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Late Holocene Paleoecology of Southeastern Iowa: Development of Riparian Vegetation at Nichols Marsh[1]

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Pollen, vascular plant and bryophyte macrofossils from peat and silt deposits that filled an oxbow lake near Nichols, Iowa provide a 2500-year record of wetland succession and of upland habitats. Radiocarbon dates of 2320 ± 90 yr B.P. (BETA 12514) near the base and 1260 ± 70 yr B.P. (BETA-12513) midway up one section, and 1050 ± 70 (BETA 12515) in another provide chronologic control.

The pollen diagram indicates substantial changes in local wetland habitats, but less change in upland vegetation in the last 2500 years. Plant macrofossils record changes from a deep to a shallow oxbow lake during the first few hundred years after the meander was cut off. About 1600 yr B.P. marsh vegetation began to encroach as the lake filled with sediment. A somewhat weedy marsh that existed from about 1400 to 900 yr B.P., developed into a rich mire that persisted until the 1840's, when Europeans began cultivating the upland areas. A rise of ragweed pollen (from 7 to 25%) documents the beginning of cultivation in the area, and is accompanied by a sudden increase in diversity and in numbers and taxa of weedy species on the marsh.

The presence of abundant charcoal and macrofossils of such prairie taxa as *Amorpha* and *Petalostemum* imply warmer conditions from about 1400 to 900 B.P.; their absence and the appearance of the bryophyte *Meesia* suggest cooler conditions during the last thousand years. Key Words: Paleoecology, Holocene, Plant Macrofossils, Palynology, Pollen, Bryophytes, Marsh Flora, Wetland Evolution, Archaeology.

INTRODUCTION

The dearth of information on Holocene paleoenvironments south of the Wisconsinan ice border reflects the paucity of depositional sites. In Iowa, most suitable localities for pollen and plant macrofossil analysis are situated on the Des Moines Lobe in the north-central part of the State, where glaciers left numerous depressions that became lakes or marshes. However, the rediscovery of peat deposits (Roosa et al, 1984) in southeastern Iowa (Fig. 1), led to this investigation begun in the summer of 1984.

The study site, herein designated Nichols Marsh, is located in southeastern Iowa about four km southeast of Nichols in Muscatine County (SE ¼, NW ¼ Sec. 23, T.77N., R.4 W.; 41° 27′ 30″ N, 91° 17′ W). Nichols Marsh occupies a filled oxbow lake formed by either the Cedar River or its tributary, Wapsinonoc Creek (Fig. 1). The original meander cut into a nine-meter terrace along the Cedar River. At the present time, the oxbow is overgrown, mainly with marsh vegetation, and no natural pond remains, although open water is present where peat is being mined. The owner of the commercial peat operation has probed the deposit and reports that the thickest section is adjacent to the upland west of the marsh, on the outside edge of the meander (Ross McGlothlen, oral communication, 1984) (Fig. 2).

The primary purpose of this study is to provide the first detailed reconstruction of Late Holocene vegetation south of the Wisconsinan ice margin by documenting the paleoenvironment of this filled oxbow and of the surrounding area. This paper will 1) record the wetland succession beginning with the time of abandonment of the meander, using evidence from the analysis of pollen and plant macrofossils (mostly seeds and fruits of vascular plants, and fragments of bryophytes), 2) provide a continuous pollen sequence to interpret the upland vegetation of the last 2300 years, and 3) try to distinguish which vegetational changes are caused by wetland succession and which are caused by climatic change and/or the impact of human activities. The results will be interpreted with reference to the present-day vegetation. In addition, this study provides a control site (uninfluenced by human occupation) for a series of archaeological sites along Highway 218 about 18 km west of Nichols (Lensink, 1986). Both the archaeological sites and Nichols Marsh contain records dating back about 2500 years.

METHODS

We sampled the sediments in August, 1984, when the water table had been lowered for peat mining, and approximately 1.3 m of peat were exposed at low water level. Two sites about 15 m apart were sampled. Site 1, about 20 m east of the upland was primarily for pollen analysis. Samples were dug out of the peat face from the surface down to the water table, and then cored with a modified Livingstone Corer with an inside diameter of about 5 cm. Site 2, mainly for plant macrofossils, was cored near the valley wall to maximize the number of upland macrofossils. The sediment stratigraphy, core lengths, and radiocarbon dates show that the sections are very comparable. Samples were wrapped in Saran Wrap and aluminum foil, and returned to the laboratory.

Pollen samples 1 cm^3 in size were taken from section 1 using a modified syringe (Maher, 1981). A tablet containing 16,180 ± 1500 *Eucalyptus* grains was added to each sample, and the samples were processed by standard methods (Faegri and Iverson, 1975). Pollen samples were mounted in silicone oil. A minimum of 300 pollen grains of upland taxa were counted for each level. Section 2 was washed in 10-cm segments through screens with 0.5 and 0.1 mm openings, and the residues were picked for macrofossils.

The pollen diagrams (Figs. 2 and 3) from site 1 were divided by visual inspection into four zones, each with a characteristic assemblage of pollen and spores. The zones probably represent changes mainly of marsh vegetation (see Discussion) and are thus of local, rather than regional importance. Regional pollen types did not fluctuate sufficiently to warrant zonation. The macrofossils were zoned separately

[1]Iowa Quaternary Studies Group Contribution no. 3.

(Tables 1 and 2, Figure 4) on the basis of the characteristic assemblage of fossils in each zone.

Pollen diagrams are generally used to reconstruct upland vegetation, so pollen or spores of aquatic vegetation, and other local lowland taxa are excluded from the pollen sum (Maher, 1972). However, at Nichols Marsh it is difficult to decide which pollen types are local and which are regional in origin; therefore, on the pollen diagram, curves are plotted in two ways. The darker curves are plotted excluding Cyperaceae, aquatic taxa, spores, and algae from the pollen sum. On the lighter curves Gramineae has also been excluded from the pollen sum, because macrofossil evidence suggests that Gramineae pollen is mostly derived from local aquatic taxa (see Discussion).

Three radiocarbon dates were obtained from the two sample sites. From site 1, organic silt from 305-310 cm was dated at 2320 ± 90 yr B.P.(Beta 12514), and peat from 185-190 cm was 1260 ±70 yr B.P.(Beta 12513). Peat surrounding the uppermost in a series of sand lenses from 160 to 170 cm in site 2 was dated at 1050 ± 70 yr B.P.(Beta 12515). The interpolated date from site 1 for this interval would be 945 yr B.P., or 105 years off from the dated interval. This correlation suggests that the interpolation is within the range of error for these dates. Dates for the zone boundaries undated by radiocarbon analysis are interpolated using the sedimentation rate between radiocarbon dates. The base of the section is estimated to be about 2500 years B.P. on the basis of extrapolation from the sedimentation rate between the two radiocarbon dates from site 1.

Surveys of the extant flora were carried out during several visits in the growing seasons of 1984-1986 by Roosa and Pusateri, and were supplemented with visits by Baker in August, 1984, by Horton, and by Baker and Horton in September, 1986. Voucher specimens are deposited as follows: vascular plants are in the herbaria of the University of Iowa (IA) and the University of Northern Iowa (ISTC); pollen and vascular plant macrofossils are in the Paleontological Repository of The University of Iowa SUI; bryophytes and bryophyte macrofossils are in IA.

Authority names for the vascular plants generally follow Gleason and Cronquist (1963), while those for the bryophytes are mostly according to Crum and Anderson (1981), and Stotler and Crandall-Stotler (1977).

Author responsibilities for the paper are as follows: Kim analyzed the pollen and produced the pollen diagrams; Witinok and Sullivan picked and counted the macrofossils and made routine identifications; Roosa and Pusateri surveyed the modern flora; Horton identified fossil and modern bryophytes and assisted with revision of the manuscript; Baker identified most of the macrofossils, added to the survey of the modern flora, and authored the manuscript.

RESULTS

Nichols Marsh presently supports a diverse flora (Table 1) in which *Typha latifolia* (broad-leaved cattail) is a dominant species, in places in

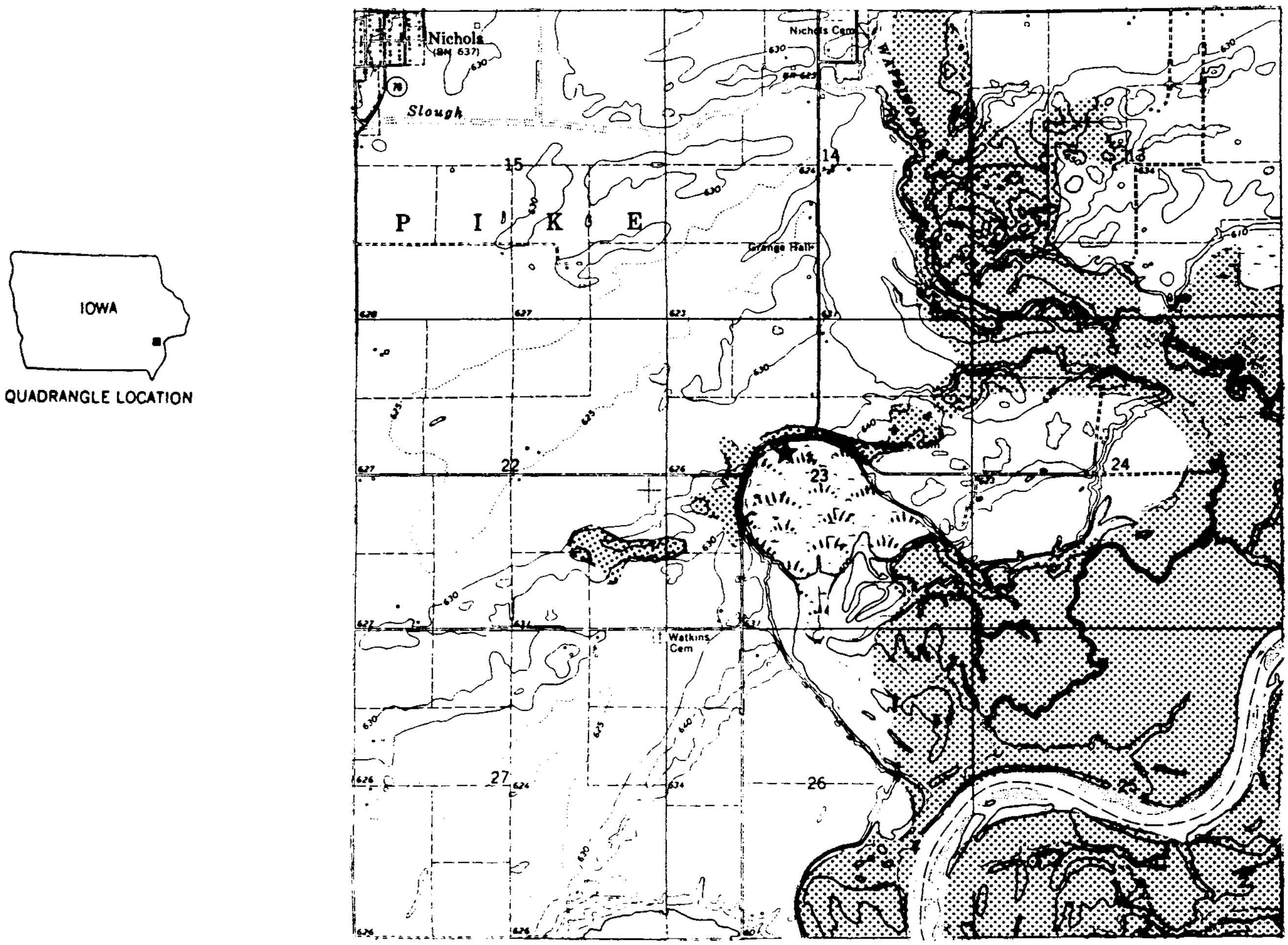

Figure 1. Topographic map of the Nichols area, Iowa, showing the sampling sites (star), and the present forest cover (shaded). The original forest cover was apparently similar to the modern distribution (Iowa State Planning Board, 1935, Figure 16.)

