



Groundwater Controls on Wetland Vegetation of a Ridge-and-Swale Chronosequence in a Lake Michigan Embayment

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Abstract

A chronosequence of wetland swales between beach ridges in the Manistique/Thompson embayments of Lake Michigan contains plant communities that differ across the strandplain. We characterized vegetation in 33 swales and compared distribution with previously reported groundwater flow systems. Older swales near a groundwater divide created by the peak Nipissing ridge receive local flows and hold sedge/leatherleaf floating mats that transition to swamp. Farther lakeward, another groundwater divide is created by discharge of calcareous waters released by termination of an underlying clay confining layer, resulting in swales dominated by northern white cedar. Cedar swamp continues lakeward in swales having flow-through calcareous groundwater, but several swales are perched above those flows. Farther lakeward, a large amalgamated beach ridge creates another groundwater divide with discharges that again support cedar swamp. Calcareous discharge from the confined aquifer, with downslope flow-through waters, then supports more cedar swamp. Flow-through waters meet yet another calcareous discharge, resulting in ponding and development of floating mats. Finally, a deep regional aquifer discharges at the Lake Michigan shore and supports marsh/shoreline species. Our results have implications for assessing potential responses to climate change, interpretation of past climate changes in paleoecological studies, and management of wetlands facing future climate changes.

Keywords Ridge/swale wetlands · Lake Michigan · Wetland vegetation · *Thuja occidentalis* · Groundwater hydrology · Climate change

Introduction

The importance of groundwater to wetlands is well-known (e.g., Winter and Rosenberry 1995; Winter et al. 1998; Winter 1999; Hayashi and Rosenberry 2002; Euliss Jr. et al. 2014), and its role in groundwater-dependent ecosystems (Hatton and Evans 1998), including wetlands, was reviewed by Klove et al. (2011). Although the relation of groundwater to wetland vegetation has been addressed quite thoroughly for

fen peatlands (e.g., Glaser et al. 1990; Drexler et al. 1999; Drexler and Bedford 2002; Glaser 2002a, 2002b), other freshwater wetlands have received less attention. Early work in the Laurentian Great Lakes region of North America by Wilcox et al. (1984, 1986) found that the location and composition of peatland and marsh plant communities in a wetland complex near the shore of Lake Michigan were associated with groundwater flows. In Wisconsin, Kurtz et al. (2007) also tied groundwater discharges with position of marsh communities. Carlson Mazur et al. (2014) studied hydrology in swales across a Lake Huron strandplain at Negwegon State Park, Michigan, and Carlson Mazur et al. (2020) correlated groundwater hydrology at the site with wetland plant communities, which were mostly dominated by hardwood trees but some by herbaceous vegetation. They concluded that groundwater discharges might provide buffering capacity for wetland response to climate change.

Climate is a major driver of water levels in the Great Lakes. As reviewed in Wilcox et al. (2007), major droughts and low lake levels are correlated with climatic events, such as the

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Medieval Warm Period, that also affected the western Great Lakes and Great Plains (Booth et al. 2006). Prolonged high lake levels have been correlated with reconstructions of bog surface moisture and inland lake records from across the Great Lakes region (Booth and Jackson 2003; Booth et al. 2004). Paleo lake-level reconstructions for Lake Michigan over the past 6100 years confirm the timing of major, longer-term, high and low lake levels with known climatic periods (Baedke and Thompson 2000; Argyilan et al. 2018).

Strandplains containing ridge-and-swale wetlands in embayments of the Great Lakes provide ideal locations to assess climate change, as they represent chronosequences of wetlands that get progressively younger nearer the lake (Fig. 1a) (Thompson 1992). Sedimentological studies at multiple strandplains using vibracores of beach ridges were used to develop paleohydrograph proxies for climate change (Baedke et al. 2004). At Manistique, Michigan along the northwestern shore of Lake Michigan, we also studied vegetation change in wetlands across the strandplain. Paleoecological studies (Singer 1996) identified past plant communities that were similar to vegetation in modern swales so that projections could be made regarding wetland response to future climate changes.

