that these peatlands are old leatherleaf bogs. Not only is the underlying peat composed of a thick stratum of *Sphagnum* (Swinehart & Parker 2000), but the present Sphagna are the same species that characterize leatherleaf bogs. In wet areas, *S. cuspidatum* is common. In moist areas, *S. recurvum* forms carpets, and low hummocks harbor *S. magellanicum.* A few other species, namely *S. affine* and *S. palustre,* indicate more shaded and mineral-rich conditions. *Leucobryum albidum,* common in moist, shaded areas, was found in Blueberry Bog and represents a new Indiana record (Swinehart & Andrus 1998).

Forested peatland: Forested peatlands are characterized by a canopy dominated by *Acer rubrum. Larix laricina* was present in all of the sites included in the present study, but many individuals were dead and most of the living specimens were etiolated and depauperate as a result of shading by *A. rubrum.* Other members common in the tree layer include *Acer saccharinum, Prunus serotina, Quercus palustris* and *Ulmus americana. Betula allegheniensis, Fagus grandifolia, Fraxinus pennsylvanica, Liriodendron tulipifera, Nyssa sylvatica* and *Sassafras albidum* were infrequent locally. *Pinus strobus* was a dominant member of the canopy at Mount Pleasant Bog, and the presence of individuals in both the shrub and herbaceous layers suggests that the species will persist well beyond the demise of *Larix,* which never reproduces in the understory of these forested peatlands. A single individual of *P. strobus* was also found at Ropchan Memorial Bog. The shrub canopy in forested peatlands is dominated by *Acer rubrum, Aronia melanocarpa, Ilex verticillata, Nemopanthus mucronatus, Toxicodendron vernix* and *Vaccinium corymbosum. Amelanchier laevis, Lindera benzoin* and *Rosa palustris* are more local. Other shrubs include *Gaylussacia baccata* and *Nyssa sylvatica.* The herbaceous flora is characterized by *Bidens cernua, Maianthemum canadense, Osmunda cinnamomea* and *Trientalis borealis.* Other notable but more local herbaceous species include *Carex trisperma, Coptis trifolia, Cypripedium acaule, Dryopterus spinulosa, Isotria verticillata, Lycopodium lucidulum, L. obscurum, Mitchella repens* and *Rubus hispidus. Acer rubrum* seedlings are always abundant, indicating the importance of this species in the long-term composition of the tree canopy. The most characteristic and abundant bryophyte of forested peatlands in Indiana is *Pallavicinia lyellii.* Although it often forms on decaying tamarack root-stocks, it also forms hummocks on exposed peat. The hummocks are composed almost entirely of the undecomposed tissue of dead individuals, while the surface is colonized by living individuals. The species is considered an acidophile (H.A. Crum, pers. commun.); and, consequently, it is usually found on peat having a pH between 3.5–4.5. Other common bryophytes include *Mnium affine* var. *ciliare, Rhynchostegium serrulatum, Sphagnum affine, Tetraphis pellucida* and *Thuidium delicatulum.* Additional species are more local in distribution (see Table 6).

Variability of the vascular plant communities.—Alkalinity (indicative of the magnitude of groundwater influence) and woody plant cover (indicative of seral stage in terms of substrate density and moisture saturation) explained 21.5% of the variability in the plant communities of the herbaceous layer.

Alkalinity: Canonical Correspondence Analysis (CCA) of herbaceous-vascular flora (composition and cover) distinctly separated fens (Binkley, Kiser and Svoboda) from all other peatlands on the basis of alkalinity and pH (Fig. 2). Leatherleaf bogs were tightly clustered at the mineral-poor end of the gradient, but the other peatland types were more loosely clustered (Fig. 2). This tight clustering is attributed to the fact that leatherleaf communities have become as acid and mineral-poor as climatic and edaphic conditions will allow, favoring plant assemblages of close compositional affinity. In the case of fens, acidification of the substrate by brown mosses, and continued separation from the effects of groundwater due to sedimentation, will cause some peatlands to progressively migrate to the mineral-poor end of the spectrum. Binkley Fen, already exhibiting large expanses of colonizing *Sphagnum* mosses, is an example of this process, hence its position on the lower end (relatively) of the alkalinity gradient (Fig. 2). In contrast, Kiser Lake Fen is far removed from Binkley Fen because it is extremely mineral-rich due to an artesian water supply and the presence of marl under the peat. The tall-shrub bogs and forested peatlands, due to their variable origins (having arisen from either fens or bogs), are loosely clustered, each showing either mineral-rich or mineral-poor