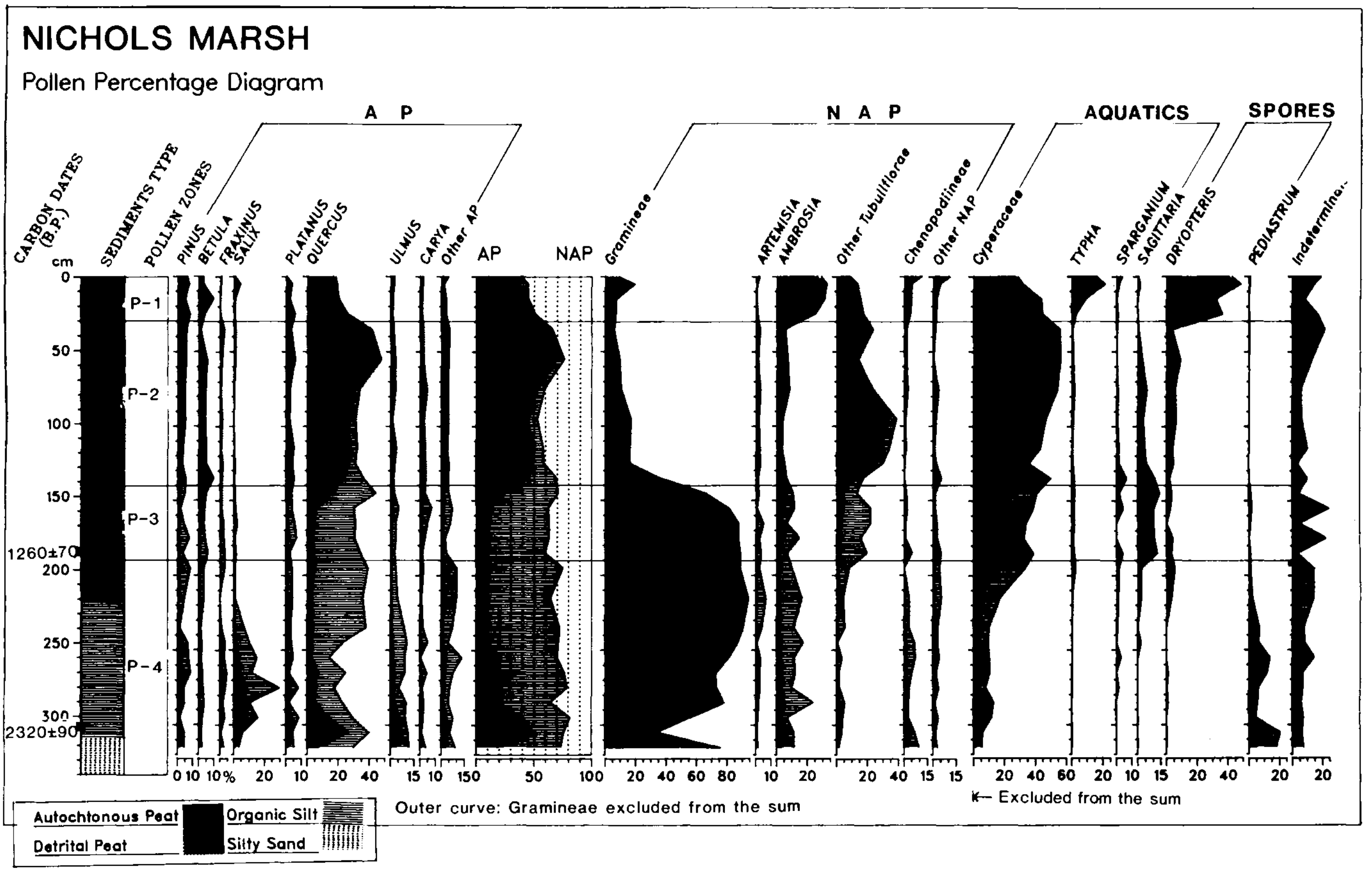

Figure 2. Pollen percentage diagram from Site 1, Nichols Marsh.

almost pure stands, but elsewhere with a diverse component of marsh sedges, grasses, and forbs. Other species that are locally important include *Carex lacustris* and other *Carex* species (sedges), *Bidens cernua* (beggar ticks), *Leersia oryzoides* (rice cutgrass), *Polygonum punctatum* (smartweed), *Pilea fontana* (clearweed) and *Dulichium arundinaceum* (three-way sedge). Most of the marsh vegetation is herbaceous, but *Betula nigra* (river birch) is scattered sparsely across the surface, and a few small patches are dominated by shrubs, mainly *Cornus stolonifera* (dogwood), *Spiraea alba* (meadow-sweet), *Amorpha fruticosa* (lead-plant), and *Salix discolor* (pussy-willow). Bryophytes represent a relatively minor component of the vegetation, but several taxa, including *Amblystegium riparium, Hypnum lindbergii, Helodium blandowii* var. *elodioides* and *Aneura pinquis,* are locally abundant.

The wetland vascular plants include substantial elements of marshes, sand marshes, alluvial forests, fens, and *Sphagnum* mats (Lammers and Van Der Valk, 1978). The bryophytes all are characteristic of marshes and/or rich mires. In general, the species present are typical of southeastern Iowa wetlands (Lammers and Van Der Valk, 1977, 1978), although a few rare species like *Menyanthes trifoliata* (buckbean) and the bryophyte, *Calliergonella cuspidata,* are at or near the southern limit of their range.

The forest along the edge of Nichols Marsh is typical of Iowa floodplain and valley-margin forests, with *Betula nigra, Acer saccharinum* (silver maple), *A. negundo* (boxelder), *Ulmus americana* (American elm), *Robinia pseudoacacia* (black locust), *Morus rubra* (red mulberry), *Quercus alba* (white oak), *Q. marcrocarpa* (bur oak), *Q. palustris* (swamp white oak), and scattered *Carya cordiformis* (bitternut hickory) and *Fraxinus pennsylvanica* (green ash).

The pollen percentage diagram for site 1 is plotted on Fig. 2; the pollen concentration diagram (grains/cc of sediment) is plotted on Fig. 3. Percentages mentioned below refer to the light outer curves on Fig. 2 in which grass is removed from the pollen sum (see Methods). Zone P-4 (326 to 190 cm) is defined by high Gramineae (= Poaceae; grass) pollen percentages and concentrations (up to 90% and 295,000 grns/cm^3, respectively), and low percentages of Cyperaceae (sedges) and Other Tubuliflorae (Compositae or Asteraceae). Minor peaks of *Salix* (willow) and *Pediastrum* (a green alga) also are present. Arboreal pollen (AP) generally is above 70%, and the trees with low but consistent pollen percentages include *Pinus* (pine) *Betula, Fraxinus, Platanus* (sycamore), *Ulmus,* and *Carya.* This zone ranges in age from about 2550 to 1260 yr B.P. (see Methods).

Zone P-3 (190-140 cm) is characterized by continuing high percentages and concentrations of Gramineae pollen, increasing percentages and concentrations of Other Tubuliflorae and Cyperaceae, and a maximum in *Sagittaria* (arrowhead) pollen percentages. Arboreal pollen concentration drops from about 14,000 to about 10,000 grn/cm^3 at the base of the zone, but percentages of tree pollen remain at about the same levels as below. This zone ranges in age from about 1260 to 930 yr B.P.

Zone P-2 (140 to 30 cm) is defined by a decline in Gramineae pollen percentages to low levels, coupled with a rise in Other Tubuliforae and Cyperaceae pollen percentages and concentrations to their highest levels. Arboreal pollen declines, generally to less than 70%, and the individual tree taxa mentioned above continue at low percentages. This zone dates from 930 yr B.P. to the time of cultivation by European settlers in the mid-1800's.

Zone P-1 (0 to 30 cm) is defined by the widespread *Ambrosia* (ragweed) peak, recognized throughout much of central United States as a post-settlement phenomenon caused by invasion of weeds on disturbed and cultivated soil. In addition, prominent peaks in *Typha*

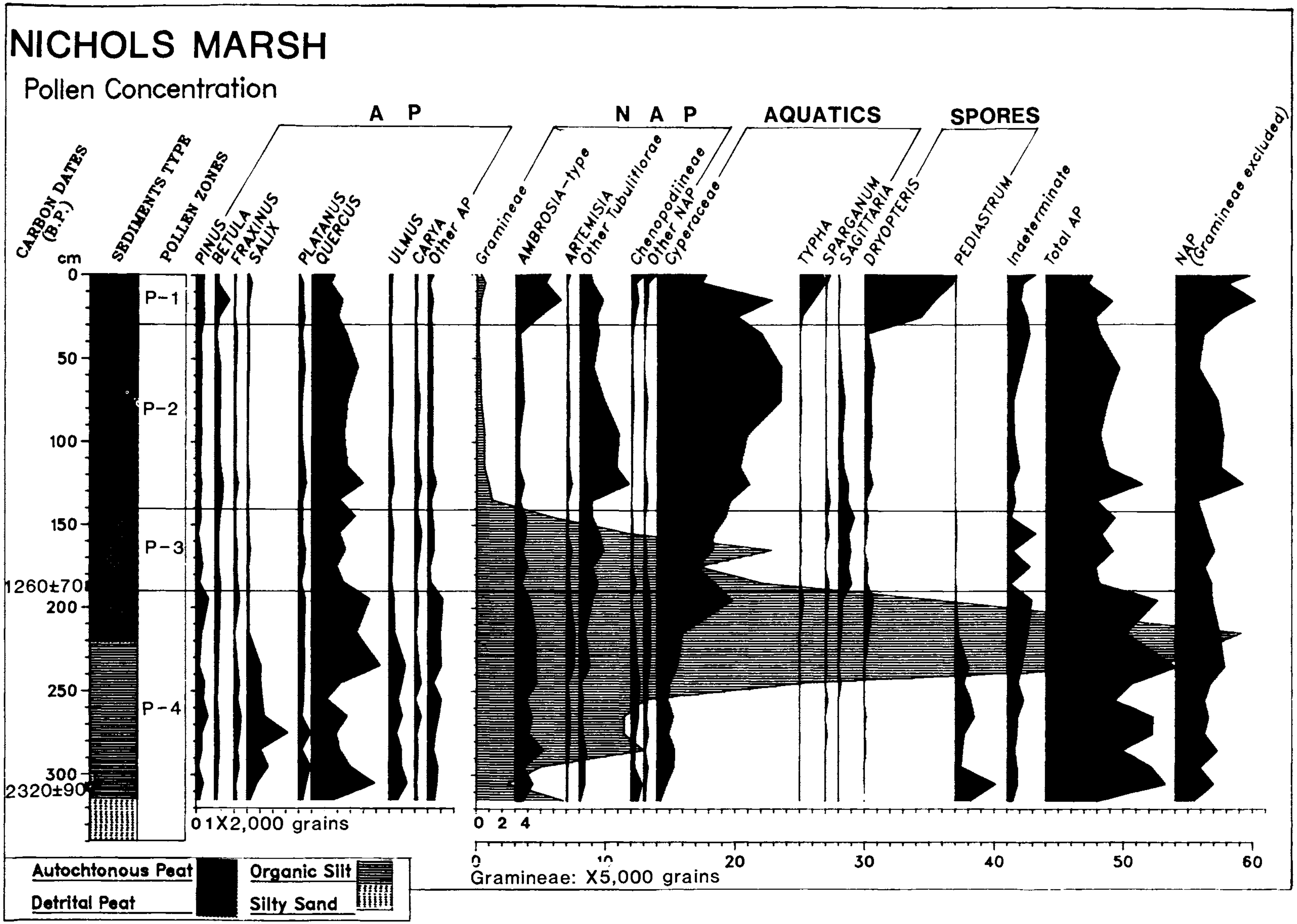

Figure 3. Pollen concentration diagram from Site 1, Nichols Marsh. Gramineae curve is shaded to show overlap across other curves.

pollen and *Dryopteris*-type (probably *Thelypteris palustris*, marsh fern) spores occur in this zone. This zone ranges in age from about 1845 to the present.

