

1-1-1987

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A CHRONOSEQUENCE OF AQUATIC MACROPHYTE COMMUNITIES IN DUNE PONDS

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(Accepted for publication 7 January 1987)

ABSTRACT

Wilcox, D. A. and Simonin, H. A., 1987. A chronosequence of aquatic macrophyte communities in dune ponds. *Aquat. Bot.*, 28: 227-242.

Differences in macrophyte community composition in a chronosequence of spatially separated dune ponds near the south shore of Lake Michigan were examined and related to environmental variables. Five ponds from each of five pond rows were sampled. In each pond, the cover of each plant species and water and sediment depth were sampled using a stratified random design. Radio-carbon dates were obtained from selected ponds.

Ordination of the vegetation data by detrended correspondence analysis revealed similarities in the plant communities of ponds in the same row and community differences between ponds in different rows. Younger ponds (<300 years) were dominated by *Chara* spp. and *Najas flexilis*, middle-age ponds (2100 years) by *Myriophyllum* spp. and *Nymphaea tuberosa*, and older ponds (3000 years) by *Typha angustifolia*. Distribution of macrophyte communities was most closely correlated with water depth, which generally decreased with increasing age of the pond row. Some sediment chemistry differences were found between pond rows, but there were no significant differences in water chemistry.

Although a linear succession pattern is suggested, we think that anthropogenic disturbance played a major role in determining the vegetation differences observed. Thus, a chronosequence of spatially separated ponds can provide valuable information on hydrarch succession, but it may be misleading and actually represent succession affected by disturbance history.

INTRODUCTION

The definitions and interpretations of succession in wetland and shallow aquatic plant communities have recently been reviewed by van der Valk (1982). He described one of the major impacts on wetland ecology of the Clementsian successional model as 'the tendency to interpret zonal patterns in wetlands as indicators of future successional trends'. He also suggested that the

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practice of assuming that zonation presages succession was sometimes abused. A review of the literature will verify that a large proportion of hydrarch succession studies have, in fact, focused on zonation patterns (e.g. Pearsall, 1920; Gates, 1926; Graham and Henry, 1933; Wilson, 1935, 1941; Lindeman, 1941). Other studies have utilized paleobotanical methods (Walker, 1970; Jankovska, 1978), seed bank analyses (van der Valk and Davis, 1976, 1978, 1979) and short-term site evaluations (Macan, 1977; Larson et al., 1980; Danell and Sjöberg, 1982).

Studies of plant succession in chronosequences of spatially separated aquatic habitats have been rare (van der Valk and Bliss, 1971; Crawford, 1977), probably because suitable sites are also rare. One well-known (Odum, 1953; Golley, 1977) example of such a chronosequence is the series of dune ponds bordering the south shore of Lake Michigan that was studied by Shelford (1911, 1913). Although he was investigating the animal communities of the ponds, Shelford did report non-quantitative observations on the differences between macrophyte communities in successively older rows of ponds. His assessment of the plant communities was aided by Cowles, who had conducted pioneering terrestrial plant succession studies on the sand dunes of the region (Cowles, 1899, 1911). The low dune ridges that separate the pond rows were utilized in further studies of plant succession by Olson (1958) and Henderson and Long (1984).

The purpose of this paper is to quantitatively test the existence of a successional sequence in these ponds and relate it to changes in environmental variables. We also seek to explain the observed species distribution patterns among ponds and to determine if changes in environmental factors with time or disturbances, or both, have given rise to the observed patterns.

STUDY SITE

The inter-dunal and intra-dunal ponds used in this study are located within the Miller Woods section of Indiana Dunes National Lakeshore in Lake County, Indiana. There are over 150 ponds in this 360-ha area, and they represent the last minimally disturbed remnants of the extensive pond system studied by Shelford (1911, 1913). The ponds were formed in rows on the Calumet Lake Plain as ancestral Lake Michigan receded northward. Thus, the ponds to the north are younger than the ponds to the south. Although Shelford (1911) reported as many as 58 linear rows of ponds, only five recognizable rows (numbered 1–5, north to south) now remain in the national lakeshore (Fig. 1). The surrounding lands have succumbed to industrial and residential development.