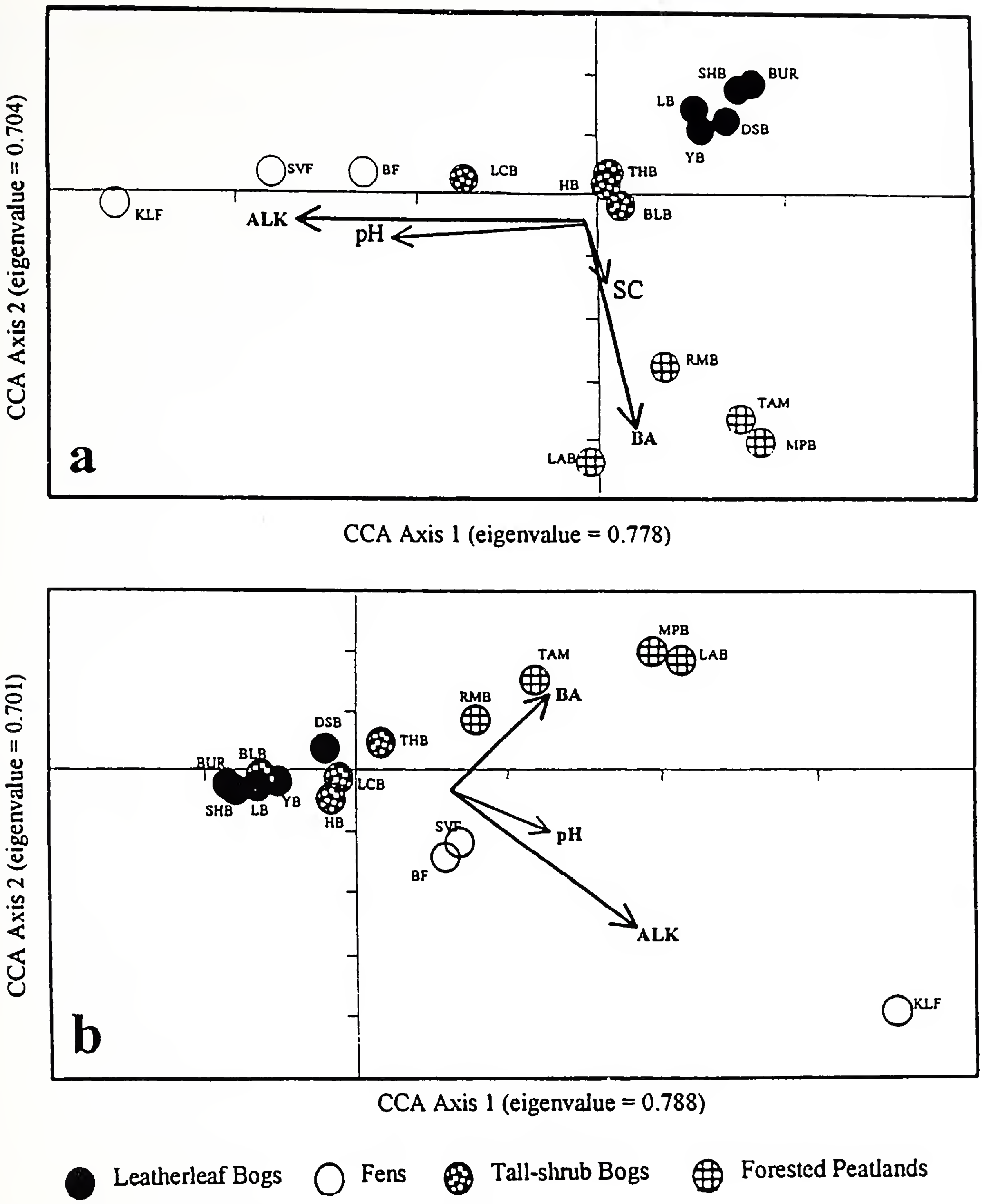

Figure 2.—Canonical Correspondence Analysis (CCA) showing the relationship of the vegetation composition and cover and four environmental variables in 16 Indiana peatlands. Plot "a" is vascular flora, and plot "b" is bryophyte flora. Length of arrows represents represents relative strength of the regression for the respective variables.

affinities according to their respective developmental pathways. This is supported by the stratigraphic and palaeoecological data presented by Swinehart & Parker (2000).

Woody plant cover: In addition to groundwater influence, seral position was a major source of variability in the herbaceous vegetation of the peatlands. Seral position in these lake-fill peatlands is indicated by the amount of shrub and tree cover. Growth of this woody vegetation is favored by build-up of sediment to the point where the surface becomes dryer and firm enough to support the weight of the plants. As a consequence of this drying, decomposition accelerates and increases nutrient availability (Kratz & Dewitt 1986). With the colonization of dense shrubs or a forest canopy, light becomes limiting for heliophilic species.

Forested peatlands were distinctly separated from the other peatlands (Fig. 2). The distinction between the herbaceous vegetation in the forested peatlands and the tall-shrub bogs suggests that either light and/or edaphic conditions were significantly different. The response of the bryophytes to forest and shrub cover, discussed below, would suggest that moisture was the primary factor distinguishing the herbaceous vegetation of these peatlands.

Variability of the bryophyte communities.—*Alkalinity:* The four types of peatland were not as clearly separated on the basis of the response of the bryophyte community to alkalinity (Fig. 2). The character of *individual* peatlands along the gradient was more apparent, suggesting that the bryophyte flora is a better indicator of trophic condition than the vascular flora. According to Crum (1988), vascular plants have a higher trophic plasticity than mosses and, therefore, mosses are better indicators of habitat.

Leatherleaf bogs were clustered tightly at the mineral-poor end of the gradient (Fig. 2). Bryophyte communities of tall-shrub peatlands and forested peatlands shared affinities with either mineral-rich or mineral-poor conditions, depending on their seral origin (fen or bog, respectively). Kiser Lake Fen was distinctly separated from the other fens and forested peatlands due to its extreme mineral-rich, artesian water flow.

Woody plant cover: Shrub cover was a relatively insignificant factor in the ordination of the peatland bryophyte communities ($r^2 < 0.2$). However, tree basal area distinguished the bryophyte communities of forested peatlands from all other peatland types. While thick tree cover may have influenced the bryophyte communities by limiting light, the presence of a forest infers a dryer substrate, and this may have been a more important factor. Many of the bryophyte communities of tall-shrub bogs, which exhibited nearly impenetrable shrub canopies, are closely associated with leatherleaf bogs in the ordination. Since light in these tall-shrub bogs is significantly reduced (as it is in forested peatlands), it might be concluded that the moisture saturation of the substrate is a more important factor in distinguishing the bryophyte communities of forested peatlands and tall-shrub bogs. The progressively firmer and dryer substrate that favored the establishment of trees also favored a transition from bog and fen bryophytes to lowland forest species.

