8-1988

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A PALEOECOLOGICAL TEST OF A CLASSICAL
HYDROSERE IN THE LAKE MICHIGAN DUNES[1]

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Abstract. Aquatic vegetation varies along a chronosequence of dune ponds at Miller Woods, Indiana Dunes National Lakeshore. Submersed and floating-leaved macrophytes dominate the vegetation of the youngest ponds. Older ponds contain mixed assemblages of submersed, floating-leaved, and emergent plant taxa. The oldest ponds are dominated by emergent plants, especially *Typha angustifolia.* We conducted paleoecological studies at one of the oldest ponds to test the hypothesis that the modern vegetational array along the pond chronosequence represents a hydrarch successional sequence. Macrofossil stratigraphy of the 3000-yr-old pond indicates no significant changes in pond vegetation following early colonization until <150 BP. Pond vegetation before 150 BP consisted of a diverse assemblage of submersed, floating-leaved, and emergent macrophyte taxa. Pollen and macrofossil data indicate a major, rapid vegetational change at <150 BP, evidently in response to local human disturbance. Pollen data reveal that the extensive *Typha* stands in the older ponds have developed recently, following postsettlement disturbance. Modern vegetational differences along the chronosequence reflect differential effects of disturbance rather than autogenic hydrarch succession. This study illustrates a major pitfall in inferring successional trends from spatial sequences of vegetation.

Key words: aquatic macrophytes; chronosequence; disturbance; hydrosere; Indiana Dunes; paleoecology; plant macrofossils; pollen; ponds; succession; vegetation dynamics; wetlands.

INTRODUCTION

Most models of ecological succession are inferred from studies of chronosequences, in which comparisons are made among land surfaces differing in age or in time elapsed since most recent disturbance. Spatial vegetational patterns among sites are assumed to represent temporal vegetational patterns at a fixed site. The critical assumption underlying this approach is that there are no ecologically significant differences among sites in the spatial array except age (or time since last disturbance) and degree of successional development. Whenever possible, independent tests of this assumption or of successional sequences inferred from spatial chronosequences are needed. A record of the actual temporal changes at one or more sites in the spatial chronosequence can provide such a test (Oldfield 1970, Walker 1970).

Among the earliest and most influential applications of the chronosequence approach were the studies of Cowles (1899, 1901, 1911) and Shelford (1907, 1911, 1913) in the Indiana Dunes region along the southern shore of Lake Michigan. Recognition that age of the land surface increased inland from the lakeshore provided the basis for successional models of terrestrial vegetation (Cowles 1899, 1901) and animal communities (Shelford 1907, 1913). Similarly, Shelford (1911, 1913) used the spatial sequence of dune ponds to develop a descriptive model of hydrarch vegetational and faunal succession. Detailed quantitative vegetational studies of dune ponds in the region have recently confirmed the spatial patterns described by Shelford (Wilcox and Simonin 1987).

We tested the hypothesis that the modern vegetational array along the pond chronosequence represents a hydrarch successional sequence by conducting paleoecological studies of a dune pond in the Indiana Dunes region.

STUDY AREA

Our study site is located in the Miller Woods section of Indiana Dunes National Lakeshore (Lake County,
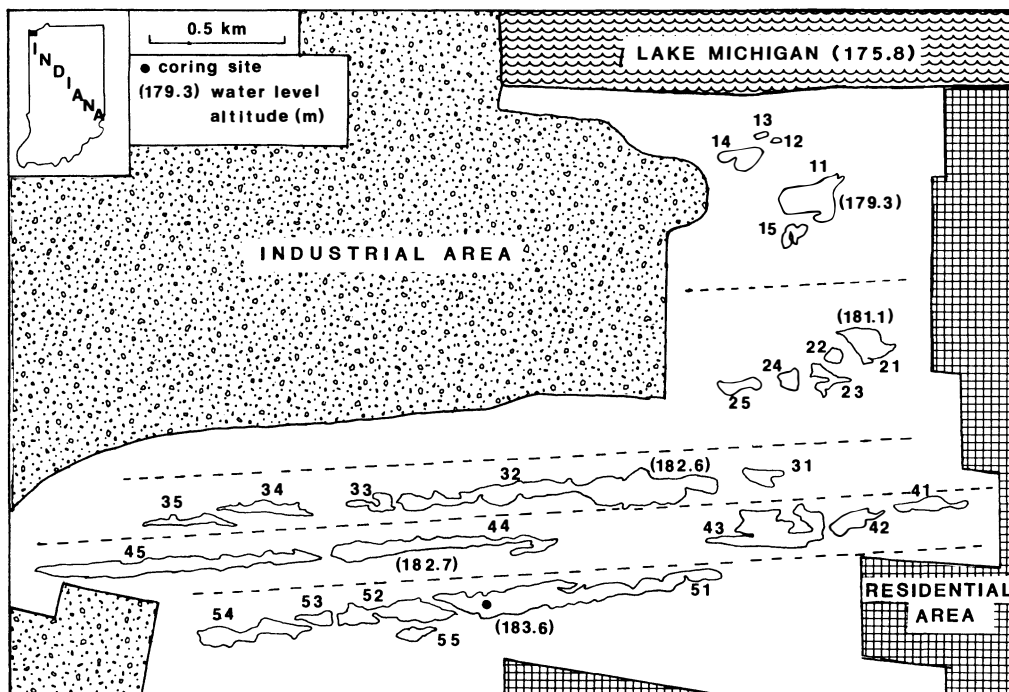
Fig. 1. Map of the Miller Woods area showing locations of Pond 51 (bottom center) and other ponds studied by Wilcox and Simonin (1987). Not all ponds in the area are included. Numbers in parentheses refer to altitudes (m above mean sea level) of pond and lake water levels. Dashed lines depict approximate boundaries between pond rows.