The three southern-most rows of ponds in the study area are inter-dunal ridge and swale formations. The two northern-most rows of ponds are intra-dunal formations (Reshkin, 1981). The ponds vary from intermittently ponded depressions of about 10 m² area to permanent bodies of water as large as 6.7 ha. Most of the permanent ponds are in basins with a maximum depth of 2 m;

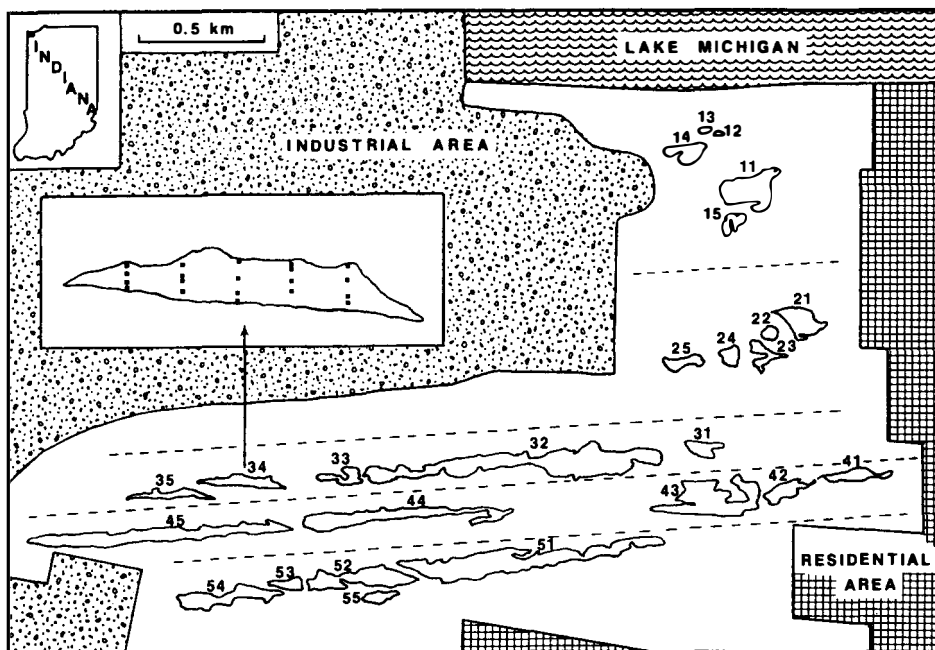


Fig. 1. Map of the Miller Woods study area showing numbered, selected study ponds, surrounding development and schematic diagram of sampling design.

the relative water and sediment depths in the basins vary with age. Water levels are maintained by the north-flowing feed of calcareous ground water through the region. Pond vegetation varies from *Chara*-dominated younger ponds to floating-leaved and submersed species in middle-age ponds to *Typha*-dominated older ponds. The dunes are dominated by black oak woodlands.

METHODS

Five ponds from each of the five pond rows were randomly selected from pools of 7, 12, 8, 12 and 7 ponds per row (1–5). The ponds in the selection pool were all permanent ponds not known to be directly affected by the surrounding industrial and residential development. The selected ponds were given two-digit identification numbers, with the first digit referring to the pond row (Fig. 1). A stratified random sampling scheme was designed with five equally spaced north-south transects across each pond and four randomly spaced 1 m² quadrats on each transect, for a total of 20 quadrats per pond (see Fig. 1). At each sampling quadrat, data were collected on plant species occurrence and percentage cover. All plant names used conform to the nomenclature of Swink and Wilhelm (1979). Authorities for all species are listed (see Table II). Water

and sediment depths (to sand bottom) were also measured. All sampling was conducted in the second half of August 1982.

Mid-depth water chemistry samples (two per pond) were collected at randomly selected locations on the eastern- and western-most transects of each pond in mid-April, mid-July and late October 1983. The sampling times were chosen to provide data from periods before spring plant growth, during mid-summer growth and during senescence in the autumn. Specific conductance, pH, alkalinity, calcium and magnesium determinations were carried out according to APHA (1975). Analyses for dissolved phosphorus, $\text{NO}_2 + \text{NO}_3$ nitrogen, $\text{NH}_4 +$ organic nitrogen, and potassium were conducted by standard U.S. Geological Survey laboratory procedures (Brown et al., 1970).

Sediment chemistry samples (eight per pond) were collected from two randomly selected locations on all pond transects except the center transect of each pond. The samples were collected from the upper 20 cm of sediment in early April 1984, prior to spring plant growth. The samples were dried and then analyzed on a dry weight basis by the Purdue Soil Testing Laboratory for Bray No. 1 phosphorus, nitrate nitrogen, ammonia nitrogen, exchangeable potassium, pH and percentage organic matter. Samples for radiocarbon dating were taken from the bottom of sediment cores collected at the deepest identified parts of ponds 21, 32, 44 and 51.