The results of the analyses of plant macrofossils from site 2 are shown in Table 2. Zone M-5 (326 to 240 cm) is characterized by aquatic taxa such as *Potamogeton amplifolius* (pondweed), *P. foliosus* (pondweed), *Najas flexilis* (naiad), *Myriophyllum* sp. (water milfoil), *Ceratophyllum demersum* (coontail), *Ranunculus aquatilis* (water crowfoot), and *Zizania aquatica* (wild rice), along with charophytes, aquatic molluscs, fish scales, and ostracodes. Other taxa present, including *Leersia oryzoides*, *Sagittaria cuneata* and the mosses, *Drepanocladus aduncus* and *Amblystegium serpens*, generally grow on moist substrates, but they will tolerate standing water or soils that change seasonally from wet to dry. Such plants are classified here as dampground perennials (Table 2). A few weedy annuals (disturbed-ground plants), such as *Amaranthus* (amaranth) and *Chenopodium* (goosefoot), also are present. The total number of specimens of vascular plant and bryophyte macrofossils in this zone is low (mean = 11/level, range = 6-21), and diversity is also low (mean = 6 taxa/level). This zone represents the time from 2550 yr B.P. (extrapolated from site 1) to about 1685 (interpolated from site 1) yr B.P. (see Methods).

In zone M-4 (240 to 210 cm), most aquatic plant taxa decline in importance, but *Zizania aquatica* and *Najas flexilis* continue to be prominent, and *Nymphaea* sp. (white water lily) appears for the first time. Dampground perennial species become more common and more diverse. The most abundant of these are *Carex comosa*, *Carex* with trigonous achenes but no perigynia (also possibly *C. comosa*), *Eleocharis palustris* (including *E. calva*) (spikerush), *Leersia oryzoides*, *Sagittaria latifolia* and *Scirpus validus* (including *S. acutus*) (bullrush). Some weedy species of vascular plants also are present, especially *Bidens cernua* and *Pilea pumila*. The first prairie species, *Lespedeza capitata* (bush clover) appears as well. Although the species of mosses, *Drepanocladus aduncus* and *Amblystegium serpens*, are the same in zone 4 as in zone 5, there is an increase in abundance of *Drepanocladus* in zone 4. The total number of specimens in this zone increases dramatically (mean = 114/level, range = 58-178), as does diversity (mean = 18 taxa/level). Zone M-4 represents the time from about 1685 yr B.P. to about 1410 yr B.P. (interpolated from site 1).

In zone M-3 (210 to 151 cm), seeds of weedy annual plants become common, and a diverse vascular-plant flora is present (Table 2). For example, *Bidens cernua* and *Pilea pumila* become more abundant, and *Amaranthus albus*, species of *Cyperus* (umbrella-sedge) and *Polygonum* are present at several levels. Although they are not dominant in the flora, weedy taxa reach an early peak in diversity and abundance in this zone. Dampground perennials continue to dominate in abundance of seeds, and *Carex* spp., *Eleocharis palustris*, and *Scirpus validus* along with *Leersia oryzoides*, *Panicum* (switchgrass) species and *Zizania aquatica* make this a sedge-grass dominated assemblage. However, the diversity of other dampground perennials is high. Among the bryophytes, *Drepanocladus* is most abundant in this zone, indicating that marshy conditions predominate. However, *Calliergonella cuspidata*, an indicator of rich mire conditions, also is present for the first time. The occurrence of *Dulichium arundinaceum* in this zone demonstrates that other elements of rich mire vegetation also are present. Aquatic taxa are absent at the top of this zone, and prairie species, such as *Amorpha* sp. (not *A. fruticosa*), *Petalostemum candidum* (white prairie clover), and *Rudbeckia* cf. *hirta* (brown-eyed susan) occur sparsely, and

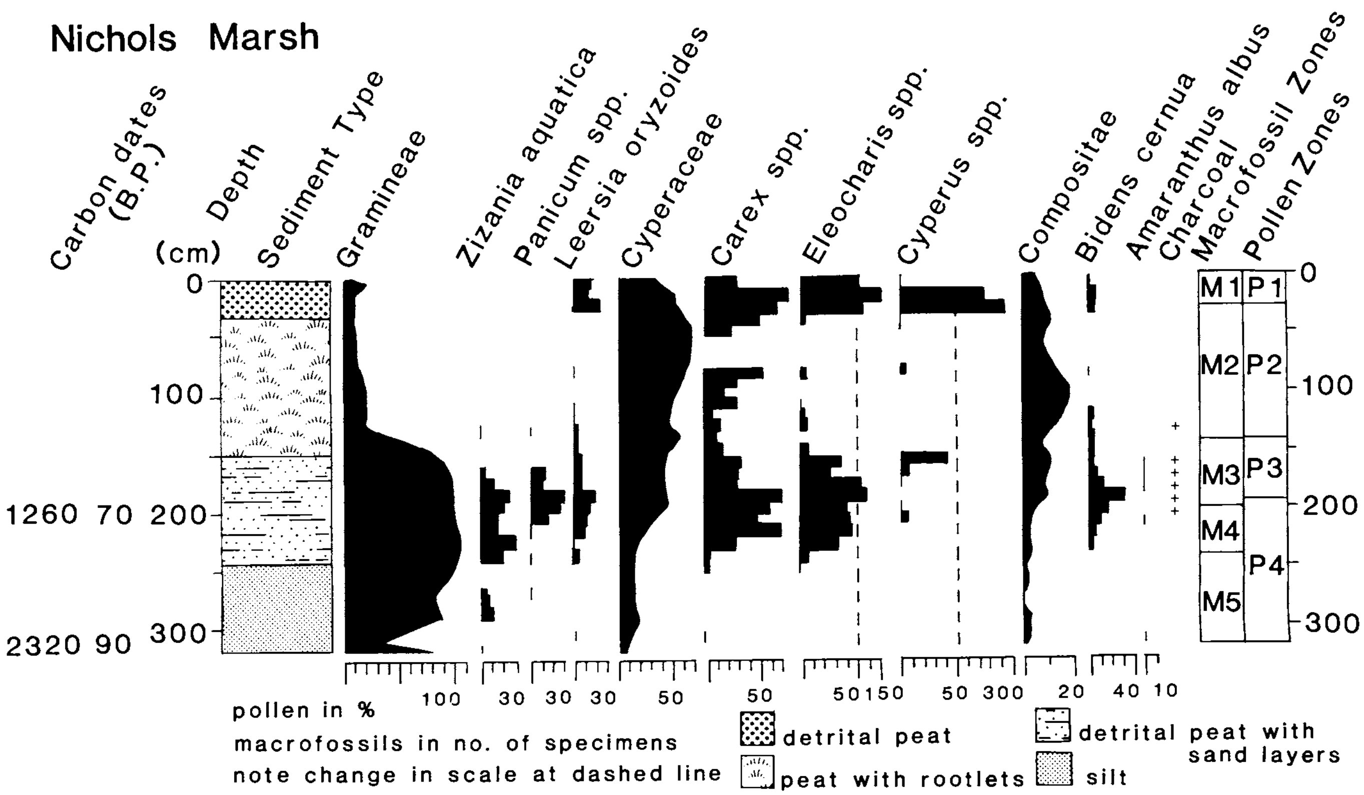

Figure 4. Comparison of selected pollen and plant macrofossil curves from Nichols Marsh. Curves represent percentages; bars represent numbers of plant macrofossil specimens.

Table 1. List of plants identified from the vicinity of Nichols Marsh (modern flora by DMR and WPP), and as fossils from the sediments (by RGB).

w = wetland, a = disturbed ground, f = forest, p = prairie, o = other or widespread, s = pollen or spore identification only	In Modern Habitat	In Modern Flora	In Fossil Flora, by Zone: Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
HEPATICOPHYTA							
ANEURACEAE							
Aneura pinguis (L.) Dumort.	w	x	-	-	-	-	-
RICCIACEAE							
Riccia fluitans L.	w	x	-	-	-	-	-
BRYOPHYTA							
AMBLYSTEGIACEAE							
Amblystegium riparium (Hedw.) BSG	w	x	-	-	-	-	-
A. serpens (Hedw.) BSG	w	x	x	-	x	x	x
A. trichopodium (Schultz) Hartm.	w	x	-	-	-	-	-
Calliergon sp.	w	-	-	x	-	-	-
Calliergonella cuspidata (Hedw.) Loeske	w	x	-	x	x	-	-
Campylium chrysophyllum (Brid.) J. Lange	w	x	-	-	-	-	-
C. radicale (P. -Beauv.) Grout	w	x	-	-	-	-	-
Drepanocladus aduncus (Hedw.) Warnst.	w	-	x	x	x	x	x
BRACHYTHECIECEAE							
Brachythecium cf. *mildeanum* (Schimp.) Schimp. ex Milde	w	-	-	x	-	-	-
B. sp.	w?	-	-	x	-	-	-
BRYACEAE							
Leptobryum pyriforme (Hedw.) Wils.	w	x	-	-	-	-	-
Plagiomnium cuspidatum (Hedw.) T. Kop.	f	x	-	-	-	-	-
P. ellipticum (Hedw.) T. Kop.	w	x	-	-	-	-	-
HYPNACEAE							
Hypnum lindbergii Mitt.	w	x	-	-	-	-	-
MEESIACEAE							
Meesia triquetra (L. ex Richt.) Angstr.	w	-	x	x	-	-	-
THUIDIACEAE							
Helodium blandowii (Web. & Mohr) Warnst. var. *elodioides* (Ren. & Card. ex. Roell.) Crum, Steere & Anderson	w	x	-	-	-	-	-
EQUISETOPHYTA							
EQUISETACEAE (Horsetail Family)							
Equisetum arvense L.	o	x	-	-	-	-	-
E. hyemale L.	o	x	-	-	-	-	-
E. sp.	o	-	x	-	-	-	-
POLYPODIOPHYTA							
ADIANTACEAE (Maidenhair Fern Family)							
Adiantum pedatum L.	f	x	-	-	-	-	-
ASPLENIACEAE							
Asplenium platyneuron (L.) Oakes ex. D.C. Eaton	f	x	-	-	-	-	-
Athryium angustum (Willd.) Presl.	f	x	-	-	-	-	-
A. thelypterioides (Michx.) Desv.	f	x	-	-	-	-	-
Cystopteris bulbifera (L.) Bernh.	f	x	-	-	-	-	-
C. protrusa (Weath.) Blasdell	f	x	-	-	-	-	-
Dryopteris cristata (L.) Gray	f	x	-	-	-	-	-
Onoclea sensibilis L.	w	x	-	-	-	-	-
AZOLLACEAE							
Azolla mexicana Presl.	w	x	-	-	-	-	-
DENSTAEDTIACEAE							
Pteridium aquilinum (L.) Kuhn	f	x	-	-	-	-	-
OPHIOGLOSSACEAE (Adder's-tongue Fern Family)							
Botrychium dissectum Spreng. var. *dissectum*	f	x	-	-	-	-	-
B. dissectum Spreng. var. *obliquum* (Muhl.) Clute	f	x	-	-	-	-	-
B. virginianum (L.) Sw.	f	x	-	-	-	-	-