Indiana). Most of the ponds originally studied by Shelford have been destroyed by urban and industrial development; the Miller Woods section contains nearly all of the dune ponds remaining in the Indiana Dunes region (Wilcox and Simonin 1987).

The Miller Woods ponds occur in five relatively discrete rows parallel to the Lake Michigan shoreline (Fig. 1). Age of the ponds increases with distance of the pond rows from the lakeshore (Futyma 1985, Wilcox and Simonin 1987). The two rows closest to the Lake Michigan shore (rows 1 and 2) are in areas of irregular, hummocky sand dunes. Dune crests are 4–21 m above the water surface of the ponds. These dunes developed ≈2000 BP as Lake Michigan receded from the Algoma stage to its present level (Reshkin 1981). The three pond rows farthest from the lakeshore (rows 3, 4, and 5) are separated by narrow sand ridges. These ridges represent low beach dunes associated with shorelines formed successively during recession to the Algoma stage between 3000 and 2000 BP (T. A. Thompson, *personal communication*). Ridge crests in this area are 2–6 m above the pond surfaces.

Terrestrial vegetation surrounding the ponds in rows 2–5 consists today of open woodlands dominated by *Quercus velutina* (Henderson 1982). Presettlement woodlands probably also included significant amounts of *Pinus strobus* and *P. banksiana* (R. P. Futyma, *personal observation*). Terrestrial vegetation in the vicinity of row 1 consists of dune grasses (*Ammophila brevili-gulata, Calamovilfa longifolia, Andropogon scoparius*)

and occasional individuals of *Populus deltoides*. Presettlement vegetation near rows 1 and 2 included significant numbers of *Pinus strobus, P. banksiana, Populus tremuloides,* and *Quercus velutina* (Bacone et al. 1980). Apparent successional relationships of the terrestrial vegetation are described by Cowles (1899, 1901), Olson (1958), Henderson (1982), Henderson and Long (1984), and Futyma (1985).

Physical and chemical characteristics of the Miller Woods ponds are described in detail by Wilcox and Simonin (1987). Ponds in rows 1 and 2 are irregular in shape, while those in rows 3–5 are long and narrow, paralleling the intervening sand ridges and the lakeshore. The ponds in rows 1 and 2 are generally smaller than those farther from the lakeshore. Water depth varies inversely with pond age; sediment thickness and percent organic content increase with pond age. All of the ponds are hardwater; water chemistry does not vary significantly among pond rows. Water levels are controlled by groundwater. Water levels fluctuate from year to year; the overall magnitude of fluctuation during the past decade is estimated at <40 cm.

Variation in vegetation along the pond chronosequence comprises a gradient ranging from submersed macrophyte assemblages (youngest ponds) through mixed assemblages of submersed and floating-leaved macrophytes to vegetation dominated by emergent macrophytes with some submersed and floating-leaved plants (oldest ponds) (Wilcox and Simonin 1987). Ponds in rows 1 and 2 contain abundant *Chara* spp., *Najas*

flexilis, Potamogeton spp., *Myriophyllum* spp., and *Utricularia vulgaris. Nitella* spp. and *Utricularia gibba* are also frequent. A few floating-leaved (*Nuphar* spp.) and emergent taxa (*Eleocharis* spp., *Scirpus acutus, Polygonum coccineum*) are frequent, but none are as abundant as the submersed taxa (Wilcox and Simonin 1987). Pond rows 3 through 5 represent a gradient from vegetation dominated by submersed (*Myriophyllum* spp., *Utricularia vulgaris*) and floating-leaved taxa (*Nuphar* spp., *Nymphaea tuberosa*) with scattered emergents (*Proserpinaca palustris, Scirpus acutus, Sparganium chlorocarpum, Typha angustifolia*) (row 3) to emergent-dominated vegetation with submersed and floating-leaved species present in small numbers (row 5) (Wilcox and Simonin 1987). *Cephalanthus occidentalis,* a wetland shrub, is prominent in several row 5 basins.