Water and sediment chemistry and water and sediment depth data were analyzed by analysis of variance and Student-Newman-Keuls multiple range tests. The mean values reported for pH were calculated from hydrogen ion concentrations, but the ANOVAs were run on the actual pH values, which have more homogeneous variances. The vegetation data were summarized by pond as importance values (IV), calculated as the sum of relative frequency and relative mean cover. The $\text{IV} \times \text{pond}$ matrix was analyzed by detrended correspondence analysis (DCA using DECORANA) to give ordinations of both ponds and species. Since our interests were in more general community patterns, rather than rare species occurrences, the total number of species used in the ordination was reduced from 89 to 51 by adherence to the following criteria: species were dropped if the frequency was less than 10 quadrats (out of 500) unless, (1) they were found in more than one pond and one cover value was at least 20%, or (2) they were found in only one pond but in five or more quadrats. The qualifiers were added to retain species that might be considered indicators. Due to problems associated with collecting and identifying a large number of specimens, *Chara* and *Myriophyllum* observations were each grouped. The common species identified were *Chara vulgaris* L. and *Myriophyllum verticillatum pectinatum* Wallr. Stands of dead *Typha* (cattails) were common in many ponds and were therefore recognized and classed separately.

TABLE I

Results of SNK sequential range tests ($\alpha=0.05$) based on one-way ANOVAs for water and sediment depths at individual sites by pond row

	Water ¹					Sediment ²				
Pond row	5	1	4	3	2	1	2	3	4	5
Mean depth (cm)	<u>12.9</u>	<u>26.3</u>	<u>27.5</u>	<u>40.8</u>	<u>55.3</u>	<u>13.6</u>	<u>20.7</u>	<u>27.0</u>	<u>38.5</u>	<u>55.7</u>

¹ $F_{0.05(4,495)} = 40.32, P=0.0001.$

² $F_{0.05(4,495)} = 139.46, P=0.0001.$

RESULTS

Pond age and water/sediment depth

Radiocarbon dates from the bottom of sediment cores collected from ponds in Rows 2–5 support the concept that the pond rows formed sequentially. The minimum pond ages in years before present (± 1 S.D.) were as follows: Pond 51, 3000 ± 93 ; Pond 44, 2400 ± 70 ; Pond 32, 2100 ± 80 ; Pond 21, 2100 ± 123 . The sample from Pond 21 contained marly organic muds that were acid treated to remove carbonates prior to dating. However, the presence of a calcareous, marl-depositing environment at the time the organic materials were produced may also have induced plant uptake of ancient carbon from bicarbonates (Wetzel, 1975). This would have resulted in an artificially older radiocarbon date for that pond. The core collected from Row 1 Pond 13 contained too much sand and not enough organic matter for dating. The ponds in Row 1 are thought to be no more than a few hundred years old (Futyma, 1985).

The mean basin depth for ponds in Rows 2–5 is about 70 cm, and it is partitioned between varying depths of water and sediment (Table I). Ponds in Row 1 are influenced by blowing sand from active dunes, and the mean basin depth is about 40 cm. Mean sediment depth increased significantly ($\alpha=0.05$) in older ponds. The corresponding mean water depths decreased significantly with age from 55 to 13 cm in Rows 2–5. The exception was Row 1, where numerous shallow water sites were encountered in wind-blown areas, reducing average water depths to 26 cm. Casual observations in other years suggest that pond water levels may vary by as much as 20 cm between dry and wet years.

Vegetation

Differences were seen in the plant communities of each pond row as identified by the mean importance values and the numbers of ponds in which individual species occurred (Table II). The most common species in Row 1 were *Chara* spp., *Najas flexilis* and *Potamogeton gramineus*. The most common spe-

TABLE II

Number of ponds per row each plant species occurred in (frequency) and mean importance value of species in pond row (given in parentheses)