Table 1 Continued

OSMUNDACEAE							
Osmunda regalis L.	w	x	-	-	-	-	-
THELYPTERIDACEAE							
Thelypteris palustris Schott	w	x	-	-	-	-	-
PINOPHYTA							
CUPRESSACEAE (Cypress Family)							
Juniperus virginiana L.	f	x	-	-	-	-	-
MAGNOLIOPHYTA: LILIATAE							
ALISMATACEAE (Water Plantain Family)							
Alisma plantago-aquatica L. var. *parviflorum* Schult.	w	x	-	-	-	x	x
Sagittaria cuneata Sheld.	w	-	-	-	-	-	x
S. latifolia Willd.	w	x	x	x	x	x	-
ARACEAE (Arum Family)							
Acorus calamus L.	w	x	-	-	-	-	-
COMMELINACEAE (Spiderwort Family)							
Commelina communis L.	a	x	-	-	-	-	-
Tradescantia bracteata Small	p	x	-	-	-	-	-
T. ohioensis Raf.	o	x	-	-	-	-	-
T. virginiana L.	o	x	-	-	-	-	-
CYPERACEAE (Sedge Family)							
Carex atherodes Spreng.	w	x	-	-	-	-	-
C. comosa Boott.	w	-	-	-	x	x	-
C. grayii Carey	f	x	-	-	-	-	-
C. hystericina Muhl.	w	x	x	x	x	x	-
C. lacustris Willd.	w	x	x	x	-	-	-
C. lasiocarpa Ehrh. var. *americana* Fern.	w	x	x	x	x	-	-
C. prairea Dew.	w	-	x	x	x	-	-
C. stricta Lam	w	x	-	-	-	-	-
C. vulpinoidea Michx.	w	x	-	-	-	-	-
C. spp. (biconvex)	w	-	x	x	x	x	x
C. spp. (trigonous)	w	-	x	x	x	x	x
Cyperus acuminatus Torr. & Hook.	w	-	-	-	x	-	-
C. diandrus Torr.	w	x	x	x	x	-	-
C. engelmanni Steud.	w	-	x	x	x	-	-
C. erythrorhizos Muhl.	w	x	-	-	-	-	-
C. esculentus L.	w	x	-	-	-	-	-
C. filiculmis Vahl.	o	x	-	-	-	-	-
C. odoratus L.	w	-	x	-	-	-	-
C. schweinitzii Torr.	o	x	-	-	-	-	-
C. strigosus L.	w	x	-	-	-	-	-
C. sp.	w	-	x	-	-	-	x
Dulichium arundinaceum (L.) Britton	w	x	-	-	x	-	-
Eleocharis acicularis (L.) R.&S.	w	x	-	-	-	-	-
E. palustris (L.) R.&.S.	w	-	x	x	x	x	x
E. tenuis (Willd.) Schult.	w	-	x	x	x	-	-
Scirpus atrovirens Willd.	w	x	-	-	-	-	-
S. cyperinus L.	w	x	-	-	-	-	-
S. fluviatilis (Torr.) Gray	w	x	-	-	-	-	-
S. validus Vahl. var. *creber* Fern.	w	x	x	x	x	x	x
IRIDACEAE (Iris Family)							
Iris schrevei Small	w	x	-	-	-	-	-
Sisyrinchium campestre Bickn.	o	x	-	-	-	-	-
JUNCAECEAE (Rush Family)							
Juncus acuminatus Michx.	w	x	-	-	-	-	-
J. dudleyi Wiegand	w	x	-	-	-	-	-
J. effusus L.	w	x	-	-	-	-	-
J. interior Wieg.	o	x	-	-	-	-	-
J. nodosus L.	w	x	-	-	-	-	-
J. tenuis Willd.	a	x	-	-	-	-	-

Table 1 Continued

J. torreyi Cov.	w	x	-	-	-	-	-
J. sp.	w?	-	-	x	-	-	-
LEMNACEAE (Duckweed Family)							
Lemna minor L.	w	x	-	-	-	-	-
Spirodela polyrhiza (L.) Schleiden	w	x	-	-	-	-	-
LILIACEAE (Lily Family)							
Allium canadense L.	f,p	x	-	-	-	-	-
Asparagus officinalis L.	a	x	-	-	-	-	-
Erythronium albidum L.	f	x	-	-	-	-	-
Polygonatum biflorum (Walter) Ell.	f	x	-	-	-	-	-
Smilacina racemosa (L.) Desf.	f	x	-	-	-	-	-
Smilax ecirrhata (Engelm. ex Kunth) S. Watson	f	x	-	-	-	-	-
S. herbacea L.	f	x	-	-	-	-	-
S. hispida Muhl.	f	x	-	-	-	-	-
Uvularia sessilifolia L.	f	x	-	-	-	-	-
NAJADACEAE (Pondweed Family)							
Najas flexilis (Willd.) R.&S.	w	-	-	-	x	x	x
Potamogeton amplifolius Tuckerm.	w	-	-	-	-	-	x
P. foliosus Raf.	w	-	-	-	x	-	x
POACEAE (Gramineae; Grass Family)							
Agropyron repens (L.) Beauv.	a	x	-	-	-	-	-
A. gigantea Roth	o	x	-	-	-	-	-
A. hyemalis (Walter) BSP	o	x	-	-	-	-	-
A. perennans (Walter) Tuckerman	o	x	-	-	-	-	-
A. smithii Rydb.	o	x	-	-	-	-	-
A. trachycaulum (Link) Malte	o	x	-	-	-	-	-
Andropogon gerardii Vitman	p	x	-	-	-	-	-
Aristida basiramea Engelm. ex Vasey	o	x	-	-	-	-	-
A. dichotoma Michx.	o	x	-	-	-	-	-
A. oligantha Michx.	o	x	-	-	-	-	-
A. tuberculosa Nutt.	o	x	-	-	-	-	-
Avena sativa L.	a	x	-	-	-	-	-
Bouteloua curtipendula (Michx.) Torrey	p	x	-	-	-	-	-
Brachyelectrum erectum (Schreb.) Beauv.	o	x	-	-	-	-	-
Bromus ciliatus L.	o	x	-	-	-	-	-
B. commutatus Schrader	a	x	-	-	-	-	-
B. inermus Leysser	a	x	-	-	-	-	-
B. japonicus Thunb. ex Murray	a	x	-	-	-	-	-
Bromus kalmii Gray	o	x	-	-	-	-	-
B. latiglumis (Shear) Hitchc.	o	x	-	-	-	-	-
B. pubescens Muhl. ex Willd.	o	x	-	-	-	-	-
B. secalinus L.	a	x	-	-	-	-	-
B. tectorum L.	a	x	-	-	-	-	-
Calamagrostis canadensis (Michx.) Beauv.	w	x	-	-	-	-	-
Calamovilfa longifolia (Hooker) Schribn.	p	x	-	-	-	-	-
Cenchrus longispinus (Hackel) Fern.	a	x	-	-	-	-	-
Cinna arundinacea L.	o	x	-	-	-	-	-
Dactylis glomerata L.	a	x	-	-	-	-	-
Danthonia spicata (L.) Beauv. ex R.&S.	o	x	-	-	-	-	-
Diarrhena americana Beauv.	o	a	-	-	-	-	-
Digitaria sanguinalis (L.) Scop.	a	x	-	-	-	-	-
Echinochloa crusgalli (L.) Beauv.	a	x	-	-	-	-	-
Elusine indica (L.) Gaertn.	a	x	-	-	-	-	-
Elymus canadensis L.	p	x	-	-	-	-	-
E. villosus Muhl. ex Willd.	o	x	-	-	-	-	-
E. virginicus L.	o	x	-	-	-	-	-
Festuca octoflora Walter var. *tenella* (Willd.) Fern.	o	x	-	-	-	-	-
Glyceria striata (Lam.) Hitchc.	w	x	-	-	-	-	-
Hordeum jubatum L.	a	x	-	-	-	-	-
H. pusillum Nutt.	o	x	-	-	-	-	-
H. vulgare L.	a	x	-	-	-	-	-
Hystrix patula Moench	a	x	-	-	-	-	-

Table 1 Continued

Koeleria micrantha (Ledeb) Schultes	o	x	-	-	-	-	-
Leersia oryzoides (L.) Sw.	w	x	x	x	x	x	x
Leptoloma cognatum (Schult.) Chase	o	x	-	-	-	-	-
Melica nitens (Scribn.) Nutt.	o	x	-	-	-	-	-
Miscanthus sacchariflorus (Maxim.) Haeckel	a	x	-	-	-	-	-
Muhlenbergia frondosa (Poiret) Fern.	o	x	-	-	-	-	-
M. glomerata (Willd.) Trin.	w	x	-	-	-	-	-
M. schreberi J.F. Gmelin.	w	x	-	-	-	-	-
Oryzopsis racemosa (Smith) Ricker	o	x	-	-	-	-	-
Panicum capillare L.	o	x	-	-	-	-	-
P. dichotomiflorum Michx.	o	x	-	-	-	-	-
P. virgatum L.	o	x	-	-	-	-	-
P. sp. (large)	w?	-	-	-	x	x	-
P. sp. (small)	w?	-	-	x	x	x	x
Paspalum setaceum Michx. var. *stramineum* (Nash) D. Banks	o	x	-	-	-	-	-
Poa compressa L.	o	x	-	-	-	-	-
P. pratensis L.	o	x	-	-	-	-	-
Phalaris arundinacea L.	w	x	-	-	-	-	-
Phleum pratense L.	a	x	-	-	-	-	-
Schizachrium scoparium (Michx.) Nash	p	x	-	-	-	-	-
Setaria glauca (L.) Beauv.	a	x	-	-	-	-	-
S. viridis (L.) Beauv.	a	x	-	-	-	-	-
Spartina pectinata Link	w	x	-	-	-	-	-
Sporobolus asper (Michx.) Kunth	o	x	-	-	-	-	-
S. cryptandrus (Torr.) A. Gray	o	x	-	-	-	-	-
Stipa spartea Trin.	p	x	-	-	-	-	-
Tridens flavus (L.) Hitch.	o	x	-	-	-	-	-
Triplasis purpurea (Walt.) Chapm.	o	x	-	-	-	-	-
Zizania aquatica L.	w	-	-	x	x	x	x
Other Gramineae	w?	-	x	x	x	x	x
PONTEDERIACEAE (Pickerelweed Family)							
Pontederia cordata L.	w	x	-	-	-	-	-
TYPHACEAE (Cattail Family)							
Typha latifolia L.	w	x	-	-	-	-	-
T. x *glauca* Godron	w	x	-	-	-	-	-
T. sp.	w	-	x	x	x	-	-
MAGNOLIOPHYTA: MAGNOLIATAE							
ACANTHACEAE							
Ruellia humilis Nutt.	p,f	x	-	-	-	-	-
ACERACEAE (Maple Family)							
Acer negundo L.	f	x	-	-	-	-	-
A. saccharinum L.	f	x	-	-	-	-	-
AIZOACEAE (Carpetweed Family)							
Mollugo verticillata L.	a	x	x	-	x	x	-
AMARANTHACEAE (Amaranth Family)							
Amaranthus albus L.	a	x	-	-	x	-	x
A. graecizans L.	a	x	-	-	-	-	-
A. retroflexus L.	a	x	-	-	-	-	-
ANACARDIACEAE (Cashew Family)							
Rhus aromatica Ait.	o	x	-	-	-	-	-
Rhus glabra L.	o	x	-	-	-	-	-
Toxicodendron radicans (L.) O. Ktze ssp. *negundo* (Greene) Gillis	o	x	-	-	-	-	-
APIACEAE (Umbelliferae; Parsley Family)							
Cicuta bulbifera L.	w	x	-	-	-	-	-
C. maculata L.	w	x	-	-	-	-	-
Conium maculatum L.	w	x	-	-	-	-	-
Daucus carota L.	a	x	-	-	-	-	-
Osmorrhiza claytonii (Michx.) Clarke	f	x	-	-	-	-	-
Oxypolis rigidior (L.) Raf.	w	x	-	-	-	-	-
Pastinaca sativa L.	a	x	-	-	-	-	-