Patterns of vegetation along the Miller Woods pond chronosequence are similar to those described by Shelford (1911, 1913), who proposed that succession in the ponds follows a course from bare sand bottoms to submersed vegetation to mixed submersed/floating-leaved/emergent vegetation to emergent-dominated vegetation to shrub-dominated vegetation. The mechanism driving these changes was postulated to be progressive accumulation of organic sediments derived from organisms growing within the pond basin (Shelford 1911, 1913). The consequent progressive shallowing of the basin would thus facilitate development of each successive vegetational stage.

Human disturbance of the landscape within the Miller Woods area began at least as early as 1851 with the construction of a railroad corridor through the tract (Ball 1900, Moore 1959). Additional railroad rights-of-way, sidings, and connectors were developed in 1874 and the early 1900s. Railroad construction was confined to pond rows 3, 4, and 5 and resulted in alterations of pond morphology and drainage in some cases. Several large ponds were cut into two or more isolated basins by causeways. These activities were accompanied or preceded by cutting of forests throughout the area for fuel and lumber. The area originally studied by Shelford had a similar disturbance history (Shelford 1911:130 and Map II).

METHODS

Study site

Detailed pollen and plant macrofossil studies were carried out on sediments from Pond 51 (numbering after Wilcox and Simonin 1987) in pond row 5. The pond is ≈1100 m × ≤100 m. Pond 51 is the easternmost of four basins isolated from each other by construction of railroad rights-of-way and connectors in the mid-to-late 19th century. Most of the pond basin is occupied by dense stands of *Typha angustifolia.* The scattered open-water areas in the pond contain a diverse assemblage of macrophytes, including *Potamo-*

geton spp., *Utricularia vulgaris, Polygonum coccineum, Nuphar* spp., *Sparganium chlorocarpum, Sagittaria latifolia, Calamagrostis canadensis, Equisetum fluviatile, Proserpinaca palustris, Ranunculus flabellaris,* and *Scirpus acutus. Cephalanthus occidentalis* occurs in shallow water along the shore.

The sediment core was taken from open water (115 cm depth) near the west end of Pond 51. The core was obtained by Futyma and Wilcox using a Livingstone piston corer (7 cm diameter).

Pollen

Pollen sample preparation and counting followed standard procedures (details in Futyma 1985). Pollen percentages were calculated based on a sum of all terrestrial, wetland, and aquatic taxa. Confidence intervals (95%) for pollen percentages were determined using the procedure of Moore and Webb (1978).

Plant macrofossils

Samples for macrofossil analysis were obtained by slicing the core into sections 3 cm long, yielding cylindrical samples ≈115 cm³ in volume. Samples were disaggregated by gentle agitation in water and then washed through a nest of sieves (707-μm mesh, 420-μm mesh, and 200-μm mesh). Residues from each sieve fraction were stored separately in ≈25% ethanol.

The 707-μm and 420-μm sieve residues were analyzed for each of 12 depth intervals. The 200-μm sieve fraction was not examined. Samples were placed in a white enamel pan and scanned at 12× magnification using a Wild M5 stereomicroscope. Abundant, readily identifiable morphotypes (*Najas* seeds, *Pinus* needles, *Chara* and *Nitella* oospores) were tallied during the initial scanning. All other potentially identifiable macrofossils were removed, stored separately, and examined in detail later. All seeds, fruits, oospores, conifer needles, and microsporangia were identified and tabulated. Bryophytes, although abundant in all samples, were not examined owing to inadequate reference material. Determinations of all macrofossils were made by comparison with herbarium-documented reference specimens. All taxa represented in the core were assumed to be modern constituents of the northwestern Indiana flora (Peattie 1930, Deam 1940, Fernald 1950, Wilhelm 1980). Most identifications were made to the lowest taxonomic level possible based on morphology, preservation state, and available reference collections.

All of the *Pinus* spp. needles were fragmented. Needle fragments were tallied and summed according to the procedure outlined by Jackson and Miller (1983).

Usage of "sp.," "cf.," "-type," and "/" in presenting macrofossil data follows Birks and Birks (1980). Vascular plant nomenclature follows Fernald (1950). Notes on certain macrofossil determinations are included in an Appendix.