Species	Row 1	Row 2	Row 3	Row 4	Row 5
<i>Calamagrostis canadensis</i> (Michx.) Nutt.	—	—	2 (3.0)	5 (7.5)	4 (10.1)
<i>Carex stricta</i> Lam.	—	—	1 (1.0)	3 (1.4)	—
<i>Cephalanthus occidentalis</i> L.	—	—	—	2 (1.0)	3 (5.7)
<i>Chara</i> spp.	5 (89.9)	5 (82.9)	1 (0.2)	2 (4.2)	2 (2.3)
<i>Cladium mariscoides</i> (Muhl.) Torr.	3 (4.6)	—	1 (6.4)	1 (0.2)	2 (0.6)
Cyperaceae	—	—	—	—	2 (0.6)
<i>Drepanocladus</i> spp.	—	2 (2.3)	—	—	—
<i>Dryopteris thelypteris</i> (Lawson) Nakai	—	—	1 (0.2)	2 (1.9)	4 (1.0)
<i>Dulichium arundinaceum</i> (L.) Britt.	—	—	1 (0.2)	1 (0.7)	3 (2.6)
<i>Eleocharis acicularis</i> (L.) R. & S.	1 (3.4)	2 (0.9)	2 (0.7)	2 (0.5)	3 (5.4)
<i>Eleocharis elliptica</i> Kunth	1 (2.8)	—	—	—	—
<i>Eleocharis rostellata</i> Torr.	—	—	—	—	1 (3.4)
<i>Eleocharis</i> spp.	4 (7.2)	—	1 (7.6)	3 (3.4)	2 (0.4)
<i>Elodea canadensis</i> Michx.	1 (2.0)	—	—	—	—
<i>Iris virginica</i> (Small) E. Anders.	—	—	2 (1.4)	1 (0.9)	2 (0.6)
<i>Myriophyllum</i> spp.	—	5 (12.6)	3 (31.0)	5 (51.5)	3 (15.8)
<i>Najas flexilis</i> (Willd.) Rostk. & Schmidt	4 (27.2)	5 (14.7)	2 (6.6)	1 (3.0)	—
<i>Nitella</i> spp.	—	3 (4.1)	2 (1.0)	1 (0.5)	2 (2.2)
<i>Nuphar advena</i> (Ait.) Ait. f.	—	3 (4.8)	3 (6.5)	2 (1.9)	—
<i>Nuphar variegatum</i> Engelm.	1 (0.4)	2 (5.0)	4 (9.8)	4 (9.5)	3 (4.0)
<i>Nymphaea tuberosa</i> Paine	—	1 (2.9)	3 (25.8)	4 (4.2)	1 (2.1)
<i>Phragmites communis</i> (Fourn.) Fern.	—	—	—	1 (0.3)	2 (0.9)
Poaceae	2 (2.4)	—	—	—	—
<i>Polygonum amphibium</i> (Coleman) Fern.	—	1 (0.3)	2 (3.3)	3 (2.4)	3 (3.6)
<i>Polygonum coccineum</i> Muhl.	—	4 (4.5)	2 (2.0)	5 (4.1)	5 (12.8)
<i>Polygonum hydropiperoides</i> Michx.	—	—	—	1 (0.2)	3 (4.4)
<i>Pontederia cordata</i> L.	—	—	—	2 (1.7)	2 (1.3)
<i>Potamogeton amplifolius</i> Tuckerm.	—	3 (7.9)	—	—	—
<i>Potamogeton foliosus</i> Raf.	2 (1.7)	2 (5.4)	2 (2.3)	2 (5.7)	—
<i>Potamogeton gramineus</i> L.	4 (14.5)	—	2 (0.8)	2 (0.5)	3 (3.9)
<i>Potamogeton illinoensis</i> Morong	—	—	1 (0.6)	2 (3.5)	—
<i>Potamogeton natans</i> L.	—	1 (0.2)	2 (4.0)	—	—
<i>Potamogeton nodosus</i> Poir.	—	2 (2.6)	3 (3.7)	2 (0.4)	—
<i>Potamogeton pectinatus</i> L.	2 (12.3)	1 (1.0)	1 (0.6)	1 (1.2)	—
<i>Potamogeton pusillus</i> L.	—	1 (1.6)	1 (1.8)	1 (0.2)	1 (1.5)
<i>Proserpinaca palustris</i> Fern. & Griseb.	—	—	3 (3.9)	4 (5.1)	5 (19.5)
<i>Ranunculus flabellaris</i> Raf.	1 (0.5)	—	—	2 (0.5)	5 (5.6)
<i>Sagittaria graminea</i> Michx.	—	—	1 (2.7)	—	—
<i>Sagittaria latifolia</i> Willd.	1 (0.3)	—	1 (1.1)	3 (1.4)	4 (14.8)
<i>Scirpus acutus</i> Muhl.	4 (7.7)	2 (1.8)	2 (1.2)	5 (7.7)	4 (7.7)
<i>Scirpus americana</i> Pers.	5 (4.2)	—	—	—	—
<i>Scirpus cyperinus</i> (L.) Kunth	—	—	—	—	2 (0.6)
<i>Sparganium chlorocarpum</i> Rydb.	—	3 (3.2)	3 (2.3)	5 (6.0)	5 (5.3)
<i>Sparganium eurycarpum</i> Engelm.	—	—	—	2 (1.1)	1 (0.2)
<i>Typha angustifolia</i> L.	1 (0.3)	—	3 (5.6)	5 (23.1)	4 (25.9)
<i>Typha</i> (dead)	1 (1.9)	—	4 (19.1)	5 (18.9)	4 (11.1)
<i>Typha</i> (hybrid)	—	—	2 (12.4)	2 (5.6)	2 (1.5)
<i>Utricularia gibba</i> L.	3 (9.5)	3 (8.7)	1 (3.1)	—	—
<i>Utricularia vulgaris</i> L.	2 (0.8)	5 (29.9)	4 (17.1)	5 (11.1)	5 (18.8)
<i>Vallisneria americana</i> Michx.	1 (0.8)	2 (2.5)	2 (0.9)	—	—
<i>Zizania aquatica</i> L.	—	—	2 (1.3)	3 (3.9)	1 (0.1)

