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DIFFERENTIATING CLIMATIC AND SUCCESSIONAL INFLUENCES ON LONG-TERM DEVELOPMENT OF A MARSH¹

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Abstract. Comparison of long-term records of local wetland vegetation dynamics with regional, climate-forced terrestrial vegetation changes can be used to differentiate the rates and effects of autogenic successional processes and allogenic environmental change on wetland vegetation dynamics. We studied Holocene plant macrofossil and pollen sequences from Portage Marsh, a shallow, 18-ha marsh in northeastern Indiana. Between 10 000 and 5700 yr BP the basin was occupied by a shallow, open lake, while upland vegetation consisted of mesic forests of *Pinus*, *Quercus*, *Ulmus*, and *Carya*. At 5700 yr BP the open lake was replaced rapidly by a shallow marsh, while simultaneously *Quercus* savanna developed on the surrounding uplands. The marsh was characterized by periodic drawdowns, and the uplands by periodic fires. Species composition of the marsh underwent further changes between 3000 and 2000 yr BP. Upland pollen spectra at Portage Marsh and other sites in the region shifted towards more mesic vegetation during that period. The consistency and temporal correspondence between the changes in upland vegetation and marsh vegetation indicate that the major vegetational changes in the marsh during the Holocene resulted from hydrologic changes forced by regional climate change. Progressive shallowing of the basin by autogenic accumulation of organic sediment constrained vegetational responses to climate change but did not serve as the direct mechanism of change.

Key words: climate change; hydrological change; Indiana; Lake Michigan; paleoecology; plant macrofossils; pollen; succession; vegetation dynamics; wetland vegetation and dynamics.

INTRODUCTION

Ecological succession was conceived and developed largely from observations and insights by Henry Chandler Cowles and Victor E. Shelford from the Chicago region (Cowles 1899, 1901, Shelford 1907, 1911a, b, c, 1913). Cowles and Shelford recognized the dynamic nature of the regional landscape, particularly in the Lake Michigan dunes and swales, and used the temporal heterogeneity of the land surface to infer past and ongoing changes in plant and animal communities. They emphasized autogenic mechanisms as being primarily responsible for ecological change, but recognized that ecological dynamics are constrained by prevailing climate, and that climatic change could alter the trajectory of ecological succession (Cowles 1901, Shelford 1911b).

The roles of autogenic successional processes and allogenic environmental change in vegetation dynamics are still not clearly understood (Glenn-Lewin et al. 1992). Critical to understanding those roles is identification of the rate, frequency, and impact of allogenic

environmental changes relative to the rate of autogenic successional mechanisms. Ecological studies are hampered by the temporal scales (10^2 – 10^4 yr) at which those processes typically occur. However, paleoecological studies can provide information about ecological and environmental dynamics at those time scales (Schoonmaker and Foster 1991, Prentice 1992, Clark 1993).

A recent paleoecological study in the Lake Michigan dunes region by Jackson et al. (1988) shows that (1) discernible successional change did not occur in a shallow marsh during a 2800-yr period preceding Euro-American disturbance, and (2) wetland vegetation patterns along the spatial chronosequence (Wilcox and Simonin 1987) originally studied by Cowles (1901) and Shelford (1911b, c, 1913) were partly a result of 19th century human disturbance of the landscape. That study, however, did not necessarily invalidate the general hydrosere model proposed by Cowles and Shelford; successional changes within a shallow basin in the region might simply require a longer time span (e.g., 5000 or 10 000 yr). However, the postglacial history of the western Great Lakes region (i.e., the past 15 000 yr) has been characterized by climatic changes occurring at frequencies of ≈ 3000 yr related to changes in earth's orbital geometry (T. Webb et al. 1983, 1993, Baker et al. 1992, Wright 1992, Graumlich and Davis 1993). Are those changes sufficient to influence the composition of wetland vegetation (e.g., via changes

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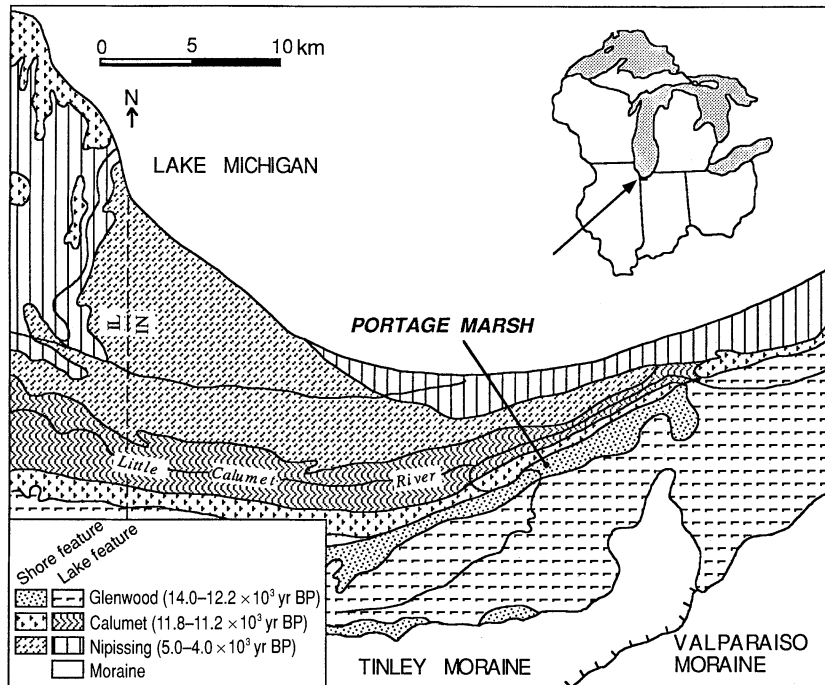


FIG. 1. Map of northwestern Indiana and northeastern Illinois, showing surficial sediments of the region (Schneider and Keller 1970) and location of Portage Marsh.

in hydrology)? To what extent are vegetation composition and successional processes of wetlands buffered against climate change? Are autogenic successional processes sufficiently rapid and/or powerful to override effects of secular climate change? What are the dominant processes governing the long-term dynamics of wetlands?

These questions can be addressed by comparing long-term records of wetland vegetation with records of regional climate. We compare plant macrofossil and pollen records of the local vegetation of Portage Marsh in northwestern Indiana (Fig. 1) with pollen records of regional upland vegetation. The macrofossil data provide a spatially and taxonomically precise record of aquatic and wetland vegetation (Watts and Winter 1966, Birks 1973, 1980, Watts 1978). Pollen of trees and other upland plants, along with microscopic charcoal, provide information on vegetation composition of the regional uplands surrounding the basin (Prentice 1988, Jackson 1994). Spatial and temporal patterns of upland pollen stratigraphy in the western Great Lakes region (T. Webb et al. 1983, 1993, Baker et al. 1992) confirm that the changes in Portage Marsh upland-pollen types are related to regional climate change. Thus, if autogenic successional processes are of primary importance in long-term dynamics of wetland vegetation, then the macrofossil and aquatic/wetland pollen sequences should be independent of changes in the upland pollen sequences. Alternatively, if climate has

controlled wetland vegetation dynamics, the changes should be synchronous and climatically consistent.