HISTORY OF AQUATIC VEGETATION IN POND 51

Our pollen and plant macrofossil data have three limitations relevant to their application in this study. The first of these is the selective representation of aquatic plant taxa in the pollen and macrofossil record. Some important taxa (e.g., *Utricularia, Potamogeton*) are poorly represented. Second, vegetational changes occurring before accumulation of organic-rich sediments in the pond are undocumented. Although pollen spectra were obtained from sandy basal sediments of the study site, interpretation is hampered by potential biases in deposition and preservation. Macrofossils were not analyzed from these sediments. Third, spatial and temporal resolution of the pollen and macrofossil data is limited. Both pollen and macrofossil assemblages sample pond vegetation over a broad area. Successional changes at a single site (e.g., 1 m²) are not documented; we can only infer vegetational changes at the spatial scale of the entire pond basin or sub-basin. Similarly, our sediment samples integrate a time span of several years (5–30 yr per pollen sample; 15–90 yr per macrofossil sample). Furthermore, neither macrofossils nor pollen were analyzed in contiguous samples of sediment. Thus, we can document long-term vegetational changes but not short-term fluctuations or cycles (cf. van der Valk and Davis 1979).

Pond 51 was formed ≈3000 BP (Figs. 2 and 3). Basal sediments from another core (Laboratory Number DE-243) yielded a ¹⁴C date of 2700 ± 70 BP (Futyma 1985).

Regional land clearance by European settlers ≈150 BP is indicated by a substantial increase in *Ambrosia* pollen percentages and corresponding decreases in tree pollen (R. P. Futyma, *personal observation*). This event marks the boundary between the *Quercus–Pinus* and *Quercus–Ambrosia* pollen assemblage zones (R. P. Futyma, *personal observation*), and is recorded at 35 cm depth in Pond 51 sediments (Figs. 2 and 3). Macrofossils of *Pinus strobus* and *P. banksiana* are consistently present in sediments below the *Ambrosia* rise, and absent above it (Table 1). Their disappearance coincides with a decline in *Pinus* pollen (R. P. Futyma, *personal observation*). These events probably record local forest clearance. In addition, gray, vitreous clinker particles (≈0.5–2 mm diameter) are abundant in macrofossil samples from sediments above 33 cm (Fig. 2). These particles are undoubtedly of local industrial origin, and were probably blown or washed in from the nearby railroads.

The macrofossil data from Pond 51 provide no clear indication of successional changes in aquatic vegetation between 3000 BP and 150 BP (Fig. 2, Table 1). Macrofossil assemblages from this interval (33–135 cm) are uniform in composition, and are characterized by consistent occurrence of *Cyperus diandrus/rivularis* achenes, *Eleocharis geniculata/olivacea* achenes, *Brasenia schreberi* seeds, *Cyperus odoratus* achenes, *Najas*

flexilis seeds, *Chara* sp. oospores, *Nitella* sp. oospores, *Eleocharis calva/palustris* achenes, *Scirpus acutus/validus* achenes, *Zizania aquatica* fruits, *Carex* sp. achenes, and *Nuphar* sp. seeds. Most samples also include *Elatine triandra/americana* seeds, *Sagittaria latifolia* achenes, *Polygonum lapathifolium* seeds, *Bidens cernua* achenes, *Eleocharis smallii* achenes, *Leersia* sp. fruits, *Polygonum hydropiperoides*-type seeds, *Dulichium arundinaceum* achenes, and *Eupatorium* sp. achenes. Most of these latter taxa are absent from the lowermost sample (132–135 cm depth), possibly indicating delayed colonization of the pond by these taxa. However, when present, these macrofossil types occur in small numbers (1–5 specimens per sample), so their occasional absence from the record may result from incomplete samples rather than absence from pond vegetation. Vegetation of the pond before 150 BP consisted of a diverse assemblage of submersed (*Najas, Chara, Nitella*), floating-leaved (*Brasenia, Nuphar*), and emergent macrophytes (*Cyperus* spp., *Eleocharis* spp., *Polygonum* spp., *Bidens, Leersia, Scirpus, Dulichium, Eupatorium, Zizania, Carex*).

Several macrofossil types undergo fluctuations in abundance below 33 cm (Fig. 2). Fluctuations of this type and magnitude are characteristic of macrofossil profiles (Watts and Winter 1966, Birks and Birks 1980), and may result from variations in transport and deposition processes within the basin, short-term fluctuations in vegetation (van der Valk 1985), or both.