Development of the hydrosere.—Analysis of the bathymetry (Swinehart 1997), stratigraphy and subfossil composition (Swinehart & Parker 2000) of peatlands in Indiana, coupled with the present floral survey of the existing representatives of the various types and stages of peatlands in the area, supports the following conclusions about their development: 1) basin-type peatlands in the southern Great Lakes region have a "monophyletic" origin as a lake or pond which, for various reasons, develops into a peat-forming fen, 2) subsequent to the open fen stage, the successional pathway becomes bi-directional; and depending on the morphometric and hydrologic characteristics of the basin (Swinehart 1997), some of the fens become mineral-poor leatherleaf bogs, while others do not, and 3) regardless of their inherent mineral richness, all Indiana peatlands are succeeded by a forest dominated by *Acer rubrum.* Open fens that were favorable to rapid, large-scale colonization by *Sphagnum* mosses developed into leatherleaf bogs (Swinehart 1997; Swinehart & Parker 2000). Leatherleaf bogs, as their substrate becomes more stable (and consequently less wet), are succeeded by a tall-shrub community characteristic of acid, relatively mineral-poor conditions (mainly *Vaccinium corymbosum, Aronia melanocarpa* and *Nemopanthus mucronatus*). Any *Larix* trees that pioneer the increasingly stable substrate are quickly displaced by *Acer rubrum.* The latter is better able to withstand the occasional flooding that results from grounding of the mat (Moizuk & Livingston 1966), and it is tolerant of shade in the understory. In contrast, *Larix* is shade intolerant and fares poorly in flooded conditions (Duncan 1954). Grounding of the mat favors decomposition of the surface of the peatland to the point where it nearly equals productivity, causing muck (rather than peat) to form. Nutrient availability is increased slightly, but the acid conditions, coupled with shade provided by the dense canopy of arborescent trees results in a sparse subcanopy cover of acid and shade tolerant herbs.

If morphometric and hydrologic characteristics of a fen basin are not favorable to rapid, large-scale colonization of the open mat by *Sphagnum* mosses, alkaliphilic shrubs invade centripetally as the substrate becomes progressively suitable for their growth. *Sphagnum* may accompany this invasion, but only as a peripheral ring or as isolated hummocks under the canopy of shrubs and small trees. Eventually, after the peat becomes dense enough to sufficiently reduce groundwater influence, *Sphagnum* may colonize the entire surface of the peatland. However, the substrate is already grounded, or nearly so, and the shrub canopy is well-developed. Shade from the shrubs and nutrients released from decomposition of the surface peat (due to grounding) will limit typical bog species and favor species typical of forested peatlands. Red maple establishes early and eventually forms a dense lowland forest (Swinehart & Parker 2000).

Unlike peatlands of the northern Great Lakes region and other northern localities in North America, conifers do not characterize the later stages of the peatland hydrosere in Indiana. In many cases, they are absent entirely, even in the early stages of peatland development. In Canada and northern Michigan, mineral-poor peatlands become dominated by *Picea mariana* and mineral-rich peatlands by *Thuja occidentalis* (Crum 1988). *Picea mariana* is not known from Indiana during historic times, and *Thuja occidentalis* is extremely rare and found only near Lake Michigan (Deam 1940).

Acer rubrum is the tentative climax species in Indiana peatlands, in southwest Michigan (Crow 1969a), and northeast Ohio (Andreas & Bryan 1990). It is dominant in the canopy and prolific in the understory. A graphic representation of the size class distribution of *Acer rubrum* trees in forested peatlands shows a classic reverse "J"-shaped curve, typical of species destined to replace themselves in their own shade. The transient nature of pioneer species such as *Betula allegheniensis* and *Larix laricina* is indicated by a bell-shaped distribution representing the eventual extinction of the species for lack of seedling and sucker survival due to shade.

The dominance of red maple in the later stages of peatland development in the southern Great Lakes region, unlike that of black spruce in the North, can be attributed to competitive success. Red maple is not an opportunist that exists in these peatlands due to uncontested survival (as in black spruce of the northern Great Lakes region (Crum 1988)), but rather it thrives and out-competes potential competitors such as *Quercus palustris*. Whether red maple is truly the ultimate edaphic climax species for the peatland hydrosere of the region is uncertain. If an equilibrium of productivity and decomposition exists in grounded peat, as suggested by Kratz & DeWitt (1986), the structure and composition of the vegetation, barring any major hydrological or elevation change or other major disturbance, would likely remain steady—favoring the continued existence of a red maple-dominated lowland forest. If, however, a slight surplus of productivity occurred as indicated by Swinehart & Parker (2000), mucky soil might eventually accumulate high enough to become relatively dry or mesic. If this happened, the existence of a complete hydrosere from open water to a forest of terrestrial affinity is not impossible. Mount Pleasant Bog (Laporte County) may be an early example of this. The substrate is firm and dry in most places, and *Pinus strobus* grows to maturity and reproduces successfully. Large specimens of *Fagus grandifolia*, the dominant species occupying the surrounding terrestrial forest, are already occasional in the pine forest.

A definitive conclusion about the nature of the steady-state or climax community in peatlands of glaciated regions is, in the final analysis, speculative due to insufficient time for full development of these communities. Perhaps application of the term "old growth" could be employed in much the same way that it is used to describe steady-state/climax upland forests. Parker (1989) defines mesic old growth forests as possessing: 1) an overstory canopy of trees older than 150 years and with little or no anthropogenic understory disturbance during the past 80–100 years, 2) an all-aged structure with multi-layered canopies, 3) horizontal structure with aggregations of canopy trees interspersed with small, all-aged canopy gaps of varying species composition, and 4) significant numbers of standing, dead snags and downed logs. The red maple peatlands meet all of these criteria accept the first. The oxygen profile in the peatland allows only the top 20–30 cm for root growth. Consequently, wind-throws are extremely common.