Table 1 Continued

Sanicula gregaria Bickn.	f	x	-	-	-	-	-
Torilis arvensis (Hudson) Link	o	x	-	-	-	-	-
Sium suave Walt.	w	-	-	-	x	x	-
APOCYNACEAE (Dogbane Family)							
Apocynum sibiricum Jacq.	a	x	-	-	-	-	-
ARISTOLOCHIACEAE (Birthwort Family)							
Asarum canadense L.	f	x	-	-	-	-	-
ASCLEPIADACEAE (Milkweed Family)							
Asclepias incarnata L.	w	x	-	-	-	-	-
A. syriaca L.	a	x	-	-	-	-	-
A. verticillata L.	a	x	-	-	-	-	-
Cynanchum laeve (Michx.) Pers.	o	x	-	-	-	-	-
ASTERACEAE (Aster Family)							
Achillea millefolium L.	a	x	-	-	-	-	-
Ambrosia artemisiifolia L.	a	x	-	-	-	-	-
A. psilostachya DC.	a	x	-	-	-	-	-
A. trifida L.	a	x	-	-	-	-	-
Antennaria plantaginifolia (L.) Richardson	f	x	-	-	-	-	-
Artemisia ludoviciana Nutt.	p	x	-	-	-	-	-
Aster azureus Lindley	o	x	-	-	-	-	-
A. cordifolius L.	o	x	-	-	-	-	-
A. ericoides L.	o	x	-	-	-	-	-
A. laevis L.	o	x	-	-	-	-	-
A. lateriflorus (L.) Britton	w	x	-	-	-	-	-
A. novae-angliae L.	w	x	-	-	-	-	-
A. ontarionis Wiegand	w	x	-	-	-	-	-
A. prealtus Poir.	w	x	-	-	-	-	-
A. simplex Willd.	w	x	-	-	-	-	-
A. sp.	w?	-	x	-	x	x	-
Bidens cernua L.	w	x	x	x	x	x	-
B. comosa (Gray) Wiegand	w	x	-	-	-	-	-
B. connata Muhl.	w	x	-	-	-	-	-
B. vulgata Greene	w	x	-	x	-	x	-
Boltonia asteroides (L.) L'Her	w	x	-	-	-	-	-
Cacalia atriplicifolia L.	p	x	-	-	-	-	-
Cichorium intybus L.	a	x	-	-	-	-	-
Cirsium altissimum (L.) Spreng.	o	x	-	-	-	-	-
C. arvense L.	a	x	-	-	-	-	-
C. discolor (Muhl.) Spreng.	o	x	-	-	-	-	-
C. vulgare (Savi.) Tenore	a	x	-	-	-	-	-
Coreopsis palmata Nutt.	p	x	-	-	-	-	-
Erigeron annuus (L.) Pers.	o	x	-	-	-	-	-
E. strigosus Muhl.	o	x	-	-	-	-	-
Eupatorium perfoliatum L.	w	x	x	x	x	-	-
E. purpureum L.	f	x	-	-	-	-	-
E. rugosum Houtt.	f	x	-	-	-	-	-
Gnaphalium obtusifolium L.	o	x	-	-	-	-	-
Helenium autumnale L.	w	x	-	-	-	-	-
Helianthus grosseserratus Martens	p	x	-	-	-	-	-
H. tuberosus L.	a	x	-	-	-	-	-
H. sp.	w?	-	x	-	-	-	-
Heliopsis helianthoides (L.) Sweet	o	x	-	-	-	-	-
Kuhnia eupatorioides L.	o	x	-	-	-	-	-
Lactuca canadensis L.	a	x	-	-	-	-	-
L. floridana (L.) Gaert.	a	x	-	-	-	-	-
Rudbeckia cf. hirta L.	p	x	-	-	x	-	-
R. laciniata L.	f	x	-	-	-	-	-
R. triloba L.	f	x	-	-	-	-	-
Silphium perfoliatum L.	w,p	x	-	-	-	-	-
Solidago canadensis L.	o	x	-	-	-	-	-
S. flexicaulis L.	o	x	-	-	-	-	-

Table 1 Continued

S. graminifolia (L.) Salisb.	w	x	-	-	-	-	-
S. nemoralis Aiton	o	x	-	-	-	-	-
Taraxacum officinale Weber	a	x	-	-	-	-	-
Tragopogon dubius Scop.	a	x	-	-	-	-	-
Vernonia baldwinii Torr.	p	x	-	-	-	-	-
Xanthium strumarium L.	a	x	-	-	-	-	-
Other Compositae	o?	-	x	x	x	x	x
BALSAMINACEAE (Touch-me-not Family)							
Impatiens capensis Meerb.	w	x	x	-	x	-	-
I. pallida Nutt.	w	x	x	x	-	-	-
BERBERIDACEAE (Barberry Family)							
Podophyllum peltatum L.	f	x	-	-	-	-	-
BETULACEAE (Birch Family)							
Betula nigra L.	f	x	x	x	x	-	x
Ostrya virginiana (Miller) K. Koch	f	x	-	-	-	-	-
BORAGINACEAE (Borage Family)							
Hackelia virginiana (L.) Johnston	o	x	-	-	-	-	-
Lithospermum canescens (Michx.) Lehm.	o	x	-	-	-	-	-
BRASSICACEAE (Cruciferae; Mustard Family)							
Brassica nigra (L.) K. Koch	a	x	-	-	-	-	-
Capsella bursa-pastoris (L.) Medicus	a	x	-	-	-	-	-
Cardamine bulbosa (Schred.) BSP	w	x	x	-	x	-	-
C. douglassii (Torrey) Britton	w	x	-	-	-	-	-
Iodanthus pinnatifidus (Michx.) Steudel	w	x	-	-	-	-	-
Lepidium campestre (L.) R. Br.	a	x	-	-	-	-	-
L. densiflorum Schrader	a	x	-	-	-	-	-
CAMPANULACEAE (Bellflower Family)							
Campanula americana L.	o	x	-	-	-	-	-
C. aparinoides Pursh	w	x	-	x	x	-	-
Lobelia cardinalis L.	o	x	-	-	-	-	-
L. inflata L.	o	x	-	-	-	-	-
L. siphilitica L.	o	x	-	-	-	-	-
Triodanis perfoliata (L.) Nieuwl.	o	x	-	-	-	-	-
CAPPARIDACEAE (Caper Family)							
Polanisia dodecandra (L.) DC.	a	-	x	-	-	-	-
CAPRIFOLIACEAE (Honeysuckle Family)							
Diervilla lonicera Miller	o	x	-	-	-	-	-
Sambucus canadensis L.	o	x	x	-	-	-	-
CARYOPHYLLACEAE (Pink Family)							
Dianthus armeria L.	a	x	-	-	-	-	-
Saponaria officinalis L.	a	x	-	-	-	-	-
Silene antirrhina L.	o	x	-	-	-	-	-
Stellaria media (L.) Cyrillo	a,w	x	-	-	-	-	-
CELASTRACEAE (Staff-tree Family)							
Celastrus scandens L.	o	x	-	-	-	-	-
CHENOPODIACEAE (Goosefoot Family)							
Chenopodium album L.	a	x	-	-	-	-	-
C. cf. *bushianum* Aellen	a	-	x	x	x	-	x
Cycloloma atriplicifolium (Sprengel) Coulter	a	x	-	-	-	-	-
CISTACEAE (Rock-rose Family)							
Helianthemum bicknellii Fern.	o	x	-	-	-	-	-
CONVOLVULACEAE (Morning-glory Family)							
Convolvulus sepium L.	a	x	-	-	-	-	-
Cuscuta gronovii Willd.	?	x	-	-	-	-	-
Ipomoea hederaceae (L.) Jacq.	a	x	-	-	-	-	-
CORNACEAE (Dogwood Family)							
Cornus drummondii Meyer	o	x	-	-	-	-	-
C. stolonifera Michx.	w	x	-	-	-	-	-

Table 1 Continued

CUCURBITACEAE (Gourd Family)							
Echinocystis lobata (Michx.) T. & G.	o	x	-	-	-	-	-
Sicyos angulatus L.	o	x	-	-	-	-	-
ELAEAGNACEAE (Oleaster Family)							
Elaeagnus angustifolia L.	a	x	-	-	-	-	-
EUPHORBIACEAE (Spurge Family)							
Acalypha gracilens Gray.	a	x	-	-	-	-	-
A. virginica L.	o	x	-	-	-	-	-
Croton glandulosus L. var. *septentrionalis* Mueller-Arg.	o	x	-	-	-	-	-
Euphorbia corollata L.	p	x	-	-	-	-	-
E. dentata Michx.	a	x	-	-	-	-	-
E. maculata L.	a	x	-	-	x	-	-
FABACEAE (Leguminosae; Bean Family)							
Amorpha fruticosa L.	w	x	-	-	-	-	-
Amorpha sp. (not *A. fruticosa*)	p?	-	-	-	x	-	-
Amphicarpa bracteata (L.) Fern.	w	x	-	-	-	-	-
Apios americana Medicus	w	x	-	-	-	-	-
Cassia marilandica L.	o	x	-	-	-	-	-
Cercis canadensis L.	f	x	-	-	-	-	-
Desmodium illinoense Gray	o	x	-	-	-	-	-
Desmodium sp.	?	x	-	-	-	-	-
Gleditsia triacanthos L.	f	x	-	-	-	-	-
Gymnocladus dioica (L.) K. Koch	f	x	-	-	-	-	-
Lathyrus palustris L.	w	x	-	-	-	-	-
Lespedeza capitata Michx.	p	x	-	-	x	-	-
Medicago lupulina L.	a	x	-	-	-	-	-
M. sativa L.	a	x	-	-	-	-	-
Melilotis alba Medicus	a	x	-	-	-	-	-
M. officinalis (L.) Lam.	a	x	-	-	-	-	-
Petalostemum candidum (Willd.) Michx.	p	x	-	-	x	-	-
Robinia pseudoacacia L.	f	x	x	-	-	-	-
Trifolium pratense L.	a	x	-	-	-	-	-
T. repens L.	a	x	-	-	-	-	-
Vicia americana Muhl.	o	x	-	-	-	-	-
FAGACEAE (Beech Family)							
Quercus alba L.	f	x	-	-	-	-	-
Q. macrocarpa Michx.	f	x	-	-	-	-	-
Q. palustris Muench.	f	x	-	-	-	-	-
Q. sp.	f	-	-	-	x	-	-
GENTIANACEAE (Gentian Family)							
Gentiana andrewsii Griseb.	w	x	-	-	-	-	-
GERANIACEAE (Geranium Family)							
Geranium carolinianum L.	o	x	-	-	-	-	-
G. maculatum L.	f	x	-	-	-	-	-
HALORAGIDACEAE (Water-Milfoil Family)							
Myriophyllum L. *sp.*	w	-	-	-	-	-	x
HYDROPHYLLACEAE (Waterleaf Family)							
Hydrophyllum virginianum L.	f	x	-	-	-	-	-
HYPERICACEAE (St. John's-wort Family)							
Hypericum mutilum L.	w	x	-	-	-	-	-
H. perforatum L.	a	x	-	-	-	-	-
H. punctatum Lam.	o	x	-	-	-	-	-
H. sp.	w?	-	-	-	x	-	-
Triadenum fraseri (Spach.) Gl.	w	x	x	-	-	-	-
JUGLANDACEAE (Walnut Family)							
Carya cordiformis (Wang.) K. Koch	f	x	-	-	-	-	-
C. ovata (Mill.) K. Koch	f	x	-	-	-	-	-
Juglans nigra L.	f	x	-	-	-	-	-

Table 1 Continued

LAMIACEAE (Mint Family)							
Agastache nepetoides (L.) Kuntze	o	x	-	-	-	-	-
Lamium purpureum L.	o	x	-	-	-	-	-
Leonurus cardiaca L.	o	x	-	-	-	-	-
Lycopus americanus Muhl.	w	x	x	x	x	-	-
L. uniflorus Michx.	w	-	x	x	-	-	-
Monarda fistulosa L.	p	x	-	-	-	-	-
M. punctata L. var. *villicaulis* Pennell	p	x	-	-	-	-	-
Nepeta cataria L.	a	x	-	-	-	-	-
Physostegia parviflora Nutt. ex Gray	w	x	-	-	-	-	-
Prunella vulgaris L.	a	x	-	-	-	-	-
Pycnanthemum virginianum	p,w	-	-	-	x	-	-
Scutellaria lateriflora L.	w	x	x	x	-	-	-
Stachys palustris L.	w	x	-	-	x	-	-
S. tenuifolia Willd.	w	x	-	-	-	-	-
LYTHRACEAE (Loosestrife Family)							
Lythrum alatum Pursh.	w	x	-	-	-	-	-
MALVACEAE (Mallow Family)							
Hibiscus militaris Cav.	w	x	-	-	-	-	-
MENISPERMACEAE (Moonseed Family)							
Menisperum canadense L.	f	x	-	-	-	-	-
MENYANTHACEAE (Buckbean Family)							
Menyanthes trifoliata L.	w	x	-	x	-	-	-
MORACEAE (Mulberry Family)							
Cannabis sativa L.	a	x	x	-	-	-	-
Morus rubra L.	f	x	-	-	-	-	-
NYCTAGINACEAE (Four-o'clock Family)							
Mirabilis nyctaginea (Michx.) Macm.	o	x	-	-	-	-	-
NYMPHAEACEAE (Water Lily Family)							
Nymphaea L. sp.	w	-	-	-	x	x	-
OLEACEAE (Olive Family)							
Fraxinus americana L.	f	x	-	-	-	-	-
F. pennsylvanica Marsh	f	x	-	-	-	-	-
ONAGRACEAE (Evening Primrose Family)							
Epilobium coloratum Muhl.	w	-	-	-	-	-	-
E. cf. *coloratum* Muhl.	w	-	x	x	x	x	-
Gaura biennis L.	p	x	-	-	-	-	-
OXALIDACEAE (Wood-sorrel Family)							
Oxalis stricta L.	a	x	-	-	-	-	-
O. sp.	w?	-	-	-	x	-	-
PAPAVERACEAE (Bloodroot Family)							
Sanguinaria canadensis L.	f	x	-	-	-	-	-
PHRYMACEAE (Lopseed Family)							
Phryma leptostachya L.	x	-	-	-	-	-	-
PHYTOLACCACEAE (Pokeberry Family)							
Phytolacca americana L.	o	x	-	-	-	-	-
PLANTAGINACEAE (Plantain Family)							
Plantago lanceolata L.	a	x	-	-	-	-	-
P. major L.	a	x	-	-	-	-	-
P. patagonica Jacq.	p	x	-	-	-	-	-
P. rugelii Dcne.	a	x	-	-	-	-	-
PLATANACEAE (Plane-tree Family)							
Platanus occidentalis L.	f	-	-	-	x	x	-
POLEMONIACEAE (Phlox Family)							
Phlox divaricata L.	f	x	-	-	-	-	-
Polemonium reptans L.	f	x	-	-	-	-	-
POLYGALACEAE (Milkwort Family)							
Polygala L.	?	-	x	-	-	x	-