Observations made while traversing the transect laid out across the strandplain while vibracoring beach ridges and summarized in a case study reported in Burkett et al. (2005) suggested changes in species dominating swale plant communities from the Lake Michigan shoreline landward. Near Lake Michigan, the wet, sandy shore was dominated by plants typical of shorelines. Not far landward were a few swales with floating sedge and leatherleaf mats (Fig. 1b). The floating mats then became shrub-dominated before phasing into cedar swamp with an herbaceous understory. Then, the cedars disappeared, and the floating mats returned. Finally, the swales transitioned into tamarack swamps. The Burkett et al. (2005) case study suggested that variable groundwater discharges and flows were likely responsible for some of the plant-community changes across the strandplain. Wilcox

et al. (2020), therefore, conducted a hydrogeologic study of the strandplain, which allowed us to correlate plant community patterns identified in past sampling with hydrology. The objectives of this paper are to report the findings of detailed vegetation studies of 33 wetland swales at Manistique and draw conclusions regarding response to groundwater discharges and flows. In doing so, we gained a further understanding of the importance of groundwater to wetland plant communities facing changes in climate.

Study Site

The Manistique and Thompson embayments along the Lake Michigan coast near Manistique, Michigan, USA contain more than 90 arcuate beach ridges forming an 8-km-wide by 5-km-deep strandplain of relict shorelines (Fig. 2). The two embayments were joined until shoreline progradation during the late Holocene intercepted a bedrock upland (Stoney Point) and isolated the two areas from combined littoral sediment accumulation. Progradation then continued on both sides of Stoney Point, and beach ridges filled both embayments. The beach ridges have relief from as little as 0.5 m to more than 10 m and are spaced on average about 45 m apart. The landward part of the strandplain is a platform of ~25 ridges that formed during the Nipissing phase of ancestral Lake Michigan as lake level rose to a peak about 4500 years ago (Thompson et al. 2014; Argyilan et al. 2018). The next ~70 beach ridges formed during the subsequent decrease in lake level down to the current elevation of Lake Michigan (Fig. 3).

The beach ridges have a core of water-lain nearshore deposits and an overlying cap of eolian sediment. Thompson and Baedke (1995, 1997) vibracored 87 ridges and used the elevation of basal foreshore deposits from the ridges and radiocarbon dates from the bases of 25 intervening swales to create a mid- to late-Holocene relative paleohydrograph for the Manistique/Thompson strandplain (Fig. 3a). Lake level rose to the peak of the Nipissing phase of ancestral Lake Michigan at 4500 years

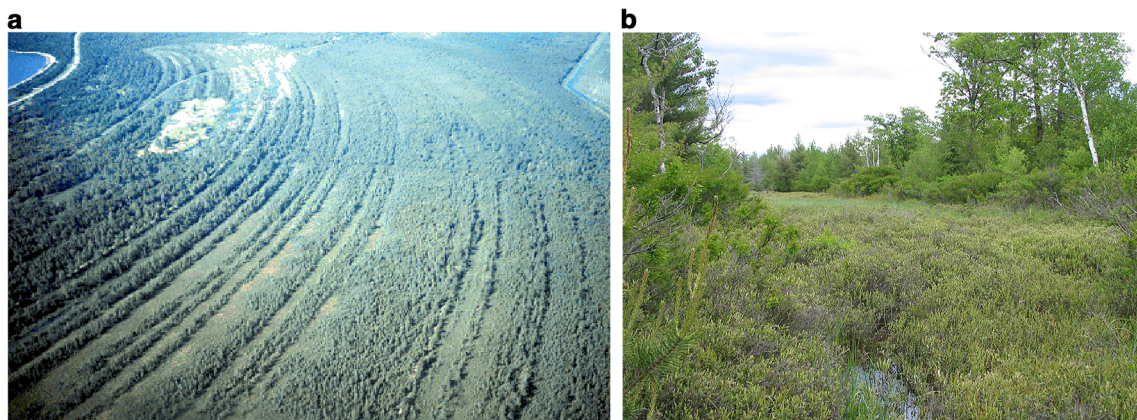


Fig. 1 a. Oblique aerial photograph of the Thompson embayment strandplain near Manistique, Michigan showing wetland swales separated by beach ridges. b. Photograph of wetland S8 between beach ridges, showing a floating mat dominated by *Chamaedaphne calyculata* and *Carex lasiocarpa*