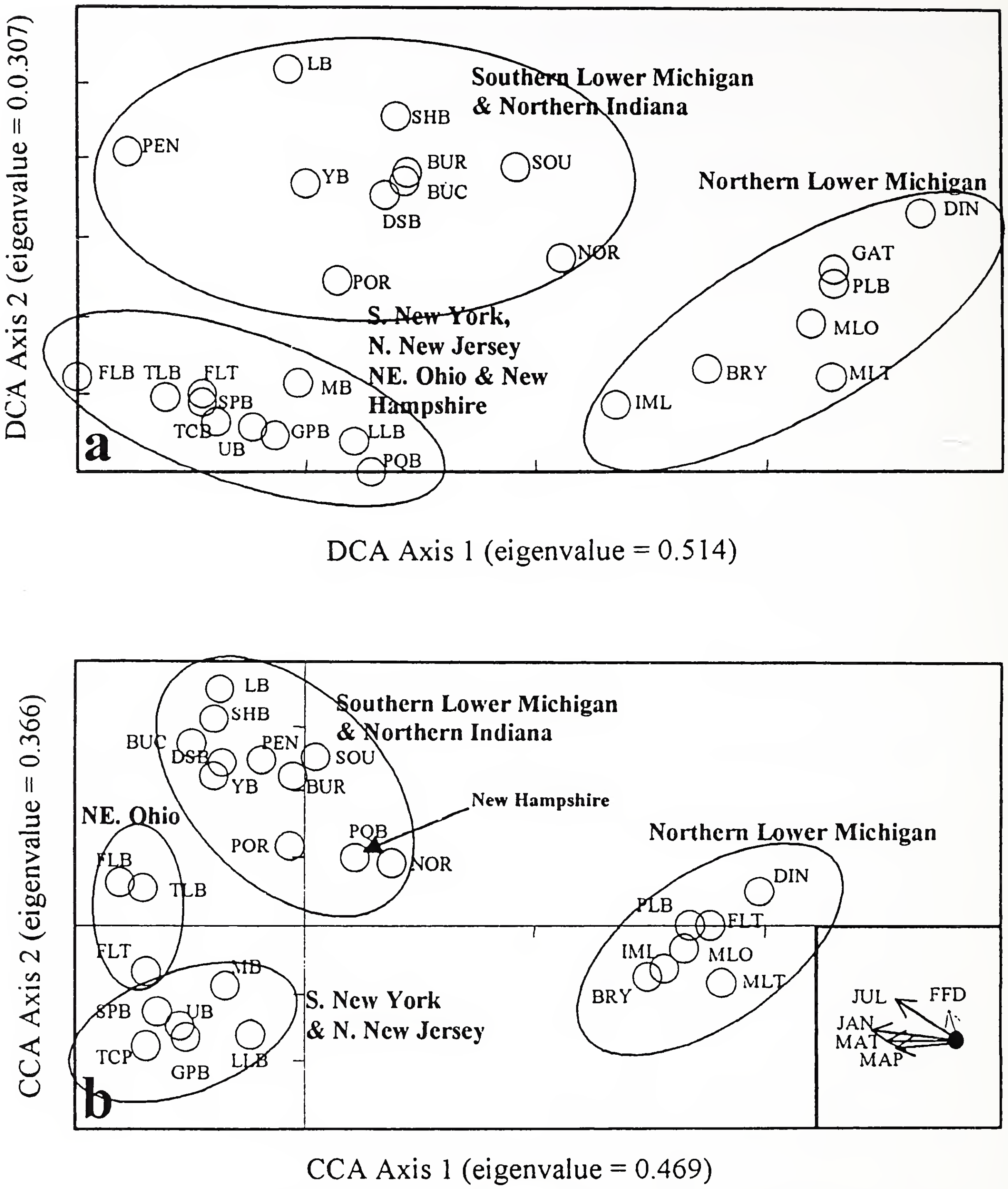

Figure 3.—Regional variation in leatherleaf bog flora (acronyms correspond with Table 8): a) Detrended Correspondence Analysis (DCA) showing the relative similarity of vegetation composition and frequency, and b) Canonical Correspondence Analysis (CCA) showing the relationship between vegetation and five climatic variables (FFD = mean number of frost-free days, JUL = mean July temperature, JAN = mean January temperature, MAT = mean annual temperature, MAP = mean annual precipitation). Length of arrows corresponds with the relative strength of the regression for the respective variables.

especially large (older) trees, and the maximum age (and size) of trees is limited by the very nature of the substrate.

Regional identity of leatherleaf bog communities.—A comparison of the vegetation of leatherleaf bogs of different regions was facilitated by: 1) relative intraregional homogeneity, 2) by the large amount of published data from different regions, and 3) a common variable in all of the studies that allowed standardization of the data for analysis. Scarcity of similar quantities of appropriate regional data on non-*Sphagnum*-dominated fens prevented statistical comparison of fens.

Table 8.—Names, locations, and sources of vegetation data for 27 leatherleaf bogs in the eastern United States. Acronyms correspond with Figure 3.