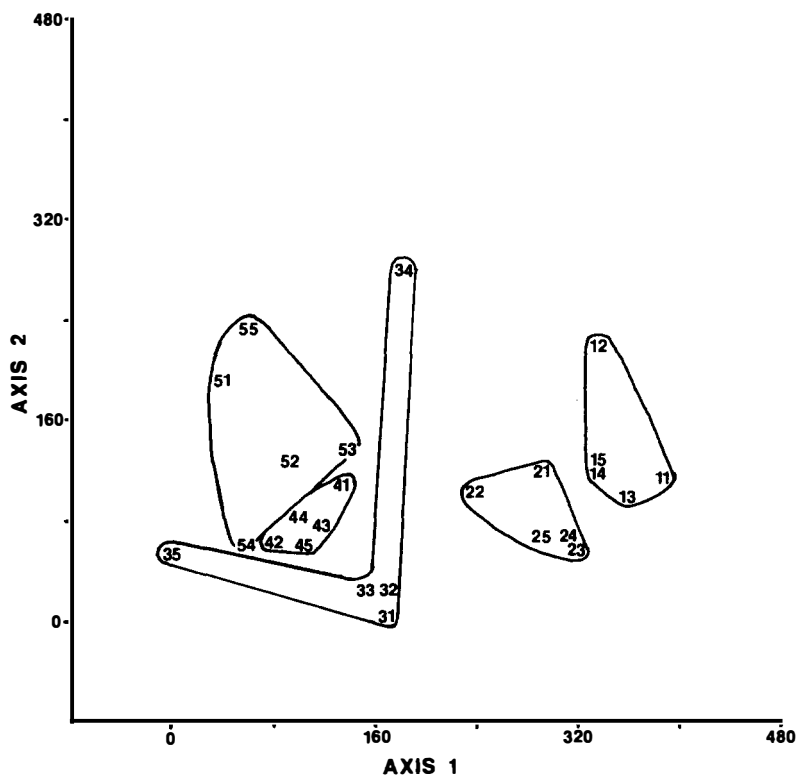


Fig. 2. Two dimensional plot of DCA ordination of the importance value \times pond matrix explaining 93.6% of the variance. Points are plotted as pond numbers.

cies in Row 2 were *Chara* spp., *Utricularia vulgaris*, *Najas flexilis* and *Myriophyllum* spp. In Row 3, the most common species were *Myriophyllum* spp., *Nymphaea tuberosa*, dead *Typha*, *Utricularia vulgaris* and *Nuphar*. In Row 4, they were *Myriophyllum* spp., *Typha angustifolia*, dead *Typha*, *Utricularia vulgaris* and *Nuphar*. The most common species in Row 5 were *Typha angustifolia*, *Proserpinaca palustris crebra*, *Utricularia vulgaris*, *Myriophyllum* spp., *Sagittaria latifolia*, *Polygonum coccineum*, dead *Typha* and *Calamagrostis canadensis*. Axis 1 of the DCA ordination clearly separated the plant communities of Row 1 ponds, Row 2 ponds, all but one (No. 35) of the Row 3 ponds, and ponds in Rows 4 and 5 (Fig. 2). The combination of Axes 1 and 2 separated the Row 4 ponds from the Row 5 ponds.

Ponds 34 and 35 are obvious outliers from the grouping of other ponds in their row, most probably because both ponds have a considerable number of shallow-water sites. The ordination scores generated by DCA for individual species can be used to assess these outliers (Fig. 3). The ordination of Pond 34 is influenced greatly by the dominance of *Eleocharis* spp., *Cladium maris-*