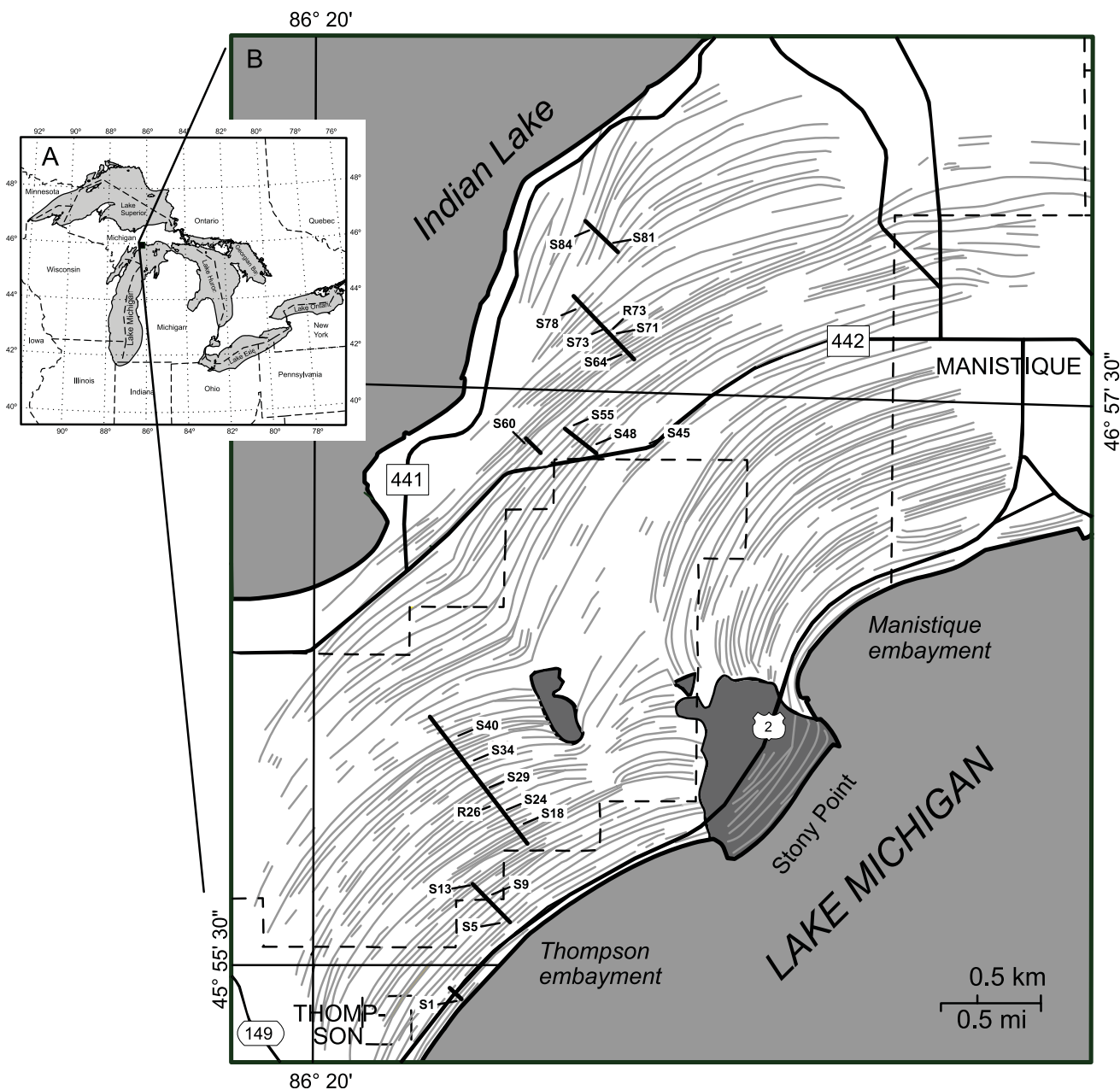


Fig. 2 Map showing the Manistique and Thompson embayments with beach ridges (black arcs) between Indian Lake and Lake Michigan. Bedrock areas shown in dark shading. Approximate locations of

transects are shown as lines crossing the ridges. Ridges R26 and R73 are labeled, as are a series of swales across the strandplain

ago and then dropped 6 m over the next 45 centuries (Fig. 3b). Because of isostatic rebound, the 6-m fall in lake-level manifests itself as a relative 11-m fall at the Manistique/Thompson strandplain. Not all of this lake-level fall is preserved in the strandplain. A 1000-year gap occurs in the strandplain chronosequence at 2700 years ago between ridges R26 and R25 (Baedke and Thompson 2000). This gap is defined by an amalgamated ridge (R26) of primarily dune sand that rises 8–9 m above surrounding ridges. Beach ridges began to form again 1700 years ago. A second gap occurs in the sequence from 1000 to about 100 years ago, followed by the recent creation of

two beach ridges in the 1970s and 1980s near the modern shoreline. Gaps in ridge formation may be due to insufficient sediment supply or erosion of previously formed ridges (Baedke and Thompson 2000).