Peatland name	Acronym	Region	Source
Burket Bog	BUR	NE Indiana	Present study
Dutch Street Bog	DSB	NE Indiana	Present study
Leatherleaf Bog	LB	NE Indiana	Present study
Yost Bog	YB	North-central Indiana	Present study
Shoemaker Bog	SHB	NW Indiana	Present study
Fern Lake Bog	FLB	NE Ohio	Andreas & Bryan (1990)
Flatiron Lake Bog	FLT	NE Ohio	Andreas & Bryan (1990)
Triangle Lake Bog	TLB	NE Ohio	Andreas & Bryan (1990)
Portage Bog	POR	SW Lower Michigan	Brewer (1966)
North Bog	NOR	SW Lower Michigan	Keough & Pippen (1981)
South Bog	SOU	SW Lower Michigan	Keough & Pippen (1981)
Pennfield Bog	PEN	SW Lower Michigan	Crow (1969a)
Buck Hollow	BUC	SE Lower Michigan	Bailey (1967)
Inverness Mud Lake	IML	N Lower Michigan	Bevis (1960)
Bryant's Bog	BRY	N Lower Michigan	Schwintzer (1981)
Dingman Bog	DIN	N Lower Michigan	Schwintzer (1981)
Gate's Bog	GAT	N Lower Michigan	Schwintzer (1981)
Mud Lake (open mat)	MLO	N Lower Michigan	Schwintzer (1981)
Mud Lake (treed)	MLT	N Lower Michigan	Schwintzer (1981)
Penny Lake Bog	PLB	N Lower Michigan	Schwintzer (1981)
Green Pond Bog	GPB	S New York	Lynn & Karlin (1985)
Spruce Pond Bog	SPB	S New York	Lynn & Karlin (1985)
Tiny Cedar Pond	TCP	S New York	Lynn & Karlin (1985)
Uttertown Bog	UB	N New Jersey	Lynn & Karlin (1985)
Mishaps Bog	MB	N New Jersey	Lynn & Karlin (1985)
Lost Lake Bog	LLB	N New Jersey	Lynn & Karlin (1985)
Pequawket Bog	PQB	Central New Hampshire	Fahey & Crow (1995)

Indirect gradient analysis (Detrended Correspondence Analysis (DCA)) of vegetation frequency (ranked) from 27 leatherleaf bogs in the eastern United States (Table 8) showed three distinct clusters: those from southern Michigan and northern Indiana, those from northern Michigan, and those from southern New York, northern New Jersey and northeast Ohio (Fig. 3). Direct gradient analysis (Canonical Correspondence Analysis (CCA)) of the vegetation and five climatic variables showed a similar clustering; however, the Ohio peatlands were more distinctly separated from the northeastern sites, and the New Hampshire bog (Pequawket Bog) associated more closely with the southern Great Lakes sites (Fig. 3).

Much of the variability separating the "southern peatlands" (southern Michigan, northern Indiana, northeast Ohio, southern New York, northern New Jersey and New Hampshire) from the "northern peatlands" (represented by northern Michigan) is explained by mean annual temperature and mean annual precipitation (both having r^2 values > 0.8). The climate surrounding the northern peatlands is colder and dryer on average. Peatlands in southern Michigan and northern Indiana were further distinguished from the northern sites by having much hotter mean July temperatures. The number of frost-free days was different between bogs from the southern Great Lakes region and bogs from the northeastern U.S.; however, this variable was relatively insignificant with an r^2 value of < 0.2.

Analysis of the frequency of the most prevalent leatherleaf bog species from all of the regions and sites listed in Table 8 revealed seven geographic groupings: 1) species common to all leatherleaf bogs in the eastern United States, 2) species characteristic of northern peatlands only, 3) species restricted to southern peatlands, 4) species found in most re-

Table 9.—Prevalent vascular plants from 27 leatherleaf bogs in six general localities in the eastern United States: 1) northern Indiana (present study), 2) southern Michigan (Bevis 1960, Brewer 1966, Bailey 1967, Crow 1969a, Keough & Pippen 1981), 3) northern Michigan (Coburn *et al.* 1932, Schwintzer 1981), 4) northeast Ohio (Andreas & Bryan 1990), 5) southern New York & northern New Jersey (Lynn & Karlin 1985), and 6) New Hampshire (Fahey & Crow 1995). Number in parentheses is the number of peatlands included for that region. Numbers in the table show the percent of the peatlands that harbored the respective taxon. In regions where only one bog was represented, a "P" indicates that a given species was present.

	1 (5)	2 (5)	3 (7)	4 (3)	5 (6)	6 (1)
Widespread species						
Acer rubrum	100	80	17	100	100	P
Andromedia glaucophylla	60	40	50	—	67	P
Calla palustris	—	20	—	67	67	P
Chamaedaphne calyculata	100	100	100	100	100	P
Drosera intermedia	40	20	17	33	100	P
Drosera rotundifolia	40	40	33	67	100	P
Gaylussacia baccata	20	—	17	33	100	—
Larix laricina	—	40	33	67	83	P
Rhynchospora alba	—	20	17	67	83	P
Sarracenia purpurea	80	40	33	67	100	P
Vaccinium macrocarpon	60	40	17	100	100	P
Vaccinium oxycoccos	60	40	33	33	100	P
Aronia melanocarpa	60	40	17	67	50	P
Northern species						
Eriophorum spissum	—	—	67	—	—	—
Ledum groenlandicum	—	—	50	—	—	—
Smilacina trifolia	—	—	33	—	—	P
Vaccinium angustifolium	—	—	83	—	—	—
Vaccinium myrtiloides	—	—	83	—	—	—
"Southern" species						
Cephalanthus occidentalis	80	—	—	—	33	P
Decodon verticillata	40	20	—	67	83	P
Dulichium arundinaceum	80	60	—	33	17	P
Hypericum virginicum	80	20	—	100	100	—
Toxicodendron vernix	80	20	—	67	50	P
Vaccinium corymbosum	40	40	—	100	100	P
Woodwardia virginica	100	60	—	100	17	P
Northern & Great Lakes species						
Betula pumila	—	20	33	—	—	—
Carex oligosperma	60	40	67	—	—	P
Northern & northeastern species						
Carex trisperma	—	—	50	100	67	P
Kalmia polifolia	—	—	67	—	50	P
Picea mariana	—	—	50	—	83	P
Northeastern species						
Carex canescens	—	—	—	100	100	P
Gaylussacia frondosa	—	—	—	—	67	—
Kalmia angustifolia	—	—	—	—	100	P
Peltandra virginica	—	—	—	33	83	P
Picea rubens	—	—	—	—	50	—
Rhododendron viscosum	—	—	—	—	100	—
Southern Great Lakes species						
Carex rostrata	80	—	—	—	—	—
Iris versicolor	60	—	—	—	—	—
Nuphar advena	60	—	—	—	—	—
Scirpus cyperinus	100	40	—	—	—	—