The apparent vegetational stasis before 150 BP is potentially an artifact of the location of the coring site in the pond. The core was obtained in deep open water ≈50 m offshore, and hence its macrofossil record may be biased toward vegetation in the deepest, central part of the basin. Successional changes occurring on shallow onshore sites may not have been registered in sediments at the coring site. However, we regard this as unlikely. Emergent macrophyte taxa are abundant in the macrofossil assemblages; most of these taxa are restricted to shallow water (<50 cm) and/or wet soils. Macrofossils of these taxa probably derive from plants that grew on or near the pond shore. Birks (1973) notes that seeds and fruits of many emergent plants (including *Eleocharis calva/palustris, Carex* spp., *Scirpus acutus/validus, Dulichium, Sagittaria latifolia,* and *Bidens cernua*) can be dispersed considerable distances (at least 100–150 m) from shore. The stratigraphic constancy of these and other taxa below 33 cm argues that vegetation of the basin did not change substantially from shortly after 3000 BP to 150 BP. Although there may have been fluctuations in vegetation controlled by climate and hydrology, there are no indications of successional change as defined by changes in species composition of the vegetation (van der Valk 1982, 1985).

The macrofossil assemblage undergoes major qualitative and quantitative changes above 33 cm depth (Fig. 2), indicating major changes in composition and structure of pond vegetation following European set-
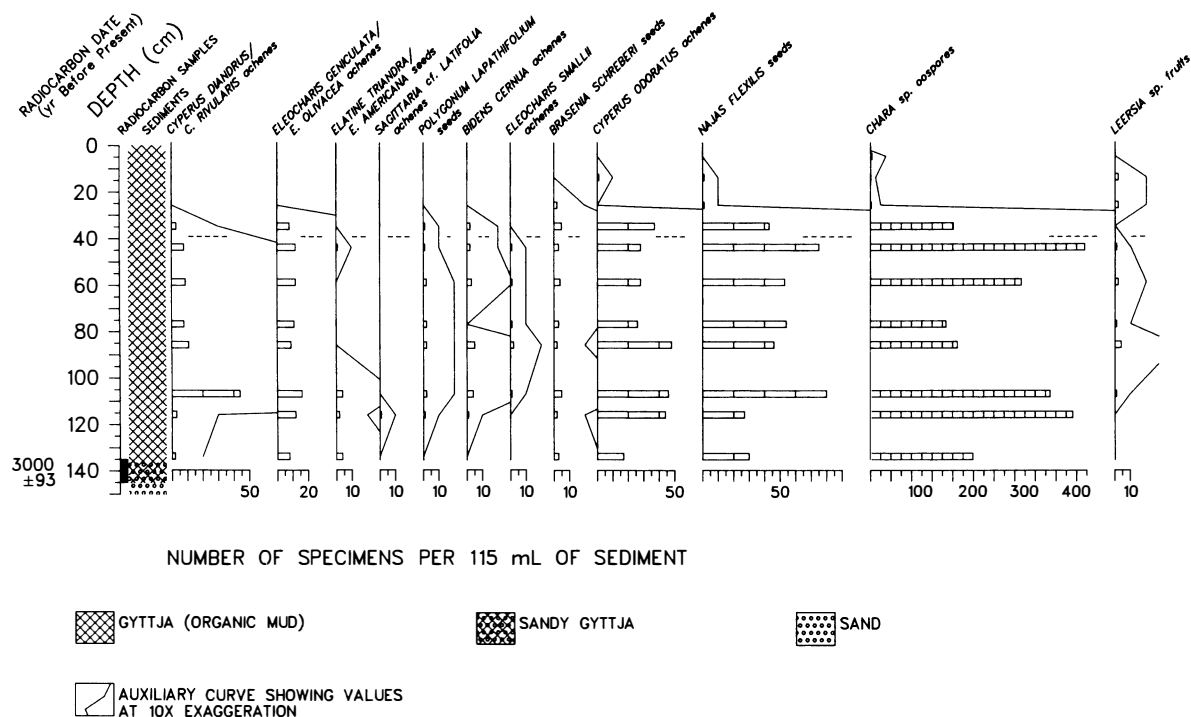
MILLER WOODS POND 51, Core A

NUMBER OF SPECIMENS PER 115 mL OF SEDIMENT

GYTTJA (ORGANIC MUD)   SANDY GYTTJA   SAND

AUXILIARY CURVE SHOWING VALUES AT 10X EXAGGERATION

FIG. 2. Plant macrofossil concentration diagram, Pond 51. A single dot in the "*Equisetum* cf. *fluviatile* stem fragments" column refers to presence in a sample. In the "Clinker particles" column, a single dot indicates <15 coal-combustion residue particles per sample, two dots ≈50 particles per sample, and three dots >150 particles per sample.

tlement of the region. Most of the characteristic pre-settlement taxa are absent or rare above 33 cm (Fig. 2). The only taxa that do not decline in abundance are *Dulichium, Leersia, Zizania, Carex,* and *Nuphar.* Several taxa absent or rare below 33 cm occur consistently in the postsettlement macrofossil assemblages: *Glyceria* sp., *Cephalanthus occidentalis, Sparganium* sp., *Ranunculus flabellaris, Proserpinaca palustris,* and *Equisetum* cf. *fluviatile.*