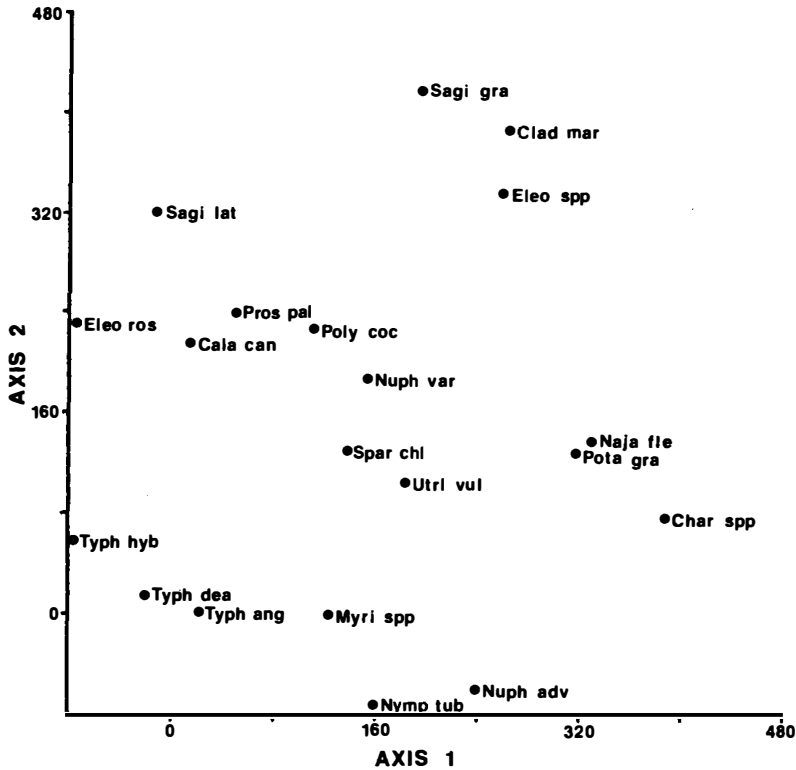


Fig. 3. Two-dimensional plot of DCA ordination of the importance value \times pond matrix explaining 93.6% of the variance. Points plotted are selected taxa.

coides, and to a lesser extent, *Sagittaria graminea*, and by the lack of *Myriophyllum* and *Nymphaea tuberosa*. Pond 35 is dominated by dead *Typha* and *Typha* hybrid, and it also lacks *Myriophyllum* and *Nymphaea tuberosa*.

Pond 12 is a less obvious outlier in Row 1. This pond also has quite shallow water and has more *Eleocharis* spp. and *Cladium mariscoides* and less *Chara* than is characteristic for other Row 1 ponds.

The scatter in the ordination among Row 5 ponds also reflects variation in species composition. Pond 51 is dominated by *Calamagrostis canadensis*, *Eleocharis rostellata* and *Sagittaria latifolia*; Pond 53 by *Sparganium chlorocarpum*; Pond 54 by dead *Typha* and *Typha angustifolia*; and Pond 55 by *Sagittaria latifolia*, *Polygonum coccineum* and *Proserpinaca palustris crebra*.

Axis 1 scores reflect the species diversity and species commonality among pond rows. Twenty-one taxa are found in the data set for Row 1 ponds used in the ordination; 22 taxa are found for Row 2 ponds (Table II). The data sets for Rows 3, 4, and 5 contain 36, 38 and 34 taxa, respectively. Thus, species richness appears to be higher in the older ponds. Rows 1 and 2 only have 10

TABLE III

Mean water chemistry determinations and standard deviations for 10 samples from each of five pond rows in Miller Woods, April 1983

Indicator	Row 1		Row 2		Row 3		Row 4		Row 5	
pH (units)	8.00		7.96		7.73		7.41		7.67	
Specific conductance ($\mu\text{s cm}^{-1}$)	419	± 33	339	± 34	344	± 37	323	± 42	330	± 59
Alkalinity as CaCO_3 ¹	166	± 32	167	± 20	166	± 16	147	± 21	152	± 39
Calcium ¹	53.9	± 12.8	49.3	± 6.1	51.8	± 7.1	49.0	± 8.4	49.4	± 9.6
Magnesium ¹	12.1	± 4.0	15.5	± 1.9	13.3	± 3.5	12.7	± 2.7	15.2	± 3.2
Potassium ¹	2.1	± 0.9	0.8	± 0.3	1.3	± 0.4	1.4	± 0.2	1.5	± 0.4
NH_4 + organic N ¹	0.25	± 0.14	0.24	± 0.08	0.33	± 0.11	0.36	± 0.18	0.43	± 0.35
Dissolved P ¹	0.004	± 0.001	0.003	± 0.001	0.005	± 0.002	0.007	± 0.002	0.006	± 0.005

¹Concentration in mg l^{-1} .

taxa in common, Rows 3 and 4 have 32 in common, Rows 4 and 5 have 31 in common, and Rows 3, 4 and 5 have 25 in common. Therefore, the separation that occurs between Row-3, -4, and -5 ponds on Axis 2 may be due largely to varying amounts of the common species rather than floristic differences.

Water and sediment chemistry

The ponds of Miller Woods are well buffered, hardwater ponds with pH values usually in the 7–8 range (Table III). Nutrient concentrations tend to be fairly low. In springtime sampling, prior to plant growth, there were no significant differences between pond rows in alkalinity, calcium, magnesium, or NH_4 + organic nitrogen. The few significant differences that occurred between pond rows in pH, specific conductance, potassium and dissolved phosphorus did not have obvious meaning. Nitrite + nitrate nitrogen was below the detection limit of 0.10 mg l^{-1} for most samples. It thus appears that there are no water chemistry conditions present that would differentially affect plant growth in the spring. Although a few significant differences between pond rows did occur in summer and autumn sampling, they were more indicative of water chemistry responses to vegetation, such as lower Ca concentrations in Rows 1 and 2 (*Chara*-dominated) in the summer. Changes in water chemistry with the seasons occurred also, but they occurred across pond rows and shouldn't differentially affect the vegetation among pond rows.