gions except for the Northeast, 5) species found in the north and northeast but absent from the southern great lakes region, 6) species found only in the Northeast, and 7) species exclusive to peatlands of the southern Great Lakes region (Table 9). Species such as *Carex canescens* and *Peltandra virginica* demonstrated the northeastern affinity of Ohio peatlands, whereas *Betula pumila* and *Carex oligosperma* showed the northern Great Lakes affinity of leatherleaf bogs in Indiana and southern Michigan.

The results of the ordinations and species groupings suggest that not only are the leatherleaf bog assemblages of the North different from those at the southern limit of the community (as concluded by Lynn & Karlin 1985), but the southern populations also have specific regional affinities. The differences between the southern sites cannot be entirely attributed to climatic variation. Some of the differences must be attributable to biogeographic history as it relates to the various lobes of ice of Wisconsin Age glaciation (see Crow 1969b).

CONCLUSIONS

Systematic vegetation sampling of 16 Indiana peatlands, including fens, tall-shrub bogs, leatherleaf bogs and forested peatlands yielded a total of 181 species. The number of species found at each site was variable, and no significant difference in species richness was noted between fens and bogs. A significant portion of the variability of the vascular and bryophyte vegetation was attributed to groundwater influence as indicated by alkalinity. Fens and bogs were distinctly separated on the basis of alkalinity. In addition to abiotic factors, temporal variables such as shrub and tree cover (indirectly indicative of seral stage, soil moisture and substrate stability) explained a significant portion of the variation. The vascular vegetation of tall-shrub bogs and forested peatlands was distinctly separated from the other sites. In contrast, shrub cover was an insignificant factor in bryophyte variability, although tree cover (Basal Area) was significant. It was thus concluded that substrate moisture rather than light accounted for most of the temporal variability in bryophytes.

Analysis of extant vegetation, along with the consideration of the palaeoecological data presented by Swinehart & Parker (2000), revealed an apparent hydrosere that begins with a lake or pond and ends with a forested peatland. All peatlands have a fen stage, but only some develop into bogs before becoming forested. Regardless of the inherent mineral-richness, all Indiana peatlands become dominated by red maple. Red maple may be the "climax" species for the peatland hydrosere in Indiana, but insufficient time has passed for a definitive conclusion. "Old-growth" might be a better descriptive term for these latter stages of peatland development.

The vascular vegetation communities of Indiana peatlands and other peatlands in the southern Great Lakes region are distinct from those in the northeast, Ohio and the northern Great Lakes. Some of this distinction is attributable to climatic factors, while others are related to biogeographic history of the region.

LITERATURE CITED

Aldrich, J.W. 1943. Biological survey of the bogs and swamps in northeastern Ohio. American Midland Naturalist 30:346–402.

Andreas, B.K. 1989. Ohio wetlands: The peatlands—Part I. On the Fringe 7:5–17.

Andreas, B.K. & G.R. Bryan. 1990. The vegetation of three *Sphagnum*-dominated Basin-type bogs in northeastern Ohio. Ohio Journal of Science 90:54–66.

Andreas, B.K. & J.D. Knoop. 1992. 100 years of change in Ohio peatlands. Ohio Journal of Science 92:130–138.

Andrus, R.E. 1980. Sphagnaceae of New York State. New York State Museum Bulletin 422, State Education Dept. Albany, New York. vi + 89 pp.

Andrus, R.E. 1987. Nomenclatural changes in *Sphagnum imbricatum sensu lato*. The Bryologist 90:217–220.

Andrus, R.E., D.J. Wagner & J.E.Titus. 1983. Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients. Canadian Journal of Botany 61:3128–3139.

Aughanbaugh, J. & O.D. Diller. 1968. Flora Of Brown's Lake Bog And Vicinity. Ohio Chapter of the Nature Conservancy. 23 pp.

Bailey, R.E. 1967. Vegetation Of Buck Hollow, Edwin S. George Reserve, Livingston County, Michigan. Student paper to W.S. Benninghoff, Department of Botany, University of Michigan, Ann Arbor. 25 pp.

Bevis, F.B. 1960. Phytosociological study of Inverness Mud Lake Bog, Cheboygan County, Michigan. Papers of the Michigan Academy of Science, Arts & Letters 45:61–74.

Brewer, R. 1966. Vegetation of two bogs in southwestern Michigan. Michigan Botanist 5:36–46.

Cain, S.A. 1928. Plant succession and ecological history of a central Indiana swamp. Botanical Gazette 86:384–401.

Collins, S.L., J.V. Perino & J.L. Vankat. 1982. Woody vegetation and microtopography in the bog meadow association of Cedar Bog, a west-central Ohio Fen. American Midland Naturalist 108:245–249.