The arcuate nature of the strandplain results in groundwater focusing (Cherkauer and McKereghan 1991; Crowe and Shikaze 2004). Thus, swales in the troughs between beach ridges often contain wetlands, which differ in plant community composition across the strandplain. Studies of the groundwater flow system showed that shallow groundwater and surface water within the swales are sourced from physically and

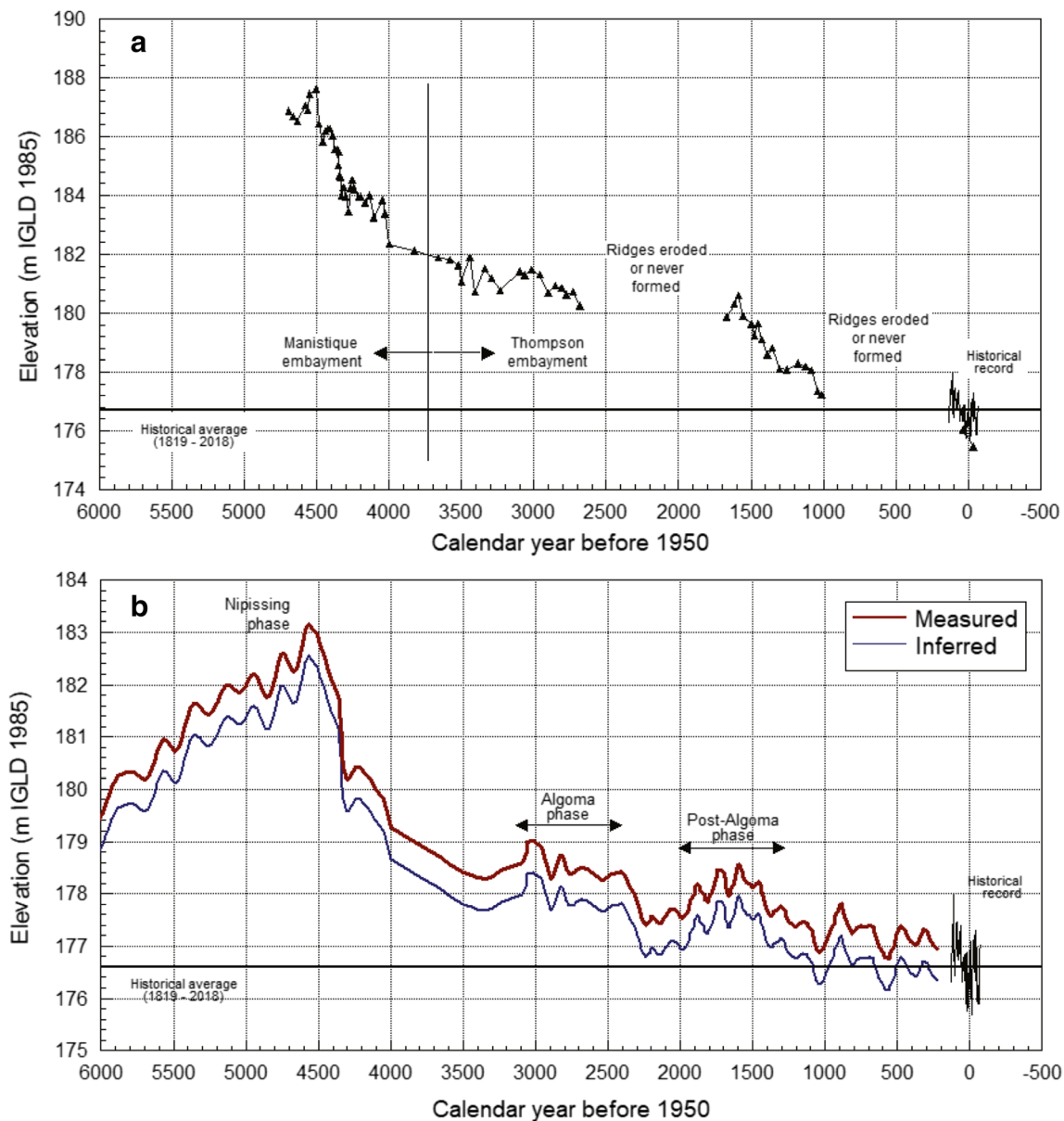


Fig. 3 a. Paleohydrograph showing relative lake level for the Manistique and Thompson embayments (Thompson and Baedke 1997) and historical lake level. Paleo lake-level data were derived from the elevation of basal foreshore deposits within each beach ridge. Note the two periods when beach ridges were eroded or never formed. The gap ending at ~1700 years ago allowed the development of an 8- to 9-m-high ridge in the Thompson

embayment where a topographically influenced groundwater divide occurs. b. Hydrograph of the late Holocene lake level and historical lake level for Lake Michigan/Huron. The top line is interpreted from beach-ridge studies, and the lower line is inferred from the average range of variation in the historical records (Baedke and Thompson 2000)

chemically distinct local, intermediate, deep, and mixed groundwater zones that are largely dependent on the distance from the modern shoreline, topography, and subsurface geology (Wilcox et al. 2020).