The pollen stratigraphy (Fig. 3) shows no significant trends in any of the aquatic or wetland taxa between 130 and 35 cm depth. The spectra are dominated by Gramineae, Cyperaceae, *Sagittaria, Nuphar, Nymphaea,* and *Brasenia. Typha latifolia* and *Typha/Sparganium* pollen is absent or rare. Pollen profiles from other cores in the pond show similar patterns (Futyma 1985). Pollen percentages of all aquatic and wetland taxa increase between 140 and 130 cm. This change may record colonization of the pond by these taxa or, alternatively, may result from poor preservation in the sandy gyttja at 140 cm.

Significant changes occur in the pollen profile above 35 cm (Fig. 3). Pollen of *Cephalanthus, Typha latifolia,* and *Typha/Sparganium* increases substantially. *Equisetum* spores also increase, while *Brasenia* pollen declines. These trends are also prominent in a second core from the center of Pond 51, and in cores from ponds in rows 3 and 4 (Futyma 1985).

Together, the pollen and macrofossil data indicate major vegetational changes in Pond 51 after 150 BP. Many of the macrophyte taxa of the pond underwent significant declines in abundance; some (e.g., *Brasenia*) became locally extinct. They were replaced in large part by macrophyte taxa previously rare or absent (*Sparganium, Ranunculus flabellaris, Proserpinaca, Equisetum, Cephalanthus, Typha*). Of particular significance is the development of large populations of *Typha.* The principal species involved was probably *T. angustifolia,* which is today the main *Typha* species in the pond. The postsettlement increase in *Typha/Sparganium* pollen is much greater than that of *T. latifolia* (Fig. 3). Numerically, *T. angustifolia* is probably the principal contributor of pollen to the *Typha/Sparganium* morphotype in sediments. The absence of a corresponding postsettlement increase in *Typha* macrofossils may represent a dispersal effect. *Typha* fruits have been shown to be rare in sediments distant from *Typha* plants in a Minnesota lake (Birks 1973). There are no *Typha* populations within 50 m of the coring site. Alternatively, *Typha* fruits may not have been retained in the 420-μm sieve fraction.

DISCUSSION

We find little evidence for successional changes at the study site before 150 BP. Successional changes undoubtedly occurred early in the history of the basin

MACROFOSSILS

POLYGONUM HYDROPIPEROIDES-type seeds · ELEOCHARIS CALVA / E. PALUSTRIS achenes · SCIRPUS ACUTUS/VALIDUS achenes · DULICHIUM ARUNDINACEUM achenes · EUPATORIUM sp. achenes · NITELLA sp. oospores · ZIZANIA AQUATICA fruits · CAREX spp. trigonous-type achenes · NUPHAR sp. seeds · GLYCERIA sp. fruits · CEPHALANTHUS OCCIDENTALIS nutlets · SPARGANIUM sp. fruits · RANUNCULUS FLABELLARIS achenes · PINUS BANKSIANA microsporangia · EQUISETUM cf. FLUVIATILE stem fragments · CLINKER PARTICLES · POLLEN ZONES

Scale: 10   50   100   30   10   10   100   200   20   20   10   20   10   10   10   10

Quercus–Ambrosia

Quercus–Pinus

analyst: S. T. Jackson, 1985

FIG. 2. Continued.

(initial colonization is obviously a successional event). These changes may well have corresponded to those proposed by Shelford (1911, 1913). However, these events cannot be inferred from the fossil record. In Pond 51, a diverse assemblage of submersed, floating-leaved, and emergent macrophytes was established by the time organic sediments began accumulating. Our inferences are of course limited with respect to a few

TABLE 1. Plant macrofossil concentrations (expressed as number of items per 115 cm³ of sediment) from Miller Wood: Pond 51. Only morphotypes not presented in Fig. 2 are included.

Depth (cm)	Pinus banksiana needles	Pinus strobus needles	Pinus banksiana microsporangia	Pinus strobus microsporangia	Pinus strobus seeds	Potamogeton subgenus Eupotamogeton fruits	Alisma sp. achene	Sagittaria cf. latifolia achene	Sagittaria sp. achenes	Alismataceae (undifferentiated) embryos	Gramineae (undifferentiated) fruits	Eleocharis cf. smallii achenes	Eleocharis sp. achenes	Carex biconvex-type achenes	Cyperaceae (undifferentiated) achenes	Polygonum amphibium/coccineum seed	cf. Polygonum hydropiperoides-type seed fragment	Polygonum sp. seeds	Hypericum sp. seeds	Myriophyllum exalbescens-type mericarp	Myriophyllum sp. leaves	cf. Hieracium achenes
0–3						1														1	1	
3–6							1				1			1								
12–15																						
24–27															2							
33–36	1	1				1					1	1	2		1							
42–45	1	1				1			1		2	1	2	3			1			1		
57–60	1	1	1								2		1			1						1
75–78	1	1	1	1							1		1					2				
84–87	1	1				1					3	1	6					1				
105–108	1	1	1	1	1						3	1	7			2	1	3	1			2
114–117	1	1				1		1	1	1			7					3	1			
132–135	1	1				1					1		6									