Recent paleoecological and paleoclimatic syntheses of the upper Mississippi Valley region by Baker et al. (1992) and Wright (1992) show a pattern of early Holocene mesic conditions, mid-Holocene drought, and increasingly mesic late Holocene conditions. This sequence contrasts with paleoclimatic sequences inferred for the northern Great Lakes region (Bartlein et al. 1984, Wright 1992) and the northeastern United States (Davis et al. 1980, Jackson 1989, R. S. Webb et al. 1993), where warmest and/or driest conditions occurred during the early Holocene. The eastern boundary of the pattern identified by Baker et al. (1992) is not clearly defined. Although Holocene pollen records already exist in the southeastern Lake Michigan region (Bailey 1972, Williams 1974, Manny et al. 1978), interpretation is hampered by dating uncertainties owing to ^{14}C -reservoir deficiencies in organic lake sediments (Williams 1974, Jackson et al. 1986). Our data provide an opportunity to define the early Holocene climate boundary.

STUDY SITE

Portage Marsh occupies a shallow, 18-ha depression ≈ 5 km south of the modern Lake Michigan shore ($41^{\circ}34'34''$ N, $87^{\circ}13'21''$ W, 189 m elevation) (Fig. 1). The marsh is on shore sediments deposited during the Glenwood II high-water phase of ancestral Lake Mich-

igan (12 200–13 000 yr BP [Hansel et al. 1985, Chrzas-towski and Thompson 1992]). The marsh basin was formed between two successive south-trending arms of a Glenwood II sandspit (Chrzas-towski and Thompson 1992), and was probably connected to a Glenwood II lagoon immediately south of the spit.

The Portage Marsh basin probably became isolated from ancestral Lake Michigan at the onset of the Two Creeks low-water phase (12 200–11 800 yr BP), when ice of the Lake Michigan Lobe retreated temporarily beyond the Straits of Mackinac, opening a northern outlet. Lake level in the Lake Michigan basin dropped, causing the Glenwood lagoon to drain. Although water levels in the Lake Michigan basin rose again during the Calumet and Algonquin phases between 11 800 and 10 000 yr BP, the shoreline was \approx 500 m north of the Portage Marsh basin, with water levels 5–10 m lower than the modern marsh surface (Bretz 1955, Fullerton 1980, Chrzas-towski and Thompson 1992). Opening of the North Bay outlet of Lake Huron 10 000 yr BP initiated the Chippewa low-water phase, during which lake level declined substantially (as much as 70–110 m) and the shoreline rapidly receded tens of kilometres north of Portage Marsh (Hansel et al. 1985, Chrzas-towski and Thompson 1992). During the early Holocene, lake level gradually rose owing to isostatic uplift of the North Bay outlet, peaking at 184 m \approx 4700 yr BP. At that time (Nipissing I high-water phase), the Lake Michigan shore was \approx 3 km north of Portage Marsh. The lakeshore has prograded steadily northward during the late Holocene.

The sediment surface of Portage Marsh today is horizontal to gently sloping. The basin contained open water (0.4–0.6 m) in June 1991 and in June and September 1994. Local residents indicated that this has been a typical summer condition for at least the past two decades, although the marsh has dried completely during some years (most recently in 1988). The basin lacks inflow and outflow channels today, and water depth is sensitive to precipitation variation. An artificial channel 20–30 cm deep has been cut through the peat in the center of the marsh along its long axis. Construction near the marsh during the past four decades may have blocked an artificial or natural high-water outlet channel. Total area of the Portage Marsh watershed (excluding the marsh) is \approx 15 ha, and total elevational relief within the watershed is $<$ 5 m.

The shore of Portage Marsh is ringed by a narrow band of trees (*Quercus* spp., *Acer negundo*, *A. saccharinum*, *Salix nigra*). Vegetation along the shallow edges of the basin consists of *Sambucus canadensis*, *Rosa multiflora*, *Iris virginica*, *Phalaris arundinacea*, and *Solanum dulcamara*. Aquatic and wetland vascular plant taxa of the marsh are listed in Table 1. The central open-water portion of the marsh is dominated by *Carex lasiocarpa* and *Calamagrostis canadensis*, with scattered monotypic patches of *Typha latifolia*, *Dulichium arundinaceum*, and *Cephalanthus occidentalis*. Float-

TABLE 1. Emergent, floating-leaved, and submersed aquatic and wetland plant species observed in Portage Marsh in August 1991 and/or August 1994.

<i>Alisma triviale</i>	<i>Lythrum salicaria</i> †
<i>Brasenia schreberi</i>	<i>Mentha spicata</i> †
<i>Calamagrostis canadensis</i>	<i>Polygonum amphibium</i>
<i>Calamagrostis stricta</i>	<i>Pontederia cordata</i>
<i>Carex chordorrhiza</i>	<i>Potamogeton gramineus</i>
<i>Carex lasiocarpa</i>	<i>Proserpinaca palustris</i>
<i>Carex pseudo-cyperus</i>	<i>Rhynchospora macrostachya</i>
<i>Carex retrorsa</i>	<i>Sagittaria graminea</i>
<i>Carex stipata</i>	<i>Salix exigua</i>
<i>Cephalanthus occidentalis</i>	<i>Salix nigra</i>
<i>Cladium mariscoides</i>	<i>Salix pedicellaris</i>
<i>Dulichium arundinaceum</i>	<i>Spiraea alba</i>
<i>Eleocharis palustris</i>	<i>Triadenum</i> sp.
<i>Glyceria borealis</i>	<i>Typha latifolia</i>
<i>Glyceria striata</i>	<i>Utricularia gibba</i>
<i>Juncus canadensis</i>	<i>Utricularia intermedia</i>
<i>Lemna minor</i>	<i>Utricularia purpurea</i>
<i>Lysimachia thyrsoiflora</i>	<i>Utricularia vulgaris</i>

† Nonindigenous in North America.

ing-leaved and submersed plants are interspersed among the emergent plants, and are especially abundant in deeper water and in small (3–4 m²) open pools. We observed little vegetational or floristic change between 1991 and 1994.

Prior to European land clearance and settlement in the 1830s, *Quercus savanna* (primarily *Q. alba* and *Q. velutina*) occupied the well-drained sandy soils of the Glenwood and Calumet lake deposits surrounding the marsh (Bacone et al. 1980). *Pinus banksiana* and *P. strobus* were important associates in drier areas (especially the dune region to the north), and *Carya* and *Ulmus* were important on finer textured sites. Ground cover consisted primarily of prairie grasses, sedges, and herbs (Lindsey 1961, Bacone et al. 1980). Upland prairie existed 5 km southeast of Portage Marsh on the well-drained soils of the Valparaiso Moraine (Lindsey 1961, Bacone et al. 1980).

The landscape surrounding Portage Marsh today, including its entire watershed, is urban. Before the 1950s, the landscape was predominantly agricultural.

METHODS

Field methods

A sediment core (7.6 cm diameter) (Core 1) was obtained from Portage Marsh in June 1991 using a land-based vibracorer (Thompson et al. 1991). Advantages of this type of coring apparatus include retrieval of sediments in a single drive and effective penetration of compact, marly late-glacial sediments, which are common in lakes and wetlands of the region (Bailey 1972, Futyma 1985). Disadvantages include compression and disturbance of sediments near the surface. To obtain better resolution of the recent history of the marsh, we obtained a second core (Core 2) of the top metre of sediment in June 1994 using a modified Livingstone piston-corer (10.2 cm diameter) (Wright et al.

1984). Both cores were taken ≈ 75 m from the northern margin of the basin, where sediments are deepest.

Macrofossil analyses

Macrofossil samples were obtained by cutting 3-cm thick sections from Core 1 and 2-cm thick sections from Core 2. The outer surface of each sample was scraped to remove any possible contaminants brought down by the coring apparatus. We removed a wedge-shaped, 50-cm³ sample from each section for macrofossil analysis. Each sample was dispersed in water and washed through a series of nested sieves (710- μ m mesh, 355- μ m mesh). A 180- μ m fraction contained few or no identifiable macrofossils.