Table 1 Continued

POLYGONACEAE (Buckwheat Family)							
Polygonum lapathifolium L.	w,a	-	-	-	x	-	-
P. pensylvanicum L.	a	x	-	-	-	-	-
P. punctatum Ell.	w	x	x	x	x	x	x
Polygonum scandens L.	w	x	-	-	-	-	-
Rumex acetosella L.	a	x	-	-	-	-	-
R. crispus L.	a	x	-	-	-	-	-
R. orbiculatus Gray.	w	x	-	-	-	-	-
R. sp.	w?	-	x	-	x	-	-
PORTULACAEAE (Purslane Family)							
Portulaca oleracea L.	a	x	x	-	-	-	-
PRIMULACEAE (Primrose Family)							
Lysimachia ciliata L.	w	x	-	-	-	-	-
L. nummularia L.	w	x	-	-	-	-	-
L. terrestris (L.) BSP	w	x	-	-	-	-	-
L. thrysiflora L.	w	x	-	-	-	-	-
L. sp.	w?	-	-	-	x	-	-
RANUNCULACEAE (Crowfoot Family)							
Anemone canadensis L.	o	x	-	-	-	-	-
A. virginiana L.	o	x	-	-	-	-	-
Aquilegia canadensis L.	f	x	-	-	-	-	-
Ranunculus abortivus L.	o	x	-	-	-	-	-
Ranunculus aquatilis L.	w	-	-	-	-	-	x
ROSACEAE (Rose Family)							
Agrimonia sp.	?	x	-	-	-	-	-
Frageria virginiana Duche.	o	x	-	-	-	-	-
Geum laciniatum Murray	o	x	-	-	-	-	-
Potentilla norvegica L.	a	-	-	-	x	-	-
Prunus virginiana L.	o	x	-	-	-	-	-
Rosa multiflora Thunb. ex Murray	a	x	-	-	-	-	-
Rubus allegheniensis Porter ex Bailey	o	x	-	-	-	-	-
R. allegheniensis Porter	o	x	-	-	-	-	-
Spiraea alba Du Roi	w	x	-	-	-	-	-
RUBIACEAE (Madder Family)							
Cephalanthus occidentalis L.	w	x	-	-	-	-	-
RUTACEAE (Rue Family)							
Ptelea trifoliata L.	f	x	-	-	-	-	-
Xanthoxylum americanum P. Miller	f	x	-	-	-	-	-
SALICACEAE (Willow Family)							
Populus deltoides Bartram ex Marsh.	f	x	x	-	x	-	x
Salix discolor Muhl.	w	x	-	-	-	-	-
S. interior Rowlee	w	x	-	-	-	-	-
S. rigida Muhl.	w	x	-	-	-	-	-
S. sp.	w?	-	-	-	-	-	x
SAXIFRAGACEAE (Saxifrage Family)							
Penthorum sedoides L.	w	x	-	-	-	-	-
Ribes missouriense Nutt. ex T. & G.	o	x	-	-	-	-	-
SCROPHULARIACEAE (Figwort Family)							
Chelone glabra L.	w	x	-	-	-	-	-
Gerardia tenuifolia Vahl.	w	x	-	-	-	-	-
Mimulus glabratus HBK	w	x	-	-	-	-	-
Pedicularis lanceolata Michx.	w	x	-	-	-	-	-
Scrophularia lanceolata Pursh.	o	x	-	-	-	-	-
Verbascum thapsis L.	a	x	-	-	-	-	-
Veronicastrum virginicum (L.) Farw.	p	x	-	-	-	-	-
SOLANACEAE (Nightshade Family)							
Physalis virginiana P. Miller	o	x	-	-	-	-	-
Solanum americana P. Miller	o	x	-	-	-	-	-
S. dulcamara L.	o	x	-	-	-	-	-

Table 1 Continued

STAPHYLEACEAE (Bladdernut Family)								
Staphylea trifolia L.	f	x	-	-	-	-	-
TILIACEAE (Linden Family)								
Tilia americana L.	f	x	-	-	-	-	-
ULMACEAE (Elm Family)								
Celtis occidentalis L.	f	x	-	-	-	-	-
Ulmus americana L.	f	x	-	-	-	-	-
URTICACEAE (Nettle Family)								
Boehmeria cylindrica (L.) Sw.	w	x	x	x	x	-	-
Laportea canadensis (L.) Wedd.	w	x	-	-	-	-	-
Pilea fontana (Lunell) Rydb.	w	x	-	-	-	-	-
Pilea pumila (L.) Gray	w	x	x	x	x	x	-
Urtica dioica L.	w	x	-	-	x	-	-
VERBENACEAE (Vervain Family)								
Phyla lanceolata (Michx.) Greene	o	x	-	-	-	-	-
Verbena hastata L.	w	x	x	-	x	-	x
V. simplex Lehm.	o	x	x	-	-	-	-
V. stricta Vent.	p	x	-	-	-	-	-
V. urticifolia L.	o	x	-	-	-	-	-
VIOLACEAE (Violet Family)								
Viola sororia Willd.	o	x	-	-	-	-	-
V. sp.	w?	-	-	x	-	-	-
VITACEAE (Grape Family)								
Parthenocissus quinquefolia (L.) Planchon	f	x	-	-	-	-	-
Vitis riparia Michx.	o	x	-	-	-	-	-

are restricted mostly to this zone. Charred seeds and wood fragments are most common in zone M-3. Total macrofossil abundance is high (mean = 208/level, range = 123-315), and diversity increases (mean = 27 taxa/level). Zone M-3 spans a time from about 1410 to about 905 (interpolated from site 1).

Zone M-2 (151 to 30 cm) is characterized by a much lower abundance and diversity of the seed flora, and a contrasting increase in bryophyte abundance and diversity. Among the vascular plants, only *Carex* spp. and *Pilea pumila* remain abundant. Most other taxa of vascular plants that are present are dampground perennial plants. *Calliergonella* is the most abundant bryophyte, and another indicator of rich mire conditions, *Meesia triquetra,* also is present. *Drepanocladus* still is relatively abundant in this zone. Macrofossil abundance drops (mean = 66/level, range = 4-122), as does total diversity (mean = 13 taxa/level), although bryophyte diversity is at a maximum. The estimated time interval represented is from about 905 yr B.P. (1045 A.D.) to approximately 1845 A.D.

In zone M-1 (30 to 0 cm), diversity and abundance of seeds are at their maxima (mean = 519 specimens/level, range = 360-689; mean number of taxa = 31/level), and there is a marked decrease in diversity and abundance of bryophytes. Dampground perennials, including *Carex* spp. and *Eleocharis palustris,* return to dominance, and other taxa like *Cardamine bulbosa* (spring-cress), *Eupatorium perfoliatum* (boneset) and *Scutellaria lateriflora* (sideflower skullcap) becomes important for the first time. Weedy annual plants are at their peak, and *Cyperus diandrus, Impatiens capensis* (jewelweed), *Pilea pumila* and *Polygonum punctatum* are the most common. One of the indicator species for rich mire conditions, the moss, *Meesia triquetra,* still is present; however, *Calliergonella* is gone. The occurrence of *Drepanocladus* and *Amblystegium* suggests that marshy conditions are more prevalent than in zone M-2. Woody vegetation is well represented for the first time, as abundant fruits and catkin scales of *Betula nigra* are present, along with minimal representation of *Populus deltoides* (cottonwood), *Robinia pseudoacacia* and *Sambucus canadensis* (elderberry). This zone represents the time from about 1845 A.D. to the present.

DISCUSSION

Upland Vegetation

The upland vegetation in the vicinity of Nichols Marsh is deduced mainly from the pollen diagrams; however, macrofossil data provide critical information at certain levels. The lower two pollen zones (zones P-4 and P-3 on Figs. 2 and 3) with their very high percentages and concentrations of Gramineae present a problem in interpretation. The grass family is large and includes species that grow in a wide range of environments. High Gramineae percentages can be interpreted as representing prairie, especially when they are accompanied by high percentages of *Artemisia* (wormwood), *Ambrosia,* Other Tubuliflorae, and Chenopodiineae pollen. Such is not the case here. Direct comparison of pollen and macrofossil evidence shows that macrofossils of *Zizania aquatica* occur in the same interval as the grass pollen peaks (Fig. 4). These macrofossils are present at the base where grass pollen percentages are high, absent between 300 and 320 cm when grass pollen percentages drop, and present again rather consistently up to 160 cm where the last high peak in grass pollen occurs (Fig. 4). The absence of *Zizania* macrofossils between about 250 and 270 cm (Fig. 4) probably is not real, but rather represents samples picked in early stages of the study, before some of us recognized this taxon. We attribute the bulk of the grass pollen in this lower zone to *Zizania,* although the peak concentration (Fig. 3) may involve *Panicum* and *Leersia oryzoides* as well (Fig. 4). Macrofossils of *Panicum* and *Leersia* appear with *Zizania* from 210 to 160 cm, where the peak in grass pollen concentration occurs. However, the peak of *Leersia* macrofossils from 0 to 30 cm is accompanied by a relatively insignificant peak in grass pollen, so similar amounts of *Leersia* macrofossils lower in the section might not indicate a substantial contribution to the broad grass pollen peak. The species of *Panicum* cannot be identified, and their environmental significance is uncertain; some species of *Panicum* do occur in wetlands. *Leersia* is a semiaquatic grass that surely was a member of the marsh community. *Zizania* is often abundant in monospecific stands that have been shown to produce extremely high pollen percentages. In the late Holocene of northwestern Minnesota it

Table 2. Vascular-plant and bryophyte macrofossils, by zone and arranged by ecological type. - = absent, x = present (<5 picked in any 10-cm interval in the zone), o = common (5-49 in any interval), + = abundant (>50 in at least 1 interval). * = byrophytes.