MILLER WOODS POND 51, Core A   POLLEN PERCENTAGE

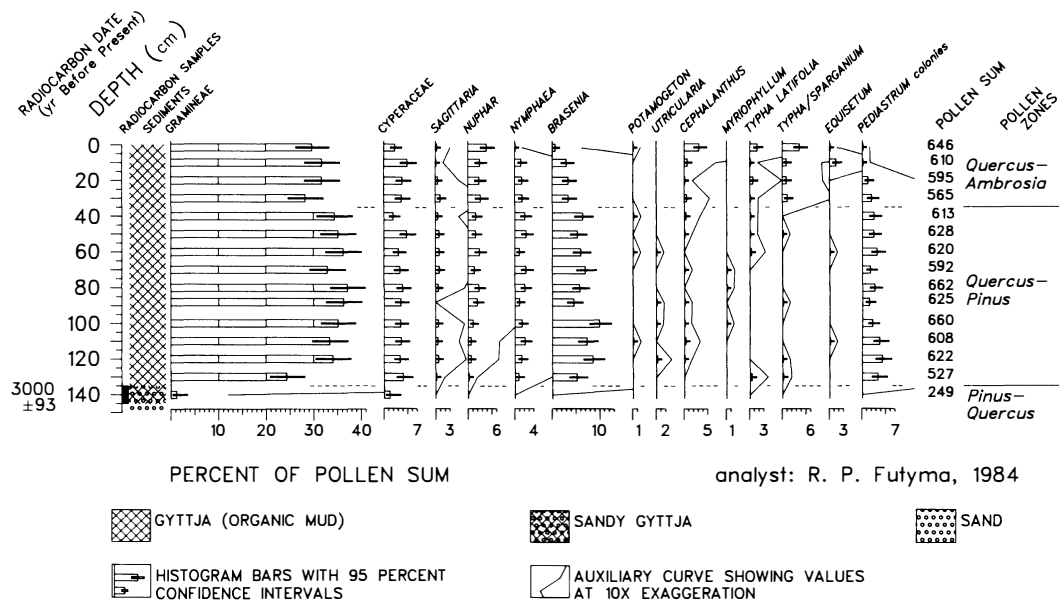

Fig. 3. Aquatic and wetland pollen percentage diagram, Pond 51.

taxa poorly represented in the pollen and macrofossil record (*Utricularia, Potamogeton, Myriophyllum*). However, data for the numerous taxa represented in the Pond 51 macrofossil record suggest strongly that pond vegetation underwent no major successional changes between 3000 and 150 BP. The only changes in composition of vegetation recorded at the study site occurred after 150 BP.

Changes in vegetation occurring after 150 BP undoubtedly resulted from human activities following European settlement of the region. Two mechanisms, operating separately or in combination, may have brought about the change in vegetation. First, construction of the railroad causeway that separates Pond 51 from Pond 52 could have directly altered the hydrology of the pond. Second, forest clearance and railroad construction may have resulted in a substantial increase in export of dissolved nutrients, dissolved and particulate organic matter, and particulate mineral material from the pond watershed into the pond (e.g., Davis 1976, Likens et al. 1977). This would, in turn, have had significant effects on water and sediment chemistry, water color and transparency, and water depth (via infilling) (see e.g., Birks et al. 1976, Brugam 1978, Davis and Norton 1978). All of these changes could potentially affect macrophytic vegetation (Hutchinson 1975, Weller 1981, Spence 1982, Barko and Smart 1983, van der Valk 1985).

Development of *Typha*-dominated vegetation following local land clearance has been documented at other midwestern lakes and ponds (McAndrews 1966, Janssen 1967, Birks et al. 1976). Janssen (1967) and Birks et al. (1976) ascribe these events to eutrophica-

tion, which is probably correct, although somewhat uninformative. Eutrophication involves a variety of biologically significant physical and chemical changes (Wetzel 1983); superimposed on these are the respective physiological and life history properties of the macrophyte species (van der Valk 1981, 1982), which may themselves influence the physical and chemical changes in the basin (Carpenter 1981). More detailed information on the nature and timing of the environmental changes in the Miller Woods ponds (e.g., paleolimnological studies) would be required to identify the specific mechanisms driving the vegetational transition.