Sieved samples were scanned at 6.5 \times magnification using a stereomicroscope. Abundant, readily recognizable fossils (e.g., *Chara* sp. oöspores, *Najas flexilis* seeds) were tallied during initial scanning. All other fossils were removed for detailed analysis at 40 \times magnification. A compound microscope with an external reflected light source was used at 100 \times magnification for detailed study of seed or achene texture of certain taxa (some Nymphaeaceae and Cyperaceae), which was necessary for identification to the lowest possible taxonomic level.

All identifiable fruits, seeds, conifer needles, microsporangia, and oöspores were identified by comparison with herbarium-documented reference specimens. Materials from the herbaria of the University of Michigan and Indiana University were used, as well as reference specimens collected in the field (deposited in the Northern Arizona University Deaver Herbarium). All specimens identified from the cores were assumed to be constituents of the modern flora of northern Indiana and southern Michigan (Peattie 1930, Deam 1940, Voss 1972, 1985, Swink and Wilhelm 1979). We used Gleason and Cronquist (1991) as the standard for taxonomic nomenclature. Notes on macrofossil identifications are presented in an Appendix.

Pollen analysis

Sediment samples (≈ 1 cm³) were prepared for pollen analysis using standard procedures for lake and wetland sediments (Fægri and Iversen 1989) and suspended in silicone oil. Pollen residues were scanned at 400 \times to a minimum count of 300 arboreal grains per sample for Core 1, and 200 arboreal grains for Core 2. *Cladium* grains were differentiated from other Cyperaceae using criteria of Fægri and Iversen (1989) for the Core 2 samples; this differentiation was not done for Core 1. Pollen percentages for terrestrial taxa are based upon a sum of all arboreal, shrub, and upland herb types. Cyperaceae were not included in that sum. Pollen percentages for wetland and aquatic plants (including Cyperaceae) were calculated from a sum of all wetland, aquatic, and upland types. Microscopic charcoal fragments (minimum diameter 15 μ m) were tallied during

pollen scans for Core 1. Charcoal data are expressed as ratios of charcoal particles to arboreal-pollen grains.

Numerical zonation

Stratigraphically constrained cluster analyses (CON-ISS) (Grimm 1987) of the pollen and plant macrofossil data were compared to determine whether major shifts in aquatic/wetland vegetation in the basin coincided with changes in the regional upland pollen assemblages. Pollen types were restricted to the following terrestrial taxa: *Abies*, *Picea*, total *Pinus*, *Acer saccharum*, *Betula*, *Carya*, *Fagus*, *Fraxinus americana*, *F. nigra*, *Juglans*, *Ostrya*/*Carpinus*, *Platanus*, *Quercus*, *Ulmus*, *Ambrosia*, *Artemisia*, Chenopodiaceae/Amaranthaceae, and Poaceae. The cluster analysis for the pollen data was based on a matrix of standardized Euclidean distances, giving equal weight to all pollen taxa regardless of their respective variances.

Macrofossil abundances of many taxa varied considerably among samples. We used presence/absence data in the numerical analysis of the macrofossil sequence to filter out this high-frequency variation. The analysis was restricted to aquatic and wetland taxa (Reed 1988) identified to the species level or to a species group. We used Euclidean distances in the macrofossil cluster analysis. Samples below 300-cm depth were omitted from both cluster analyses because of the scarcity of plant macrofossils.

RESULTS

Sediment stratigraphy and chronology

The upper 200 cm of sediment consists of dark brown, fibrous peat (Fig. 2). Compact gyttja occurs between 200 and 304 cm, and interbedded marl and marly sand occur below 304 cm. We obtained five bulk-sediment ¹⁴C dates from the peat and gyttja of Core 1 (Table 2). Although these dates are monotonically related to sediment depth (Fig. 2), the bulk dates from the gyttja are suspect because of the carbonate-rich bedrock, sediments, and groundwater of the region (Shedlock et al. 1988, 1993). Also, the timing of key events in the late-glacial and early Holocene pollen stratigraphy implied by these dates is inconsistent with records from other sites in the region (Webb et al. 1983, Jackson et al. 1986).

Accelerator mass spectrometry (AMS) dates from plant macrofossils of taxa with aerial photosynthetic organs confirmed these suspicions (Table 2, Fig. 2). We adopted an age model based on linear interpolation between the AMS date at 316–319 cm and the error-weighted average (Long and Rippeteau 1974) of the two dates (AMS and bulk) at 190–193 and 194–197 cm, and between the latter two dates and the bulk date at 85–88 cm (Fig. 2). We extrapolated the latter line to the sediment surface, rather than using the sediment surface as another dating benchmark (i.e., 0 yr BP). We did this because the *Ambrosia* pollen increase,

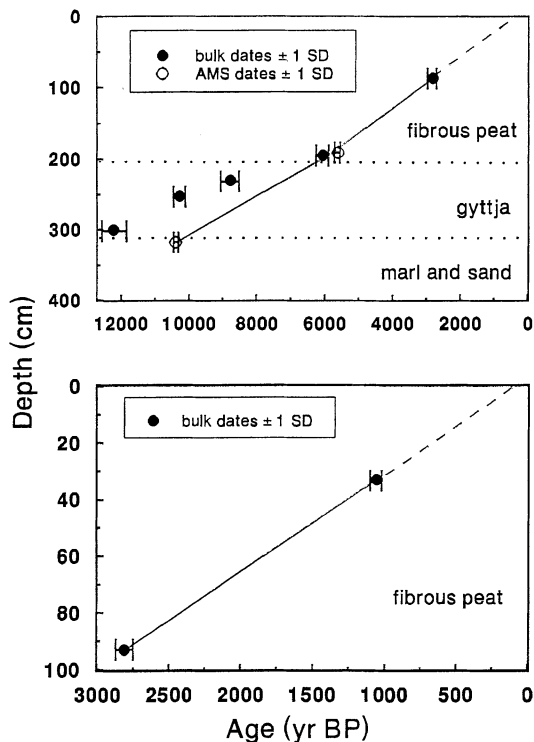


FIG. 2. Plots of radiocarbon ages vs. depth for Cores 1 (upper) and 2 (lower) from Portage Marsh. Line segments represent age models used in interpretation of pollen and plant macrofossil data. Dashed lines represent extrapolations of late Holocene age models owing to hiatus near sediment surface. AMS = accelerator mass spectrometry.

which should date ≈ 1830 AD in northwestern Indiana, occurs within 10 cm of the sediment surface of both cores (Figs. 3 and 4). In contrast, the *Ambrosia* increase occurs 25–80 cm below the sediment surface at other wetlands in the region (Futyma 1985, 1988, Jackson et al. 1988). A depositional hiatus, including erosional or oxidative loss of sediment accumulated before 1830 AD, has probably resulted from recent human activities near the basin. Our age model from Core 1 suggests that as much as 350–650 yr of recent sediment have been lost.

We obtained two bulk-sediment ^{14}C dates from the peats of Core 2 (Table 2, Fig. 2). These dates are con-

sistent with the age–depth model adopted for Core 1, and they confirm the hiatus near the sediment surface (Fig. 2). Extrapolation of the Core 2 dates suggests less sediment loss (100–200 yr) than Core 1 (Fig. 2). The differences between the cores may result from differential compaction of near-surface sediments owing to the different coring techniques used, or from differential loss of sediments at the hiatus.