Significant differences in sediment chemistry between pond rows were demonstrated in springtime sampling (Table IV). The percentage organic matter of the sediments was generally higher in older pond rows, and the corresponding sediment pH was lower. Exchangeable potassium concentrations were higher in the sediments of older ponds. Phosphorus and nitrogen concentra-

TABLE IV

Mean sediment chemistry determinations for 40 samples from each of five ponds in Miller Woods, April 1984

Indicator	Row 1	Row 2	Row 3	Row 4	Row 5
pH (units)	7.1a ¹	6.5a	5.4b	5.4b	5.4b
% O.M.	8.2a	16.7b	25.7c	36.1d	30.5cd
NH ₄ -N (mg kg ⁻¹)	17.2a	33.8a	31.3a	56.0b	29.6a
NO ₃ -N (mg kg ⁻¹)	2.3ab	1.3a	3.0b	2.7ab	3.6b
PO ₄ -P (mg kg ⁻¹)	0.8a	4.4b	5.6b	6.7b	5.7b
K (mg kg ⁻¹)	38a	39a	53a	83b	112c

¹Means followed by the same letter are not significantly different by ANOVA and SNK multiple range test ($\alpha=0.05$).

tions did not present a distinct pattern by pond row, but overall nutrient concentrations were the lowest in the sediments of Row 1 ponds.

DISCUSSION

Macrophyte communities vs. environment

Water depth, which is a function of age and sedimentation, was the most apparent environmental factor affecting the distribution of macrophyte communities among the five rows of ponds. The dominant taxa changed from submersed species in the younger, deeper ponds to submersed/floating-leaved species in the middle-aged, mid-depth ponds to submersed/floating-leaved/emergent species in the older, shallower ponds. Additionally, the ponds that were outliers in the ordination were shallower than other ponds in their rows and contained more emergent species. This distribution pattern would be expected, based on the distribution, zonation and succession studies of others (Spence, 1967; Walker and Coupland, 1968; van der Valk and Bliss, 1971; Walker and Wehrhahn, 1971; Moeller, 1985).

Fluctuations of ground-water levels also result in pond water-level fluctuations on a year-to-year basis. The survival capabilities of emergent vs. submersed/floating species could thus be affected by the resulting differential effects of drawdown or flooding in different depth ponds.

Aquatic and wetland macrophytes have been documented to utilize nutrients from both the water column and the sediment substrates (Denny, 1972), but current research stresses the importance of uptake from the sediments (see review by Spence, 1982). Water chemistry does not seem to play a role in determining species distributions among pond rows in Miller Woods because few significant differences between rows were found. The composition of the over-

all macrophyte communities may, however, be correlated to the calcareous (hard) water type (Wilson, 1935; Moyle, 1945; Spence, 1967; van der Valk and Bliss, 1971).

Differences in sediment chemistry between pond rows suggest that this factor may be correlated with plant species distributions. The general trend is towards higher pH and lower sediment nutrient concentrations in younger ponds where the nutrient cycles are 'open' or 'flow-through' (Howard-Williams, 1985). In older ponds, nutrients become progressively tied up in biomass and dead organic matter of the sediments. Walker and Wehrhahn (1971) found a correlation between sediment nutrient concentrations and variations in vegetation in Saskatchewan wetlands; van der Valk and Bliss (1971) found no correlation in oxbow lakes of Alberta. Although the species distributions among pond rows in Miller Woods may be correlated with sediment chemistry differences, this does not imply preferences or requirements. The pool of unavailable N and P in the organic matter of the sediments can serve to replenish the reserves of available forms through microbial and chemical actions. The sediment chemistry may, instead, be partly determined by the composition of the different plant communities (Davis and van der Valk, 1978a, b, 1983; Godshalk and Wetzel, 1978; Klopatek, 1978; Carignan, 1985; Twilley et al., 1985).

Percentage organic matter of the sediments has been shown to parallel succession and zonation from submersed to floating-leaved to emergent species (Pearsall, 1920, 1921; Misra, 1938; Wetzel, 1979; but see Walker and Coup-land, 1968; van der Valk and Bliss, 1971). However, Spence (1967, 1982) has never found proof of causation. There is a significant increase in percentage organic matter with age in the Miller Woods ponds, and it may relate to species distributions in the manner proposed by Barko and Smart (1983). They found greater growth inhibition in submersed species than emergent species when the organic matter content of the sediments was increased. This differential tolerance may be due to the greater rhizosphere-oxidizing abilities of the emergents, making them less susceptible to accumulations of toxic, soluble organic compounds produced during anaerobic decomposition. The lower pH values for sediments of older ponds could also affect the speciation and toxicity of the organic compounds.