Crow, G.E. 1969a. An ecological analysis of a southern Michigan bog. Michigan Botanist 8:11–27.

Crow, G.E. 1969b. A phytogeographical analysis of a southern Michigan bog. Michigan Botanist 8:51–60.

Crum, H.A. 1988. A Focus On Peatlands And Peatmosses. University of Michigan Press, Ann Arbor, Michigan. 306 pp.

Crum, H.A. 1991. Liverworts And Hornworts Of Southern Michigan. University of Michigan Herbarium, Ann Arbor. 233 pp.

Crum, H.A. & L.E. Anderson. 1981. Mosses of Eastern North America. Columbia University Press, New York. 2 vol. 1328 pp.

Dahl, T.E. 1990. Wetlands Losses In The United States 1780's To 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. 21 pp.

Damman, A.W.H. & T.W. French. 1987. The Ecology Of Peat Bogs Of The Glaciated Northeastern United States: A Community Profile. U.S. Fish and Wildlife Service Biological Report 85(7.16). 100 pp.

Davis, R.B. & D.S. Anderson. 1991. The Eccentric Bogs Of Maine. Maine Agricultural Experiment Station Technical Bulletin #146. 151 pp.

Duncan, D.P. 1954. A study of some of the factors affecting the natural regeneration of Tamarack (*Larix laricina*) in Minnesota. Ecology 35:498–521.

Dunlop, D.A. 1987. Community classification of the vascular vegetation of a New Hampshire peatland. Rhodora 89:415–440.

Fahey, L.L. & G.E. Crow. 1995. The vegetation of Pequawket Bog, Ossipee, New Hampshire. Rhodora 97:39-92.

Friesner, R.C. & J.E. Potzger. 1946. The Cabin Creek Raised Bog, Randolph County, Indiana. Butler University Botanical Studies 8:24–43.

Gates, F.C. 1942. The bogs of northern lower Michigan. Ecological Monographs 12:214–254.

Glaser, P.H. 1987. The Ecology Of Patterned Boreal Peatlands Of Northern Minnesota: A Community Profile. U.S. Fish and Wildlife Service Report 85 (7.14). 98 pp.

Glaser, P.H. 1992. Raised bogs in eastern North America—regional controls for species richness and floristic assemblages. Journal of Ecology 80: 535–554.

Glaser, P.H., J.A. Janssens & D.I. Siegel. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. Journal of Ecology 78: 1021–1048.

Glime, J.M. 1980. Northern calciphilic mosses in the Lawrence Lake Fen and Marsh (Barry Co., Michigan). Michigan Botanist 19:91–92.

Glime, J.M., R.G. Wetzel & B.J. Kennedy. 1982. The effects of bryophytes on succession from alkaline marsh to Sphagnum bog. American Midland Naturalist 108:209–223.

Hessler, R. 1896. Notes On The Flora Of Lake Cicott And Lake Maxinkuckee. Proceedings of the Indiana Academy of Science (reprinted). 14 pp.

Hull, E.D. 1937. Some Indiana bogs. The American Botanist 43:5–10.

Jeglum, J.K., A.N. Boissonneau & V.F. Haavisto. 1974. Toward a wetland classification for Ontario. Canadian Forest Service Information Report O-x-215. Sault St. Marie, Ontario.

Johnson, C.W. 1985. Bogs Of The Northeast. University Press of New England, Hanover. 269 pp.

Jones, C.H. 1941. Studies in Ohio Floristics. I. Vegetation of Ohio bogs. American Midland Naturalist 26:674–698.

Karlin, E.F. & L.M. Lynn. 1988. Dwarf-shrub bogs of the southern Catskill Mountain region of New York State: Geographic changes in the flora of peatlands in northern New Jersey and southern New York. Bulletin of the Torrey Botanical Club 115:209–217.

Keough, J.R. & R.W. Pippen. 1981. A comparison of vegetation patterns in two adjacent bogs in southwest Michigan. Michigan Botanist 20:157–166.

Keough, J.R. & R.W. Pippen. 1984. The movement of water from peatland into surrounding groundwater. Canadian Journal of Botany 62:835–839.

Knoop, J.D. 1987. Vegetational survey of Sinking Creek Fen, Clark County, Ohio. Ohio Journal of Science 87:4.

Kratz, T.K. & C.B. DeWitt. 1986. Internal factors controlling peatland-lake ecosystem development. Ecology 67:100–107.

Kuhry, P., B.J. Nicholson, L.D. Gignac, D.H. Vitt & S.E. Bayley. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany 71:10–22.

Lauschman, R. 1991. Changes in the vascular flora of Cambden (Bog) Lake, Lorain County, Ohio. Ohio Journal of Science 91(2):1.

Lesica, P. & F.W. Allendorf. 1995. When are peripheral populations valuable for Conservation? Conservation Biology 9:753–760.

Lindsey, A.A., D.V. Schmelz & S.A. Nichols.