Pollen stratigraphy: regional vegetational and climatic history

The pollen sequence is generally similar to those from other sites in northern Indiana and southern Michigan (Fig. 3; Bailey 1972, Williams 1974, Manny et al. 1978, Futyma 1985, Jackson et al. 1986). Basal pollen assemblages (Pollen Zone P-1) dominated by *Picea*, *Pinus*, and Cyperaceae are characteristic of open *Picea* woodlands. Between 11 500 and 10 000 yr BP, *Picea* woodlands throughout the southern Lake Michigan region were replaced first by mixed forest consisting of *Picea*, *Betula*, *Fraxinus nigra*, *Ulmus*, and *Ostrya/Carpinus*, and then by *Pinus*-dominated forests (Webb et al. 1983). These events are recorded in the declining *Picea* and Cyperaceae percentages and increasing *Pinus*, *Betula*, *Fraxinus nigra*, and *Ulmus* percentages towards the top of Pollen Zone P-1 (Fig. 3).

Pinus-dominated forests developed in the region by 10 000 yr BP. Most of the identifiable *Pinus* pollen at Portage Marsh was assigned to *Pinus* subgenus *Pinus* (comprising only *P. banksiana* and *P. resinosa* in the upper Midwest). Accompanying needle fragments were not identifiable to species. *Pinus banksiana* needle fragments were found in sediments dating between 11 000 and 9500 yr BP at a site 60 km southeast of Portage Marsh (Jackson et al. 1986). Macrofossils of *Pinus strobus* indicate that this species was present at Portage Marsh between 9000 and 6800 yr BP, in spite of the low pollen percentages (Fig. 3). *Quercus*, *Ulmus*, and *Carya* were also important constituents of forests during this period (Fig. 3). Low charcoal : pollen ratios (Fig. 3) indicate low fire frequencies, which suggest mesic conditions.

Overall, the pollen data indicate regional warming and development of temperate forests by 10 500 yr BP. The period from 9700 to 5700 yr BP was characterized

TABLE 2. Radiocarbon dates from Portage Marsh sediment cores.

Depth interval (cm)	Material dated	Lab number	Date (yr BP)
85–88 (Core 1)	Fibrous peat	GX-19744	2815 \pm 105
194–197 (Core 1)	Fibrous peat	GX-17971	6055 \pm 180
229–232 (Core 1)	Gyttja	GX-19745	8770 \pm 270
251–254 (Core 1)	Gyttja	GX-19746	10 285 \pm 165
299–302 (Core 1)	Gyttja	GX-17972	12 225 \pm 350
190–193 (Core 1)	397 Cyperaceae achenes	GX-20207-AMS	5608 \pm 70
316–319 (Core 1)	Conifer needle fragments	GX-20208-AMS	10 399 \pm 160
32–34 (Core 2)	Fibrous peat	GX-20479	1055 \pm 40
92–94 (Core 2)	Fibrous peat	GX-20480	2810 \pm 60

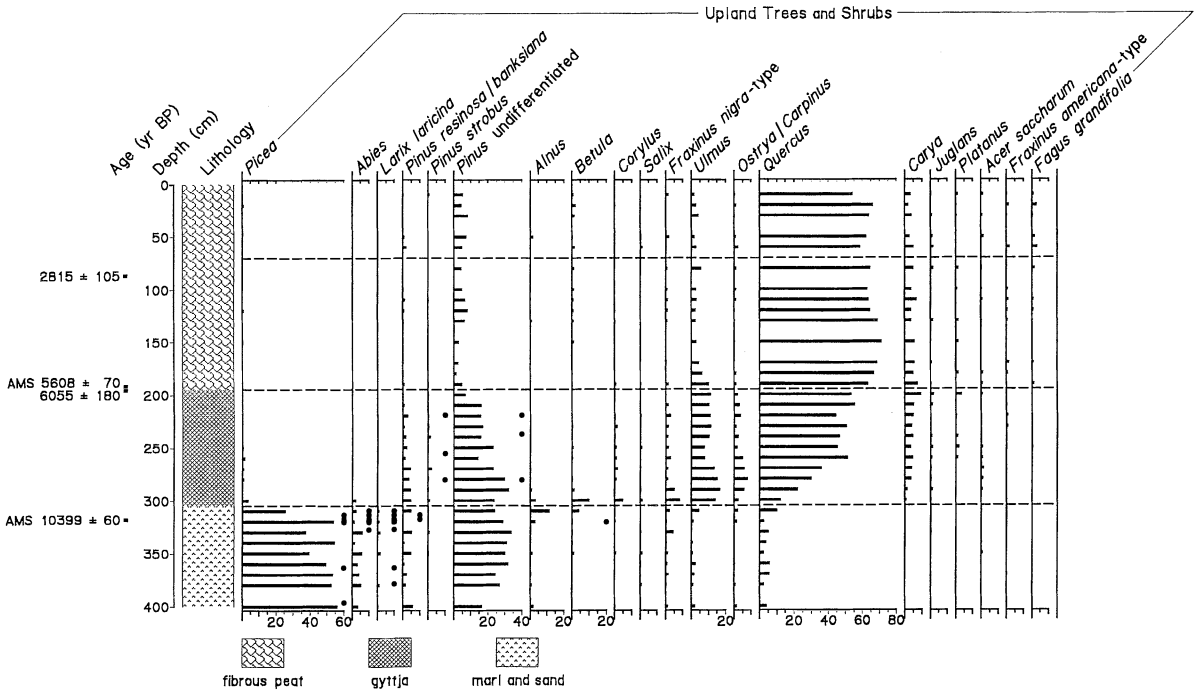


FIG. 3. Pollen percentage diagram from Portage Marsh Core 1. Closed circles in columns for *Picea*, *Abies*, *Larix*, *Pinus*, *Pinus resinosa/banksiana*, and *Pinus strobus* represent occurrences of plant macrofossils (needles, seeds, bud scales) of corresponding taxa. Closed circle in *Betula* column represents occurrence of macrofossils of *Betula papyrifera*. Closed circles in columns for *Brasenia schreberi*, *Nuphar*, *Nymphaea*, and *Potamogeton* represent pollen percentages of <2%. Charcoal column represents charcoal: arboreal-pollen ratios. Radiocarbon dates not used in age model are not shown. Rectangles to the right of the ^{14}C dates refer to depth intervals at which ^{14}C dates used in the age models were obtained. Analysts: B. J. Madsen (pollen) and D. K. Singer (macrofossils).

by temperate conditions with abundant available moisture. These inferences are consistent with other paleoclimatic records from the western Great Lakes and upper Mississippi Valley regions (T. Webb et al. 1983, 1993, Baker et al. 1992).

Other sites in the southern Lake Michigan region show a sharp decline in *Pinus* pollen before 9000 yr BP, accompanied by an increase in *Quercus* pollen (Bailey 1972, Williams 1974, Manny et al. 1978, Webb et al. 1983). In contrast, high *Pinus* percentages (>20%) persisted at Portage Marsh until after 7000 yr BP, and declined gradually from 7000 to 5700 yr BP (Fig. 3). This decrease was accompanied by increasing *Quercus* pollen. *Ulmus* pollen declined \approx 5700 yr BP.

The persistence of *Pinus* in forests near Portage Marsh well after it declined elsewhere in the region probably results from edaphic differences (e.g., Graumlich and Davis 1993). The sandy lacustrine and aeolian soils north of the Valparaiso Moraine (Fig. 1; Schneider and Keller 1970) were probably more favorable for *Pinus strobus* and *P. banksiana*; both these species are now restricted in northwest Indiana to sandy dunal soils near the Lake Michigan shore (Menges and Armentano 1985). Sites on finer textured morainal soils to the south and east were better suited for development of *Quercus/Ulmus* forests.