Zone 5	Zone 4	Zone 3	Zone 2	Zone 1	Taxon	Ecological type
x	-	-	-	-	*Myriophyllum sp.*	Aquatics
x	x	o	-	-	*Najas flexilis*	
-	x	x	-	-	*Nymphaea sp.*	
x	-	-	-	-	*Potamogeton amplifolius*	
x	-	x	-	-	*Potamogeton foliosus*	
x	-	-	-	-	*Ranunculus aquatilis*	
o	o	o	x	-	*Zizania aquatica*	
x	x	-	-	-	*Alisma plantago-aquatica var. parviflorum*	Damp- Ground Perennials
x	x	x	-	x	*Amblystegium serpens**	
-	-	x	x	x	*Boehmeria cylindrica*	
-	-	-	x	-	*Brachythecium cf. mildeanum**	
-	-	-	x	-	*Brachythecium sp.**	
-	-	-	x	-	*Calliergon sp.**	
-	-	x	o	-	*Calliergonella cuspidata**	
-	-	x	o	-	*Campanula aparinoides*	
-	-	x	-	o	*Cardamine bulbosa*	
-	o	o	-	-	*Carex comosa*	
-	o	o	o	o	*Carex hystericina*	
-	-	-	x	x	*Carex lacustris*	
-	-	x	o	x	*Carex lasiocarpa*	
-	-	o	o	o	*Carex prairea*	
x	x	x	x	o	*Carex spp. (biconvex)*	
x	o	o	o	o	*Carex spp. (trigonous)*	
x	x	o	x	x	*Drepanocladus aduncus**	
-	-	x	-	-	*Dulichium arundinaceum*	
x	o	o	o	x	*Eleocharis palustris*	
-	-	x	x	x	*Eleocharis tenuis*	
-	x	x	o	x	*Epilobium cf. coloratum*	
-	-	-	-	x	*Equisetum sp.*	
-	-	x	x	o	*Eupatorium perfoliatum*	
-	-	-	x	-	*Juncus sp.*	
x	o	o	x	o	*Leersia oryzoides*	
-	-	x	x	x	*Lycopus americanus*	
-	-	-	x	x	*Lycopus uniflorus*	
-	-	x	-	-	*Lysimachia sp.*	
-	-	-	x	-	*Menyanthes trifoliata*	
-	-	-	x	x	*Meesia triquetra**	
-	-	x	-	-	*Oxalis sp.*	
-	x	o	-	-	*Panicum sp. (large)*	
x	x	x	x	-	*Panicum sp. (small)*	
-	-	x	-	-	*Pycnanthemum virginianum*	
-	-	x	-	x	*Rumex sp.*	
x	-	-	-	-	*Sagittaria cuneata*	
-	o	o	o	x	*Sagittaria latifolia*	
x	o	o	x	x	*Scirpus validus*	
-	-	-	x	o	*Scutellaria lateriflora*	
-	x	x	-	-	*Sium suave*	
-	-	x	-	-	*Stachys palustris*	
-	-	-	-	x	*Triadenum fraseri*	
-	-	x	x	o	*Typha sp.*	
x	-	x	-	o	*Verbena hastata*	
-	-	-	x	-	*Viola sp.*	
x	-	x	-	-	*Amaranthus albus*	Weedy Annuals
-	o	o	x	o	*Bidens cernua*	
-	x	-	x	-	*Bidens vulgata*	
-	-	-	-	x	*Cannabis sativa*	
x	-	x	x	x	*Chenopodium cf. bushianum*	
-	-	x	-	-	*Cyperus acuminatus*	
-	-	x	x	o	*Cyperus engelmanni*	
-	-	-	-	x	*Cyperus odoratus*	
-	-	o	o	+	*Cyperus diandrus*	
x	-	-	-	x	*Cyperus sp.*	
-	-	x	-	-	*Euphorbia maculata*	
-	-	x	-	o	*Impatiens capensis*	
-	-	-	x	x	*Impatiens pallidus*	
-	x	x	-	x	*Mollugo verticillata*	
-	o	o	+	+	*Pilea pumila*	
-	-	-	-	x	*Polanisia dodecandra*	
-	-	x	-	-	*Polygonum lapathifolium*	
x	x	o	o	o	*Polygonum punctatum*	
-	-	-	-	x	*Portulaca oleracea*	
-	-	x	-	-	*Potentilla norvegica*	
-	-	x	-	-	*Urtica dioica*	
x	-	x	x	o	*Betula nigra*	Trees and Shrubs
-	x	x	-	-	*Platanus occidentalis*	
x	-	x	-	x	*Populus deltoides*	
-	-	x	-	-	*Quercus sp.*	
-	-	-	-	x	*Robinia pseudoacacia*	
x	-	-	-	-	*Salix sp.*	
-	-	-	-	x	*Sambucus canadensis*	
-	-	x	-	-	*Amorpha sp. (not A. fruticosa)*	Prairie Forbs
-	x	-	-	-	*Lespedeza capitata*	
-	-	x	-	-	*Petalostemum candidum*	
-	-	x	-	-	*Rudbeckia cf. hirta*	
-	-	-	-	x	*Verbena simplex*	
-	x	x	-	o	*Aster sp.*	Other
-	-	-	-	x	*Helianthus sp.*	
-	-	x	-	-	*Hypericum sp.*	
x	x	x	x	x	*Other Compositae*	
x	x	o	x	x	*Other Gramineae*	
-	x	-	-	x	*Polygala sp.*	
x	x	x	x	x	*Miscellaneous leaf fragments*	
x	x	-	-	-	*Charophytes*	
x	x	-	-	-	*Fish scales*	
x	-	-	-	-	*Molluscs*	
x	-	-	-	-	*Ostracods*	
-	x	-	-	-	*Thalloid hepatic scale**	
-	x	o	-	-	*charred plant materials*	

was identified as the predominant taxon on the basis of plant macrofossils and pollen size measurements (McAndrews, 1969).

In view of the above, Gramineae pollen probably represents aquatic taxa; therefore, grass is excluded from the pollen sum in order to produce a more accurate reconstruction of the upland vegetation. The emended pollen spectra (lightly shaded outer curves, Fig. 2) suggest a floodplain and valley-margin forest of *Quercus, Carya, Betula nigra,* and *Ulmus*, along with *Fraxinus,* and *Platanus.* The slight decline in *Quercus* percentages and concentrations between 300 and 230 cm might indicate a real decline in oak during the period between 2320 and about 1320 yr B.P. *Ulmus* was slightly more abundant than at any subsequent time; *Salix,* most likely a wetland species,was also at its peak in abundance. *Pinus* was probably never closer than it is at present (that is, in northeastern Iowa).

It seems likely that little change occurred in the regional vegetation from about 2550 to 1260 yr B.P. The few macrofossils of prairie species and the relatively common charcoal found in macrofossil zone M-3 (about 1400 to 900 yr B.P.) are the only indications of possible climatic change. They suggest that some open environments were present and hint that the climate might have been slightly warmer and drier. However, changes in vegetation and climate cannot be inferred from the pollen diagram, and if they occurred, they probably were of small magnitude and extent. For example, shifts in *Quercus* pollen concentrations and percentages in zone P-4, are unaccompanied by changes in other taxa, and cannot be unequivocally interpreted in either vegetational or climatic terms. The lack of changes on pollen curves representing upland vegetation suggests that climatic changes were not large enough to cause noticeable shifts in this vegetation. Thus, the only climatic change proposed is a slightly warmer and/or drier period from approximately 1400 to 900 yr B.P.

The rise in both Cyperaceae and Other Tubuliflorae and the drop of Gramineae pollen percentages and concentrations beginning at 1260 ± 70 yr B.P. are compared directly with the macrofossil curves in Fig. 4. Cyperaceae percentages and concentrations reflect very well the increase in macrofossils of wetland sedges (Fig. 4). The correlation of Compositae pollen and macrofossils is less apparent. This family is even larger than the Gramineae, and equally diverse in its ecological range. Pollen percentages for this taxon are quite high at Nichols Marsh, especially considering that most species are insect pollinated and don't produce much pollen. Four species occur as macrofossils (Tables 1 and 2): *Aster* sp., *Bidens cernua, B. vulgata,* and *Eupatorium perfoliatum.* All of these, with the exception of the indeterminate *Aster*, are marsh species and occur in intervals where pollen percentages of Compositae are high, although the peaks in numbers of fruits do not match closely the pollen peaks (Fig. 4). Nonetheless, Compositae pollen is interpreted as probably being derived mostly from the marsh because, 1) the high pollen percentages imply a local source in an insect-pollinated taxon, and 2) the macrofossils do occur mostly in the same zone. Thus, pollen of Cyperaceae and Other Tubuliflorae, as with that of Gramineae, is considered to be local in origin, reflecting vegetational changes on Nichols Marsh rather than on the adjacent uplands.

Pollen zone P-1 shows the effect of cultivation by the marked increase in *Ambrosia* and a slight rise in Chenopodiineae pollen percentages. The ground disturbed by plowing provided extensive new habitat for these weeds, and this pollen zone is widely recognized in the Midwest as an indicator of the time of first settlement by Europeans.

Lowland vegetation.

The development of lowland vegetation at Nichols Marsh during the Late Holocene is discussed in terms of the plant macrofossil zones, because they give better resolution; the vegetational reconstruction is deduced from both pollen and plant macrofossils. The basal plant-macrofossil zone indicates an aquatic environment. Deep-water aquatic plants such as *Potamogeton amplifolius* occur only at the base. Farther up in this zone, these are replaced by shallow-water species such as *Myriophyllum* sp. and *Ceratophyllum demersum.* Plants with wide depth ranges like *Najas flexilis* and *Zizania aquatica* also were present. Other indications of aquatic conditions in this interval include fish scales, ostracods, charophytes, aquatic molluscs, and *Daphnia* ephippia (water-flea egg-cases) (Table 2), a peak in *Pediastrum* colonies (Fig. 2), and silty, organic pond sediments. *Sagittaria, Cyperus,* and the mosses, *Drepanocladus* and *Amblystegium,* indicate that the edges of the lake supported semi-aquatic, marshy vegetation. The pond probably was bordered partially by willows as well, judging from the high pollen concentrations and percentages, and the presence of *Salix* capsules at the base. Weedy plants like *Amaranthus albus* indicate that some disturbed ground was exposed, perhaps at the cutoff of the meander during the initial formation of the oxbow lake. The site must have been a pond dominated by *Potamogeton* and *Zizania,* with a fringe of semiaquatic, marsh species and *Salix* along the shoreline from about 2550 to about 1685 yr B.P.

Macrofossil zone M-4 records the increasing abundance of perennial wetland species. This suggests that the fringing marsh around the edges of the pond was extending outward from the shoreline as the pond began to fill with sediment. The appearance of *Nymphaea* along with *Potamogeton, Najas,* and *Zizania* from the previous zone, indicates that the pond still was present. Although they probably were present earlier, the first macrofossils of the trees, *Betula nigra* and *Platanus occidentalis* gives certain evidence that they were present locally. One prairie species, *Lespedeza capitata,* suggests that some prairie openings also were present nearby. The most likely location for these would be on top of the terrace adjacent to the site. This terrace surface was unforested in 1859 (Iowa State Planning Board, 1935). From about 1685 to 1410 yr B.P., the pond, which was dominated by *Zizania* and *Nymphaea,* had partially filled in, and was surrounded by an extensive marsh dominated by *Carex* spp., *Eleocharis palustris, Scirpus validus,* and *Leersia. Betula nigra* and *Platanus* probably grew along the edge of the upland.

Macrofossils in zone M-3 indicate that, although the wetland still was dominated by sedges and grasses, many other forbs were present as well. The presence of the moss, *Calliergonella,* and the sedge, *Dulichium arundinaceum,* also suggest a fundamental change in the nature of the vegetation, from a marsh towards a rich mire. However, the continued abundance of *Drepanocladus* in this zone indicates that marshy vegetation still predominated. The upward decline of *Zizania, Najas, Nymphaea,* and *Potamogeton,* and ultimately the disappearance of all but *Zizania,* in this zone indicate that the pond finally filled in between 1410 to 905 B.P. The presence of macrofossils of the prairie taxa, *Amorpha* sp. (not *A. fruticosa), Petalostemum candidum,* and *Rudbeckia* cf. *hirta* suggests that forest less dense than at present bordered the lowland, and prairie species grew in forest openings and on the terrace surface at the top of the slopes. Weedy annual plants also were more abundant, providing additional diversity, and suggesting that disturbed ground was present nearby. Disturbed ground also is indicated by lithologic evidence; sand lenses are confined to several levels in this zone, and sand also is dispersed in the peat between sand lenses. No sand was encountered in the section at site 1, which is farther away from the upland.