Differences in modern vegetation among ponds along the chronosequence probably result from differential type and magnitude of disturbance effects. For instance, increased sediment accumulation rates would have had a greater impact on vegetation in the older, shallower ponds than in the younger, deeper basins. Also, railroad construction and logging activities were more intensive in the vicinity of the older ponds.

The vegetational history of Pond 51 from 3000 BP to the present corresponds generally to the spatial chronosequence described by Shelford (1911, 1913) and Wilcox and Simonin (1987); in both cases a mixed submersed/floating-leaved/emergent assemblage is replaced by emergent-dominated vegetation. However, many constituents of the presettlement species assemblage of Pond 51 are absent or rare in ponds of rows 1 and 2 today. *Eleocharis calva/palustris, Cyperus odoratus, Zizania aquatica, Polygonum lapathifolium, Bidens cernua, Leersia* sp., and *Dulichium arundinaceum* were not observed in any sample plots in 10

ponds of rows 1 and 2 (Wilcox and Simonin 1987), although they were present at least locally in some row 1 and 2 ponds (Wilhelm 1980). *Eleocharis geniculata/olivacea, Elatine triandra/americana,* and *Brasenia schreberi* have not been observed in any modern ponds in the Miller Woods area (Wilhelm 1980, Wilcox and Simonin 1987) and thus may have undergone local extinction following disturbance. The absence or rarity of many of the presettlement Pond 51 taxa in the modern row 1 and 2 ponds may result from environmental differences, postsettlement extirpation by human disturbance, or differences in initial floristic composition (Egler 1954) between Pond 51 and the younger ponds.

Shelford (1911, 1913) envisioned hydrarch succession in the dune ponds as being continual, gradual, and autogenic. These, in fact, are general properties of many successional models (Clements 1916, Odum 1969). However, they are not descriptive of vegetational changes at the Miller Woods ponds. Vegetation of Pond 51 persisted unchanged for nearly 2800 yr. When change did occur, it was rapid, and was ultimately controlled by allogenic processes resulting from human disturbance.

Our conclusions from the Miller Woods ponds are reasonable to apply to Shelford's (1911, 1913) study sites, in view of the similarities in the pond chronosequences, vegetation patterns, and disturbance histories. 20th century vegetation of at least the older ponds is largely a product of 19th century human disturbance. Although disturbance may have accelerated natural successional processes (e.g., basin infilling), it also distorted the resulting vegetation patterns.

V. E. Shelford was well aware of the extent and nature of 19th century human disturbance of his study area (Shelford 1911:130, 131; 1913:138, 139). However, he failed to recognize the potential effects of those disturbances on the biotic patterns he observed. Shelford assumed that the ponds were in a state of "physiographic stability" (Shelford 1911:136), meaning that they had undergone no changes in physical environment other than organic sediment accumulation since their original formation. Shelford's viewpoint that the ecological system he was dealing with was undistorted by human disturbance was characteristic of many North American ecologists of the early 20th century (Tobey 1981).

The error in inferring a successional model from the Lake Michigan dune pond chronosequence stems from the invalid assumption that the sites in the spatial sequence differ only in age and degree of successional development. Disturbance history played a dominant role in determining differences in modern vegetation among ponds. Our study underscores the point recently made by Hamburg and Sanford (1986) that careful attention must be paid to site history in ecological studies. The assumption of environmental and historical constancy among sites constitutes a major potential pitfall in chronosequence studies. Chronosequence-based successional models should be verified whenever possible by independent means. As demonstrated by this and other studies (Oldfield 1970, Walker 1970, Birks 1980, Clark and Patterson 1985), paleoecological methods can be powerful in providing such tests.

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APPENDIX

NOTES ON PLANT MACROFOSSIL DETERMINATIONS

Myriophyllum exalbescens-type includes *M. exalbescens, M. verticillatum,* and *M. spicatum.*

Polygonum hydropiperoides-type includes *P. hydropiperoides, P. hydropiper, P. punctatum, P. sagittatum,* and *P. persicaria.*

Cyperus odoratus achenes can be distinguished from those of other species by the presence of a rachilla segment clasping the basal portion of the achene (Mason 1957; S. T. Jackson, *personal observation*). These attachments are persistent and consist of corky tissues, presumably to aid dispersal by flotation. More than half of the trigonous *Cyperus* achenes observed in this study had this feature. Those lacking it were otherwise identical and were therefore assigned to *C. odoratus*; many of these in fact bore vestiges of the rachilla attachment. This morphotype may include *C. ferruginescens*; reference material for this species was not examined. Fernald (1950) views *C. odoratus* and *C. ferruginescens* as distinct but closely related species; Gleason and Cronquist (1963) lump them together under *C. odoratus.*