The transition at 5700 yr BP from a *Pinus/Quercus*

Ulmus assemblage to a *Quercus/Carya* assemblage (Fig. 3) records the development of open *Quercus* savanna near Portage Marsh. This interpretation is supported by the increase in *Ambrosia* and Poaceae percentages, although the latter may also represent development of local emergent grasses in the Portage Marsh basin. Increased charcoal: pollen ratios indicate increased fire frequency after 5700 yr BP, consistent with the development of open *Quercus* savanna (Bacone et al. 1980, Henderson 1982, Henderson and Long 1984). These changes coincide with similar trends from mesic hardwoods toward more xeric vegetation (e.g., savanna, prairie) at many sites west of the study area (Webb et al. 1983, Webb 1987, Winkler 1988, Chumbley et al. 1990, Baker et al. 1992).

Modest rises in *Fagus* and *Betula* after 3000 yr BP (Figs. 3 and 4) suggest a trend toward cooler, moister conditions in the study region. Other sites in Michigan, Indiana, and Wisconsin show more marked increases in *Fagus* and *Betula* pollen between 3000 and 2000 yr BP (Webb et al. 1983, Futyma 1985, Webb 1987, Winkler 1988). The more subtle increase in these taxa at Portage Marsh probably represents increasing populations at distant sites on fine-grained soils. Open *Quercus* savanna persisted to historic time on coarse-textured soils near Portage Marsh and to the north (Bacone et al. 1980, Henderson 1982, Futyma 1985).

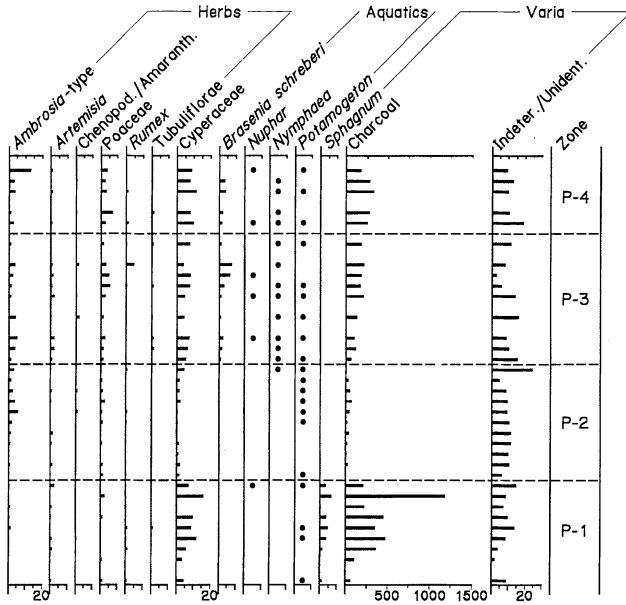


FIG. 3. Continued.

Macrofossil stratigraphy: history of local wetland vegetation

Marl-producing lake phase (>10 000 yr BP).—Macrofossils of aquatic and wetland plants are scarce before 10 000 yr BP (Fig. 5), although terrestrial macrofossils are frequent (Fig. 3). The basin may have been occupied by a deep-water lake. The marly sediments indicate that the basin was abundantly supplied by carbonate-rich groundwater.

Shallow lake phase (10 000–5700 yr BP).—Portage Marsh was occupied by a shallow, open lake from 10 000 to 5700 yr BP, as indicated by the gyttja sediments and by plant macrofossils of obligately submersed taxa (*Najas flexilis*, *Chara*) (Fig. 5). Emergent taxa are absent from the macrofossil assemblages. Because many emergent plants have well-dispersed seeds or fruits (Birks 1973), the absence of emergent taxa suggests that the entire basin was free of emergent vegetation except along the margins. The low percentages of Cyperaceae and Poaceae pollen (Fig. 3) support this inference. The occurrence of *Chara* and *Najas flexilis* indicates high pH, alkalinity, and Ca⁺⁺ and Mg⁺⁺ concentrations (Moyle 1945, Hellquist and Crow 1980), consistent with the carbonate-rich bedrock, surficial materials, and groundwater of the region (Shedlock et al. 1988, 1993).

Shallow marsh, phase I (5700–2400 yr BP).—The rapid transition from gyttja to peat deposition, together with a substantial increase in macrofossils of emergent and floating-leaved plants (Fig. 5) and an increase in Cyperaceae pollen (Fig. 3) indicate the development of a shallow marsh ≈5700 yr BP. The macrofossil assemblages deposited between 5700 and 2400 yr BP include obligate submersed taxa tolerant of shallow water (*Chara*, *Najas flexilis*, *Potamogeton*), together with floating-leaved taxa (*Brasenia*, *Nuphar*) and obligate emergents (mostly Cyperaceae; Figs. 5 and 6). Seven of the emergent species (*Cyperus erythrorhizos*, *C. odoratus*, *Eleocharis flavescens* var. *olivacea*, *Fimbristylis autumnalis*, *Fuirena pumila*, *Rhynchospora macrostachya*, *R. scirpoides*) are low-statured annuals characteristic of exposed shorelines and mud flats dur-

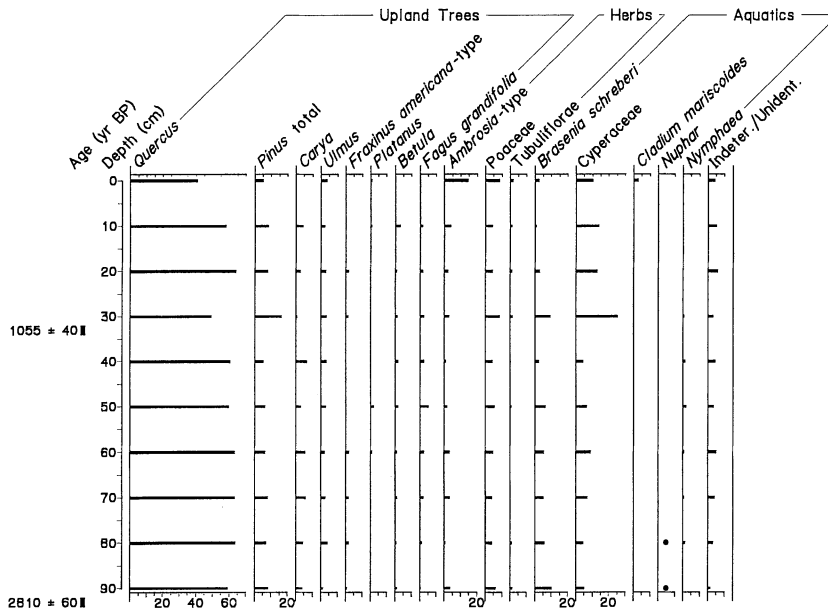


FIG. 4. Pollen percentage diagram for selected terrestrial and aquatic taxa from Portage Marsh Core 2. Closed circles in *Nuphar* column represent pollen percentages of <2%. Analyst: S. T. Jackson.