1969. Natural Areas In Indiana And Their Preservation. Purdue University Press. 594 pp.
Lindsey, A.J. 1932. The Merrillville White Pine (*Pinus strobus*) Bog, Lake County, Indiana. Butler University Botanical Studies 2:167–178.
Lynn, L.M. & E.F. Karlin. 1985. The vegetation of the low-shrub bogs of northern New Jersey and adjacent New York: Ecosystems at their southern limit. Bulletin of the Torrey Botanical Club 112: 436–444.
Markle, M.S. 1916. Phytecology of peat bogs near Richmond, Indiana. Proceedings of the Indiana Academy of Science 1915:359–375.
McCune, B. & Mefford. 1995. PC-ORD. Multivariate Analysis of Ecological Data, Version 2.0. MjM Software Design, Glenden Beach, Oregon.
McQueen, C.B. & R.M. Giesy. 1975. Comparison of the present and past bryophyte flora of Cedar Bog. Ohio Journal of Science 75:188–190.
Moizuk, G.A. & R.B. Livingston. 1966. Ecology of red maple (*Acer rubrum* L.) in a Massachusetts upland bog. Ecology 47:942–950.
NOAA. 1974. Climates Of The States, Vol. 1 (Eastern States). National Oceanic and Atmospheric Administration, U.S. Dept. of Commerce, Water Information Center, Washington. 480 pp.
Parker, G.R. 1989. Old-growth forests of the Central Hardwood Region. Natural Areas Journal 9(1):5–11.
Potzger, J.E. 1934. A notable case of bog formation. American Midland Naturalist 15:567–580.
Reichle, D.E. & W.T. Doyle. 1965. Bryophyte succession in a northern Illinois bog. The Bryologist 68:463–470.
Schaal, L.A. 1966. Climate. *In* Natural Features Of Indiana. (A.A. Lindsey, ed.). Indiana Academy of Science, Indianapolis. 600 pp.
Schwintzer, C.R. 1981. Vegetation and nutrient status of northern Michigan bogs and conifer swamps with a comparison to fens. Canadian Journal of Botany 59:842–853.
Sheviak, C.J. & A. Haney. 1973. Ecological interpretations of the vegetation patterns of Volo Bog, Lake County, Illinois. Transactions of the Illinois Academy of Science 66:99–112.
Sims, R.A., D.W. Cowell & G.M. Wickware. 1982. Classification of fens near southern James Bay, Ontario, using vegetational physiognomy. Canadian Journal of Botany 60:2608–2623.
Slack, N.G., D.H. Vitt & D.G. Horton. 1980. Vegetational gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany 58:330–350.
Sorenson, E.R. 1986. Ecology And Distribution Of Ribbed Fens In Maine And Their Relevance To The Critical Areas Program. Maine Critical Areas Program Report No. 81. 171 pp.
Starcs, H. 1961. Notes on the vascular plants of the Cabin Creek Raised Bog. Proceedings of the Indiana Academy of Science 71:302–304.
Stewart, P.M., K. Kessler & R. Dunbar. 1994. Intrafen and interfen variation of Indiana fens: Water chemistry. Proceedings of the Indiana Academy of Science 102:207–217.
Swinehart, A.L. 1994. An Ecological Investigation Of Three *Sphagnum*-bogs In Noble County, Indiana: Remnant Communities Of A Region In Transition. M.S. Thesis, Department of Biology, Central Michigan University, Mt. Pleasant. 224 pp.
Swinehart, A.L. & G.D. Starks. 1994. A record of the natural history and anthropogenic senescence of an Indiana tamarack bog. Proceedings of the Indiana Academy of Science 103:225–239.
Swinehart, A.L. 1997. The Development And Ecology Of Peatlands In Indiana. Ph.D. Dissertation, Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana. 303 pp.
Swinehart, A.L. & R.E. Andrus. 1998. New records for *Sphagnum* and other peatland bryophytes from Indiana. Northeastern Naturalist 5: 189–198.
Swinehart, A.L. & G.R. Parker. 2000. Palaeoecology and development of peatlands in Indiana. American Midland Naturalist 143:267–297.
Swink, F. & G. Wilhelm. 1994. Plants of the Chicago Region. 4th ed. Indiana Academy of Science, Indianapolis. 921 pp.
Sytsma, K.J. & R.W. Pippen. 1981. The Hampton Creek wetland complex in southwestern Michigan: II. Community classification. Michigan Botanist 20:147–156.
Sytsma, K.J. & R.W. Pippen. 1982. The Hampton Creek wetland complex in southwestern Michigan: III. Structure and succession of tamarack forests. Michigan Botanist 21:67–76.
Transeau, E.N. 1905-6. The bogs and bog flora of the Huron River Valley. Botanical Gazette. 40: 351–375, 418–448 (1905); 41:17–42 (1906).
Vitt, D.H. & P. Kuhry. 1992. Changes in moss-dominated wetland ecosystems. Pp. 178–210, *In* Bryophytes And Lichens In A Changing Environment. (J.W. Bates & A.M. Farmer, eds.). Oxford University Press, Oxford.
Vitt, D.H. & N.G. Slack. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Canadian Journal of Botany 53:332–359.
Vitt, D.H., H.A. Crum & J.A. Snider. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Michigan Botanist 14:190–200.
Waterman, W.G. 1926. Ecological problems from the Sphagnum bogs of Illinois. Ecology 7:255–272.
Welch, W.H. 1963. Bryophytes of Cabin Creek

Raised Bog. Proceedings of the Indiana Academy of Science 72:105–107.

Wilcox, D.A. 1982. The Effects Of De-icing Salts On Water Chemistry And Vegetation In Pinhook Bog, Indiana Dunes National Lakeshore. Ph.D. Dissertation, Dept. of Forestry & Natural Resources, Purdue University.

Wilcox, D.A., R.J. Shedlock & W.H. Hendrickson. 1986. Hydrology, water chemistry and ecological relations of the raised mound of Cowles Bog. Ecology 74:1103–1117.

Worley, I.A. 1981. Maine Peatlands: Their Abundance, Ecology, And Relevance To The Critical Areas Program Of The State Planning Office. Vermont Agricultural Experiment Station Planning Report 73. 387 pp.

Worley, I.A. & J.R. Sullivan. 1980. Classification Scheme For The Peatlands Of Maine. Vermont Agricultural Experiment Station, Research Report 8. 88 pp.

Manuscript received, 21 March 2001, revised 4 October 2001.