We suggest two hypotheses for the source of the sand in these lenses: 1) flooding of the river, or 2) erosion of the slopes adjacent to site 2. The absence of sand in site 1, which is closer to the Cedar River, suggests that the sands did not come from that direction; therefore, erosion of disturbed areas on the slopes or uplands seems the more likely explanation. Decreased slope stability could be caused by slightly warmer and/or drier conditions, leading to less dense vegetational cover. Warmer or drier conditions at this time are suggested by presence of macrofossils of the prairie taxa mentioned above. Other possibilities include disturbance by human activities, fires, severe storms, or perhaps higher spring runoff. Several of these factors may have acted together. For example, fires occur more frequently during drought periods (Heinselman, 1973; Anderson, 1982). Past fires are indicated in our sites by charred seeds, including some of marsh species, and charcoal fragments. The latter are concentrated in zone M-3, which suggests that fires burned in the uplands and at least partially onto the Marsh relatively frequently (Fig. 4). Disturbance by aboriginal farming is considered less likely, because pollen of cultivated crops typical in such sites (Delcourt et al., 1986) was not found (see below).

In zone M-2, vascular plants in the wetland apparently became much less abundant and diverse, while the converse is true of the bryophytes (Fig. 5). The dominance of *Calliergonella* and the occurrence of *Meesia triquetra* in this zone suggest that the shift in vegetation that began in zone M-3 culminated in the prevalence of rich mire conditions in zone M-2. Other species characteristic of rich mires also were present in this zone, including *Carex prairea* and *C. lasiocarpa*. The decrease in abundance of such species as *Drepanocladus*, *Leersia*, and *Cardamine* support the idea that marsh vegetation was less prevalent. The pond apparently had filled with sediment by this time, because aquatic plant remains are no longer present. A notable change in sediment type, from sandy peat to extremely fibrous peat made up predominantly of rootlets, occurs at the base of this zone. The changes in vegetation and sediment type could have been caused by a cooler, moister climate than that which previously prevailed. In particular, the occurrence of *Meesia triquetra* supports the hypothesis of climatic cooling. This species has a boreal-subarctic distribution at present; in the Midwest the most southerly station is northern Minnesota.

Correlation of this postulated climatic cooling with other records is difficult. The climatic changes involved are apparently small in magnitude, and their recognition from proxy data is often controversial. The entire 2500 yr record for Nichols Marsh falls within the cool Neoglacial climatic episode in Western United States (Burke and Birkeland, 1983), but correlation of the zone M-2 cooling with Rocky Mountain glacial advances is not clear. This cool period at Nichols Marsh (1045 to 1845 A.D.) is roughly correlative with the "Little Ice Age", when glaciers in Alaska expanded (Porter, 1986), and cooler conditions prevailed in the North Atlantic and northwestern Europe (Lamb, 1982). Wendland and Bryson (1974) set the boundary between the neo-Atlantic and Pacific climatic episodes at 850 yr B.P., but they do not specify the nature of the change (Fig. 5). Knox (1983) recognizes a change in stream behavior from stability to lateral channel migration in the Midwest at about 800 yr B.P., but again, the connection with climate is tenuous. Most pollen records from Iowa and adjacent areas show no consistent changes during this time (Baker and Waln, 1985; Holloway and Bryant, 1985; Kim, 1986; Semken, 1983; Van Zant, 1979; Webb et al., 1983). A 300-year record of tree rings from Iowa records several major droughts but is not considered to be sensitive to temperature (Duvick and Blasing, 1981). Wetlands may be more sensitive to small climatic shifts than previously thought; more detailed work on these late Holocene records is needed to test the hypotheses of climatic change suggested here.

In contrast with zone M-2, zone M-1 contains a very abundant and diverse assemblage of macrofossils of damp-ground perennial marsh plants, weedy annuals, and trees (Fig. 5). The Marsh continued to be dominated by Cyperaceae, but included *Cyperus* and *Eleocharis* in addition to *Carex* spp. Many forbs, such as *Aster* sp., *Eupatorium*, *Bidens cernua*, *Scutellaria*, and *Verbena* became abundant as well. The pollen diagram (Fig. 2) shows that *Typha* and *Dryopteris*-type (probably *Thelypteris palustris*) were also dominants. Zone M-1 also is characterized by a marked decrease in abundance and diversity of bryophytes, a striking contrast with zone M-2 (Fig. 5, Table 2). In zone M-1, the bryophyte flora is reduced to *Drepanocladus*, *Amblystegium* and *Meesia*. The continued presence of *Meesia* indicates that some rich mire vegetation persisted in his zone, but the *Drepanocladus*

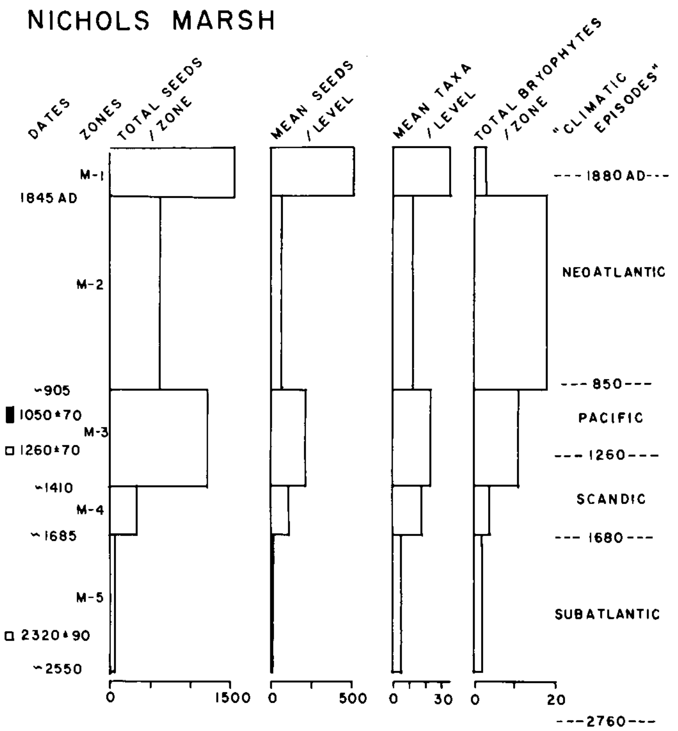

Figure 5. Summary diagram of dates, plant macrofossil abundances, and possible correlation of plant macrofossil zones with climatic episodes. Scale is numbers of specimens or taxa. Shaded box is radiocarbon date on macrofossil core; open boxes are radiocarbon dates on the nearby pollen core; date on upper zone boundary is from historical records; dates on other zone boundaries are interpolated. Climatic episodes from Wendland and Bryson (1974).

and *Amblysteguium* suggest that marshy vegetation prevailed.

It seems unlikely that correlations between the decrease in vascular plants and increase in bryophytes in zone M-2, and the converse in zone M-1 (Fig. 5), are coincidental. Bryophytes, because of their lesser stature, generally are a relatively insignificant component of the vegetation in habitats where vascular plant cover is dense and leaf litter abundant. They are more important in situations where vascular plants are less productive. At the present time on Nichols Marsh, bryophytes are virtually absent from the dense stands of *Typha*, but *Aneura*, *Hypnum*, and *Amblystegium* are relatively abundant where *Carex prairea*, *Dulichium*, and *Leersia* prevail. Therefore, it appears that the synchronous, reversed fluctuations in abundance and diversity of bryophytes and vascular plants in zones M-2 and M-1 reflect responses of the bryophytes to changes in dominance of vascular plants.

The changes in the vegetation from zone M-2 to zone M-1 are paralleled by changes in the peat, which becomes finer grained and detrital with fewer fibrous rootlets. As noted in the Results, the bases of the macrofossil zone M-1 and coincident pollen zone P-1 mark the beginning of cultivation by Europeans. This area of southeastern Iowa was opened for settlement as a result of the "Black Hawk Purchase" of 1832 (Richman, 1911, p. 113). The population of Pike township, which includes Nichols Marsh, rose from four families in 1839 to 266 people in 1850 (Hixon, 1984). Therefore, the change from fibrous to detrital peat, the abrupt increase in diversity and abundance of vascular plants, and the decrease of bryophytes, probably is related to runoff from cultivation. This runoff would substantially increase the supply of mineral nutrients to the Marsh, causing eutrophication. Such a change in nutrient status could account for the striking increase in *Typha*, for example, and indirectly, for the decrease in bryophytes. Other eastern Iowa wetlands show strong dominance by *Typha* where runoff from fields or construction impinges on them.

The forest clearance and cultivation following European settlement are known to have caused changes in the aquatic vegetation and sediment type in lakes (Birks et al., 1976; Davis, 1973, 1976; Van Zant, 1979). Chemical changes reflecting this cultural eutrophication also have been measured in lake sediments (Birks et al., 1976; Engstrom et al., 1985; Mathewes and D'Auria, 1982). However, changes in wetland vegetation and peat deposition resulting from post-settlement eutrophication are not well documented. Janssen's (1967) classical study from Stevens Pond in northwestern Minnesota is the exception; it indicates that an abrupt change from a *Picea-Larix* bog to a *Typha* marsh was initiated when the area was logged and converted to farmland. At that horizon, the sediments changed from woody peat to *Typha* peat. Tolonen (1983) also found evidence of change in local fen vegetation and sediment type following settlement in Maine.

The present vegetation of Nichols Marsh is characterized by a complex mosaic of plant communities. Much of the marsh is covered by dense stands of *Typha;* however, there are scattered patches of vegetation dominated by *Carex lacustris,* for example, or *Bidens cernua,* or *Leersia oryzoides.* In addition, there are some small areas characterized by rich mire elements, including *Carex prairea, Dulichium arundinaceum, Menyanthes trifoliata,* and the bryophytes, *Aneura pinquis, Hypnum lindbergii* and *Calliergonella cuspidata.* Therefore, it appears that elements of both zone M-1 and zone M-2 are represented in the present vegetation. This mixture suggests that the complex arrangement of plant communities reflects different rates of evolution of the wetland vegetation. Thus, relictual patches of the rich mire vegetation that dominated in zone M-2 still exist, but the present vegetation is dominated by the elements characteristic of marshy habitats that became prominent in zone M-1.

Relation to Archaeological Sites.

Several sites about 18 km west of Nichols Marsh indicate that Native American cultures were present nearly continuously during the last 4000 yr. Archaeological test excavations along the new route of Highway 218 (F-518 Corridor Project) uncovered numerous sites, and four dating back to 2500 yr B.P. have been investigated in detail (Lensink, 1986). Other sites undoubtedly were present closer to Nichols. The Cedar River and Wapsinonoc Creek were likely sites for fishing, plant gathering, and other activities, and their floodplains and terraces were potentially suitable for cultivation of crops. Thus, evidence was sought that might connect the Nichols paleoecological record with activities of early Native Americans.

Evidence for prehistoric human impact upon the native vegetation is poorly known in most areas of eastern United States (King, 1985). In eastern Canada (McAndrews, 1976) and southeastern United States (Delcourt et al., 1986; Whitehead and Sheehan, 1985), prehistoric cultivation dates back over 1000 yr. In the Little Tennessee River Valley, squash and gourd were cultivated as early as 4000 yr B.P., and maize and beans as early as 1000 yr B.P. Maize pollen, along with pollen and macrofossils of many ruderal species, were found in pond sediments on the floodplain (Delcourt et al., 1986). In southeastern Iowa at site 13WS61 in the F-518 Project, Scott (in Lensink, 1986, p. 111-112) found evidence of cultural use of *Zea mays, Carya, Juglans,* and *Crataequs* in a late-woodland site several hundred years old. Pollen samples from the upper levels of three other sites also contain *Zea* pollen, and they are similar to the upper zone at Nichols. However, their resemblance to the Nichols pollen diagram is difficult to assess because of the very different depositional (marsh vs. human occupation site) and topographic (lowland vs. hillside) contexts.

A number of plants present as fossils in the marsh are edible and could have been used by the Native American cultures present. These include *Zizania aquatica, Amaranthus, Chenopodium, Helianthus, Sagittaria, Scirpus, Typha,* and *Quercus.* However, there is no evidence here for use of these resources by the Woodland cultures. No prehistoric maize pollen, nor any evidence of other cultigens (such as squash seeds, bean seeds, or abnormally large seeds of *Iva*) has been found at the Nichols site, and the widespread use of the native plant foods, as in the Little Tennessee Valley, for example, (Delcourt et al., 1986), cannot be demonstrated here.

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