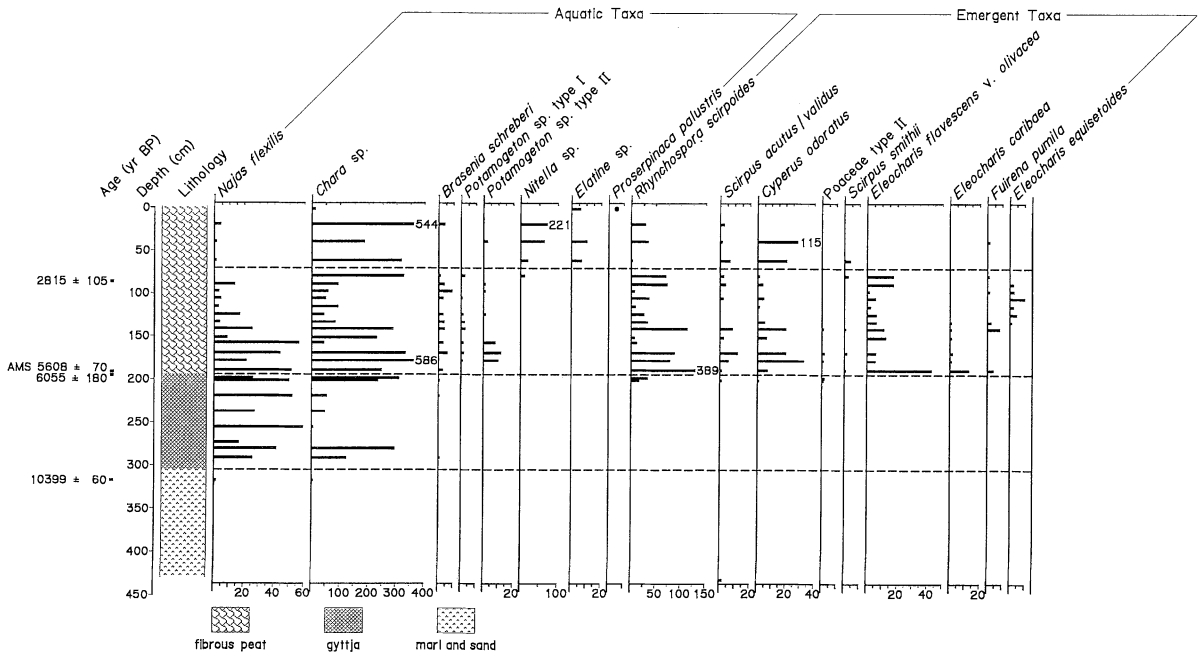


FIG. 5. Plant macrofossil concentration diagram for aquatic and wetland taxa from Portage Marsh Core 1. Macrofossils consist of seeds or fruits except for *Chara* and *Nitella*, which are oöspores. Closed circle in *Proserpinaca palustris* column represents a single occurrence. "Carbonized achenes" refers to charred Cyperaceae achenes. Analyst: D. K. Singer.

ing temporary periods of water drawdown (Voss 1972, Godfrey and Wooten 1979, Bowles et al. 1990, Wilhelm 1990, Reznicek 1994). They require periodic drawdowns to germinate and grow, and inundation to prevent site occupation by terrestrial herbs and shrubs.

The assemblage of floating-leaved and submersed aquatics together with emergent mud-flat taxa indicates that the basin was characterized by periodic fluctuations in water level. Because each macrofossil sample spans a 90–130 yr interval, sedimentary mixing of macrofossils deposited during high-water periods (submersed and floating-leaved plants) and low-water periods (shallow-water and drawdown emergents) could have yielded the mixed assemblages. Low-water periods need have occurred only infrequently to maintain the drawdown taxa; viable seeds may persist in wetland seed banks for many years (Keddy and Reznicek 1982, Leck 1989, Reznicek 1994).

Shallow marsh phase II (2400–≈150 yr BP).—Vegetation of the marsh underwent another transition with the decline of several emergent taxa and the appearance of others between 3000 and 2000 yr BP (Figs. 5 and 6). *Eleocharis flavescens* var. *olivacea* and *E. equisetoides* declined, while *E. palustris* and *Polygonum lapathifolium* increased (Fig. 6). *Cyperus bipartitus/diandrus* increased during this transition, but subsequently declined. Water-level fluctuations continued, as indicated by the persistence of several of the drawdown taxa (Figs. 5 and 6). Carbonized achenes of *Rhynchospora scirpoides* and other emergent Cyperaceae indicate that occasional fires occurred in the marsh dur-

ing drawdown periods (Figs. 5 and 6). These fires may have originated on the adjacent savanna uplands.

Modern shallow marsh phase.—The transition to the modern flora and vegetation of the marsh is not recorded owing to the depositional hiatus at 5 cm depth (Figs. 4 and 6). The marsh has undergone substantial hydrologic and ecological change within the past 150 yr (Fig. 6). Many of the taxa formerly characteristic of the marsh are absent from both the modern flora and macrofossil assemblage, and several new taxa have appeared (e.g., *Proserpinaca palustris*, *Cladium mariscoides*, *Juncus*, *Hypericum*) (Figs. 5 and 6). Seeds of species present in the top 10 cm (or more) of sediment are potentially viable seed-bank constituents (van der Valk and Davis 1976, Keddy and Reznicek 1982). Emergent drawdown taxa that were found in the seed bank but not observed during vegetation surveys in 1991 or 1994 include *Fimbristylis autumnalis*, *Fuirena pumila*, and *Rhynchospora scirpoides* (Figs. 5 and 6).

Cluster analyses

Cluster analyses for the pollen and macrofossil data (Fig. 7) confirm that major changes in local vegetation in the Portage Marsh basin coincided with regional changes in upland vegetation. For example, between 10 000 and 5700 yr BP, composition of vegetation within the basin underwent little change (Macrofossil Zone M2), while the regional vegetation underwent continual, gradual change (Pollen Zone P2). Both changed rapidly at 5700 yr BP (transitions to Zones M3 and P3). After 5700 yr BP, both local and regional vege-

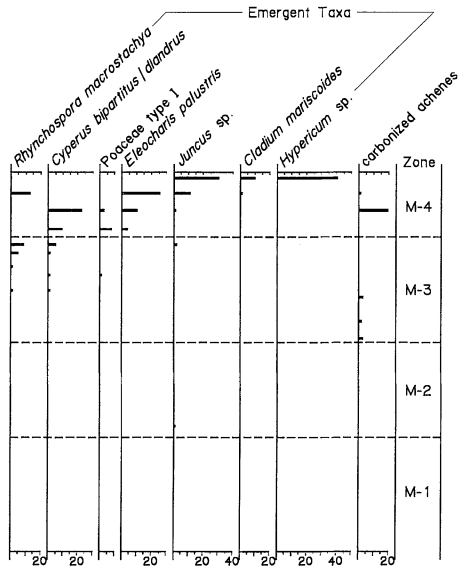


FIG. 5. Continued.

tation underwent continual and gradual change, with rapid change ≈ 2400 yr BP (transitions to Zones M4 and P4).

DISCUSSION

Mechanisms governing Holocene wetland vegetation dynamics

The shallow lake phase of the Portage Marsh basin (10000–5700 yr BP) corresponds to the period of mesic regional climate inferred from our pollen record (Fig. 3), as well as other pollen diagrams from the southern Lake Michigan region (Bailey 1972, Williams 1974, Manny et al. 1978, King 1981, Futyma 1985, 1988) and the western Great Lakes (Webb et al. 1983, Baker et al. 1992). The transition from an open, shallow lake to a marsh 5700 yr BP coincided precisely with the transition on the uplands from mesic *Quercus/Ulmus/Pinus* forest to xeric *Quercus* savanna and with an increase in regional fire frequency and/or intensity (Fig. 3). This change toward drier conditions is recorded in other pollen sequences in the southern Lake Michigan region and in the western Great Lakes and upper Mississippi Valley regions (Webb et al. 1983, Baker et al. 1992).

The coincidence of the changes at Portage Marsh with the upland vegetational changes implicates climate as the mechanism driving the transition from lake to marsh. A decrease in precipitation would have lowered water levels in the basin, allowing colonization by emergent plants. The drop in water level exposed portions of the marsh during seasonal or lower frequency droughts, and allowed establishment and seed-bank persistence of the drawdown emergents. Frequency and severity of drought years may also have increased. Water-level and vegetational response to cli-

mate-induced hydrologic change is consistent with the observed rapidity and magnitude of the macrofossil transition at 5700 yr BP. Autogenic successional mechanisms operating alone would have led to a gradual transition as the basin filled in.