Species richness vs. age

The total number of taxa recorded per pond row before the rare species were deleted from the data set (32, 23, 54, 46, 45 species in Rows 1-5, respectively) does not reflect the generally reported concept that species richness increases with pond or lake age (Godwin, 1923; van der Valk and Bliss, 1971) or decreases with water depth (Wilson, 1935, 1941; Spence, 1964, 1967; Moeller, 1985). A closer examination of the data explains the reason for this. The greatest number of taxa was recorded for Row-3 ponds; but of the 54 Row-3 taxa, 14 were

found only in Pond 34 and two only in Pond 35. These ponds were outliers in the ordination and had many more shallow-water sites than the other ponds in that row. The same reasoning can be applied to Row 1 ponds, where eight of the 32 taxa were found only in shallow Pond 12. Another five taxa were only found in water of Pond 14 that was shallower than 10 cm. Therefore, a 'corrected' comparison might show species richness that generally did increase with pond age through Rows 4–5.

Consistent with the findings of van der Valk and Bliss (1971), an increase in species richness with pond age may result from the ubiquitous occurrence of many of the younger-pond species across all pond rows. Although generally not in great abundance, these species could remain in the older ponds because of site preemption/founder effects (J. Grace, personal communication, 1986) or vegetational inertia (Gorham, 1957; Cole, 1985). The leveling-off of species richness in Rows 4 and 5 may represent reaching an equilibrium between recruitment and extinction (MacArthur and Wilson, 1967; Hutchinson, 1975) and be a response to water-level fluctuations, allelopathy, or toxic effects of more organic compounds in the sediments (Barko and Smart, 1983), as discussed previously.

Evidence for succession

In Miller Woods, differences in plant communities between pond rows did occur that seem to be correlated to time-related environmental changes, such as sedimentation and basin-filling. This may be viewed as evidence for hydrarch succession; the vegetation that occurred in increasingly older ponds will probably occur in a given pond as it ages.

In his review of succession in wetlands, van der Valk (1982) makes the point that stable, self-reproducing, climax vegetation, as proposed by Clements (1916), is illusory. In a wetland or shallow aquatic system such as the dune ponds of Miller Woods, the changes that occur in environmental conditions would probably dictate changes in vegetation, but not in a unidirectional manner. In a modification of Gleason's (1917, 1927) broad view of succession as any qualitative or quantitative change in vegetative cover, van der Valk (1981) defines succession as non-climactic, but occurring 'whenever one or more new species becomes established, when one or more species already present is extirpated, or when both occur simultaneously in a wetland'.

If the year-to-year fluctuations in water levels are not of a magnitude capable of inducing changes in the species present, then succession in these ponds could be viewed as a linear, autogenic process, simply responding to long-term changes in water depth due to sedimentation (van der Valk and Davis, 1976). However, based on research elsewhere (e.g. Walker and Wehrhahn, 1971; Davis and Brinson, 1980) and the documented disturbance history of Miller Woods (Moore, 1959; Kieffer, 1981), it is more likely that natural and anthropogenic

disturbance history has played a major role in vegetational development and that succession is, in part, allogenic.

In the early 1900s, Shelford (1911) reported that sewer, road and railroad construction had already caused water-level changes in ponds to the west of Miller Woods. Sand mining, timber harvesting, surrounding residential and industrial development, and three railroad corridors through Miller Woods provided other anthropogenic disturbances (Moore, 1959). The role of fire in the oak woodlands on the dunes has also changed in post-settlement years (Henderson and Long, 1984; Futyma, 1985), possibly altering nutrient availability and sedimentation rates. The presence of *Typha angustifolia* as the predominant cattail species in pond Rows 4 and 5 provides a clue as to the importance of disturbance. This species has been found by Smith (1967, 1986) to be restricted to unstable or disturbed sites, and it is common as an invader of disturbed wetlands (Wilcox et al., 1984; Wilcox, 1986). Additionally, paleoecological data collected by Futyma (1985) and Jackson (1985) indicate that *Typha* did not become dominant in the older ponds until the post-settlement period.

It should not be assumed that plant community differences in a chronosequence will accurately reflect the time-scale of a temporal sequence, or even the true sequence of species in a particular pond over time, because local disturbances can quickly alter the composition of the vegetation in a pond. On the other hand, disturbance is generally considered to be one of the factors affecting any succession (Drury and Nisbet, 1973; White, 1979; Glenn-Lewin, 1980).

ACKNOWLEDGMENTS

The authors wish to thank William Storm, Gail Gorka, David Cohen, Michelle Mueggler and Jon Alden for assistance in data collection; Richard Futyma for collection of samples for radiocarbon dating; Donald Franzmeier and Gary Steinhardt for facilitating sediment analyses at Purdue University; David Cohen for facilitating water chemistry analyses by the U.S. Geological Survey; Noel Pavlovic for conducting the statistical and ordination analyses; Robert Buchholz for preparing the figures; and Mary Pittman for typing the manuscript. We also thank Arnold van der Valk and Richard Futyma for their helpful reviews of the manuscript.

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