The second transition ≈ 2400 yr BP was more gradual, consisting of overlapping increases and declines in several species (Figs. 5 and 6). The basin continued to have fluctuating water levels and a rich mixture of emergent, submersed, and floating-leaved species. Successional processes may have played a role in this transition. For instance, shallowing of the basin via peat accumulation may have shifted the competitive balance among emergent species. However, the transition also coincided with a modest transition in the upland pollen record (increasing *Fagus* and *Betula*; Figs. 3 and 4). More dramatic increases in *Fagus*, *Acer*, and *Betula* occurred during the late Holocene at sites on finer textured soils in northern Indiana (Bailey 1972, Williams 1974, Futyma 1985) and southern Michigan (Manny et al. 1978). These latter increases fit a widespread pattern of increasingly cool and moist conditions in the upper Midwest after 3000 yr BP (Winkler 1988, Baker et al. 1992, Wright 1992, T. Webb et al. 1993). The stability of vegetation composition in Portage Marsh from 6000 to 3000 yr BP, followed by the synchronous changes in marsh and upland vegetation ≈ 2400 yr BP, suggest that climate change induced changes in basin hydrology. The nature of those changes is not clear from our macrofossil data, but may have consisted of changing frequency or magnitude of inundation and drawdown events.

The third transition, occurring since Euro-American settlement, is obscured by loss of the uppermost sediments. That transition appears to have had a dramatic effect on species composition of the marsh, and may have been rapid (e.g., Jackson et al. 1988). Drainage disruption, ditching, and increased surface runoff in the agricultural and later urbanized catchment probably altered the hydrology of the marsh, and led to local extirpation of some taxa and colonization by others (Keddy and Wisheu 1989, Wilcox 1995).

All three of the major Holocene transitions in vegetation and basin characteristics at Portage Marsh represent responses to hydrologic changes related to allogenic factors (climate change, human disturbance). Although the basin has accumulated organic sediments for the past 10000 yr, the rate of this autogenic process has been slow relative to the rate and magnitude of hydrologically significant climatic changes. Nevertheless, the progressive shallowing of the basin by accumulation of organic sediments has constrained subsequent responses to allogenic forcing. Accumulation of more than a metre of gyttja during the early Holocene filled the basin sufficiently that the response to the regional drying ≈ 5700 yr BP led to development of a marsh rather than a shallower lake. The marsh did not respond to greater effective moisture in the late

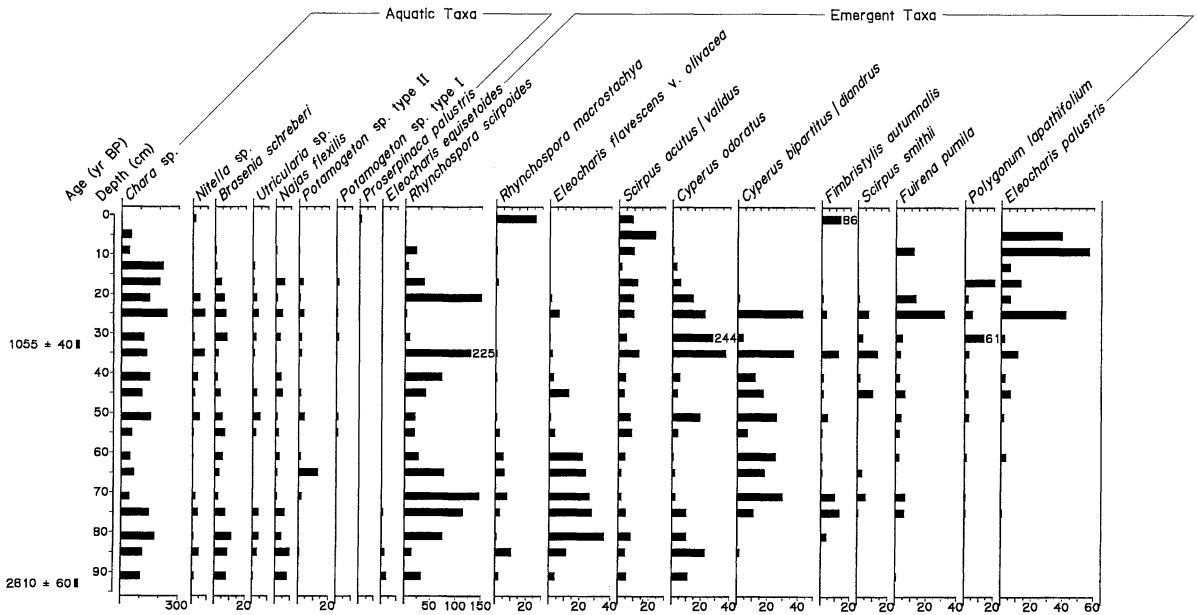


FIG. 6. Plant macrofossil concentration diagram for aquatic and wetland taxa from Portage Marsh Core 2. "Carbonized achenes" refers to charred Cyperaceae achenes (mostly *Rhynchospora scirpoides*); those that could be identified were also included in the data for the respective taxa. Macrofossils consist of seeds or fruits except for *Chara* and *Nitella*, which are oöspores. Analyst: D. K. Singer.

Holocene by returning to a shallow lake, because another 125 cm of peat had accumulated in the meantime. Instead, the vegetation composition of the marsh changed.

In the developmental history of Portage Marsh and other wetlands (Watts and Winter 1966, Janssen 1967, Walker 1970, Futyma and Miller 1986, Baker et al. 1987, Miller and Futyma 1987, Jackson et al. 1988, Winkler 1988, Lavoie et al. 1995), each successive response to a change in external forcing is contingent on preceding responses and forcings. Differences among basins in morphometry, groundwater and surface hydrology, catchment soil composition, net primary production, and other factors can lead to differences in rates of sediment accumulation, absolute water depths, and sensitivity to climate change. These factors constrain the nature of individual basin responses to external forcing. Individualistic responses of basins to climate change account for much of the "noise" observed in studies of Quaternary lake levels (Harrison 1988), mandating the use of regional networks of multiple sites in lake-level studies of paleoclimate (e.g., Harrison 1989, T. Webb et al. 1993).

Holocene climate change in the southern Lake Michigan region

Holocene climate change in the midwestern United States has been spatially complex (Webb et al. 1983, Baker et al. 1992, Wright 1992). For example, the prairie-forest border retreated westward during the mid-Holocene in western Minnesota at the same time it was expanding eastward in eastern Iowa, where prairie in-

vaded mesic forests dominated by *Ulmus*, *Ostrya*, *Tilia*, *Acer saccharum*, and *Quercus* (Chumbley et al. 1990). The latter expansion fits a more widespread pattern of increasingly dry conditions starting after 6000 yr BP in eastern Iowa, northern Illinois, and southern Wisconsin, followed by cooler and moister conditions after 3000 yr BP (Webb et al. 1983, Winkler et al. 1986, Baker et al. 1992, Wright 1992).

The pollen and plant macrofossil record from Portage Marsh indicates that the climatic pattern observed west of Lake Michigan also occurred in northwestern Indiana. The region experienced high effective moisture during the early Holocene, when summer monsoonal rainfall in the midcontinent would have been amplified by the Milankovitch summer insolation maximum (Wright 1992). Drier conditions starting 6000 yr BP were associated with dampening of monsoonal flow as summer insolation decreased. The return toward more mesic conditions after 3000 yr BP was related to cooler temperatures as summer insolation continued to decrease (Wright 1992, T. Webb et al. 1993).

This general Holocene climatic sequence is characteristic of northeastern Indiana and southwestern Michigan as well as Portage Marsh. Pollen diagrams from these regions show characteristic patterns of early Holocene pollen maxima of *Fagus* and sometimes *Acer*, followed by decreases associated with *Quercus* and *Carya* maxima, followed in turn by a late Holocene maximum of *Fagus* and *Acer* (Bailey 1972, Williams 1974, Manny et al. 1978). These patterns can be seen on the isopoll maps of Webb et al. (1983). The apparent timing of these events differs by as much as 1500 yr

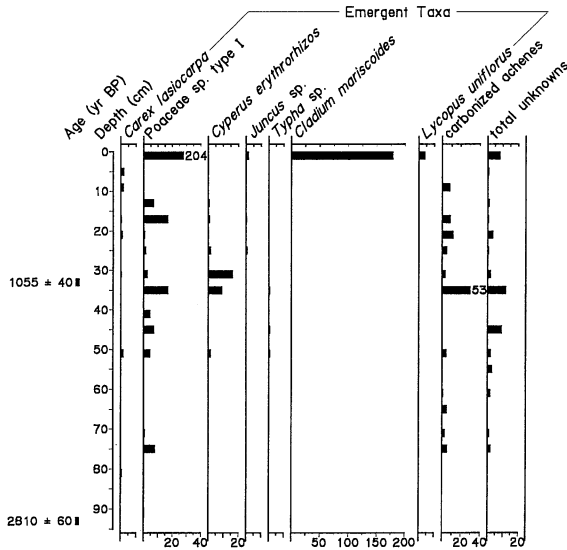


FIG. 6. Continued.

among sites. Much of this variation results from dependence of age models on ¹⁴C-dating of bulk sediments in this region of carbonate-rich groundwater and surficial sediments (e.g., Jackson et al. 1986, MacDonald et al. 1991). Pollen sequences with AMS-based age models are needed to resolve the climate and vegetation history of southern Michigan and adjacent Indiana. Such resolution will clarify the boundary between eastern regions that experienced maximum

drought in the early Holocene (Webb 1990, R. S. Webb et al. 1993) and western regions where conditions were driest in the mid-Holocene (Baker et al. 1992, Wright 1992).

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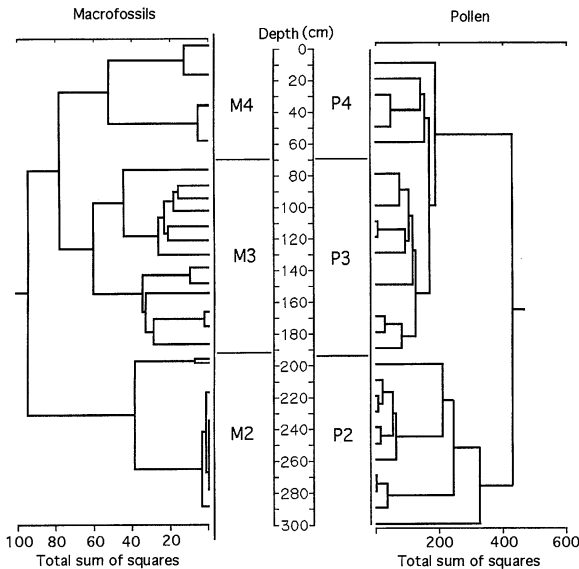


FIG. 7. Stratigraphically constrained cluster diagrams for macrofossil data (left) and pollen data (right) from Portage Marsh Core 1, with macrofossil and pollen zonation and sediment depths in the center. Macrofossil zonation is based on presence/absence of aquatic and wetland taxa; pollen zonation is based on percentages of selected upland pollen types (see Methods for details).

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APPENDIX

NOTES ON PLANT MACROFOSSIL DETERMINATIONS

Cyperus erythrorhizos achenes were distinguished from other *Cyperus* species of the region based on (a) unequally trigonous cross section, with the broadest face gently to strongly concave and the others planar, (b) length of 0.7–1.0 mm, (c) broadly elliptic shape in longitudinal view, and (d) absence of persistent corky wings. *C. odoratus* achenes were characterized by their obovoid–oblong longitudinal shape and the presence of persistent, corky rachilla segments clasping the basal portion of the achene (Jackson et al. 1988).

Two features distinguish *Eleocharis equisetoides* achenes from those of most other species: lenticular cross-sectional shape and vertical rows of transversely elongate cells. Achenes of *E. quadrangulata* and *E. robbinsii* are similar in these respects, but the achene apex is constricted to a neck that extends beyond the achene body. The apex of *E. equisetoides* is flush with the achene body or nearly so. *E. caribaea* achenes can be differentiated from those of *E. flavescens* var. *olivacea* based on the following features: (a) *E. caribaea* has

a shiny black achene surface (well preserved in fossil specimens), while *E. flavescens* var. *olivacea* has a dull achene surface. (b) *E. caribaea* achenes are narrower (0.6 ± 0.1 mm for *E. caribaea* vs. 0.8 ± 0.1 mm for *E. flavescens* var. *olivacea*). (c) The achene faces of *E. caribaea* are more compressed (achene thickness 0.35 mm) than in *E. flavescens* var. *olivacea* (0.45 mm).

Fimbristylis autumnalis achenes can be separated from most other Cyperaceae of the Great Lakes region by their small size (0.55 mm length). *F. autumnalis* achenes are trigonous. The translucent achene surface has vertical rows of transversely elongated cells. Achenes of *Bulbostylis capillaris*, although similar, are larger (0.75 mm long) and have opaque surfaces. Achenes of *Eleocharis microcarpa* lack transversely elongated cells and also have opaque surfaces.

Fuirena achenes differ from other Cyperaceae by the presence of three persistent, blade-like perianth scales. These scales are usually preserved in fossil achenes. The trigonous achene has concave sides that may split from each other in fossil specimens yet remain identifiable. Scales of *F. pumila* are ≈ 2.5 mm long including a narrow bristle-like apex, while scales of *F. squarrosa* are ≈ 2 mm long including an acuminate apex (Godfrey and Wooten 1979: Figs. 211 and 212). The translucent yellow-golden color of *F. pumila* achenes is unique among Cyperaceae of the central Great Lakes region and was observed in fossil achenes and fragments.

Rhynchospora scirpoides was characterized by lengthwise

striae on the lenticular achene, and by the persistent broad tubercle, which is equal in width to the achene. The angles between the achene faces are covered by a ridge of corky tissue that is continuous with the tubercle. The tubercle of *R. scirpoides* is equal to or greater than the achene in length, and has a style that frequently persists on fossil specimens. The tubercle of *R. nitens* is about one-third the achene length, and the style is deciduous.

Rhynchospora macrostachya achenes were distinguished from most other *Rhynchospora* based on their large size (4.5–5.5 mm, not including the tubercle, which is 16–22 mm long). Persistent bristles of *R. macrostachya* are longer than the achene, while those of *R. corniculata* are shorter than the achene. We could not separate *R. macrostachya* from *R. inundata* based on achene morphology. However, the modern range of *R. inundata* is along the Atlantic Coast from Massachusetts to Delaware, with no known populations in the Great Lakes region.

We distinguished *Scirpus smithii* achenes from other *Scirpus* species based on the following features: (a) broadly ovate shape, (b) glossy dark surface (well preserved in fossils), and (c) length (1.3–1.9 mm). *S. cespitosus* achenes are similar but have a prominent dorsal keel.

Most Poaceae seeds could not be identified to genus. Two distinct morphotypes were recognized (Poaceae Type I and Type II). *Potamogeton* fruits could not be reliably identified to species. Two morphotypes representing at least two species were recognized (Type I and Type II).

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