Methods

In July 1992–1993, vegetation was sampled in 33 swales that contained wetlands, beginning at Swale 1 (S1) near the Lake

Michigan shore and ending with S84 (Fig. 2). Little or no wetland occurred in 51 swales, and they were not sampled. To sample the wetland swales, a baseline was established perpendicular to established suites of ridges and swales, and four transects crossing the swales were set at distances 1 to 50 m from the baseline selected from a random number Table. A nylon rope was staked at the lakeward edge of a swale, stretched tautly, and staked at the landward edge. A 1-m-wide belt transect on the west side of the rope was then sampled, using a meter stick to judge transect width.

Trees having a diameter at breast height (dbh) of 5 cm or greater within the belt transects were identified and dbh measured. The sums of trees of each species across all four transects in each swale were divided by transect swale width to provide data in trees per meter swale width for use in floristic assessment. All shrub and herbaceous species occurring within the belt transect were identified (usually to species level) and listed on field data sheets; abundance of individual taxa along the transects was scored using the Braun-Blanquet method (Braun-Blanquet 1932, 1964), using values for each taxon derived by consensus from two field-crew members (single crew). Taxonomy was later adjusted to conform with eFlora.com.

Sampling data using the Braun-Blanquet scale were converted to the van der Maarel scale (van der Maarel 1979; Jager and Looman 1987), and the sums of those values across all four transects per swale were used to assess floristics. The total of 214 taxa was reduced to 162 (Appendix Table 3 with taxonomic authorities) by including only those that were identified to species level and sampled in more than one swale (unless van der Maarel value ≥ 5). A non-metric multidimensional scaling (NMS) ordination was performed using sums from the reduced data set with PC-ORD 6.0, the Sorensen (Bray-Curtis) distance measure, and autopilot set to slow and thorough (McCune and Grace 2002). Axis 1 and axis 2 scores were graphed to show similarities and dissimilarities in species composition and dominance among swales, with groupings based on known hydrology.

Results

Trees

Trees having a dbh ≥ 5 cm were found in belt transects of 25 swales (Table 1). The dominant tree species across much of the strandplain was *Thuja occidentalis*. The swales having large numbers of *T. occidentalis* showed marked patterns. Many were found in S10, S13, S17, S18, S24, and the seven wetlands between S29 and S49. Few cedar trees occurred farther landward until a reappearance in S63 and S64.

Larix laricina was found in 13 wetlands between S9 and S49 and was common in S9, S13, S24, S28, S45, S81, and S84. A similar pattern of occurrence was seen for *Alnus incana*, which was present in most wetlands between S9 and S49 and most prevalent in S17, S24, S29, S30, S31, S37, and S40, as well as S82. *Picea mariana* and *Pinus strobus* were found in many wetlands between S9 and S45 but were not prevalent. *Abies balsamea* was common in S37, S40, and S82.

Shrub and Herbaceous Vegetation

The NMS ordination of shrub and herbaceous species sorted swales across the strandplain having recognizable differences in

plant communities (Fig. 4). Wetlands S1 and S2 near the Lake Michigan shore plotted far from the other swales. They had 13 species in common and were dominated by moist soil/shallow water emergents *Juncus arcticus*, *Schoenoplectus pungens*, *Dasiphora fruticosa*, and *Juncus alpinoarticulatus* (Table 2). Wetlands S4 and S8 also plotted separately and had 17 species in common. However, S4 was partially ponded by beavers and was dominated by *Nuphar lutea ssp. variegata*, *Carex stricta*, and *Myrica gale*. Nearby S8 held a floating sedge mat and was dominated by *Chamaedaphne calyculata* and *Carex lasiocarpa*. Shrubs and small trees were prevalent in the nine wetlands from S9 to S28, which had 10 species in common to all, 10 in common to eight, and 12 in common to seven. The shrub overstory contained *A. incana*, *Ilex verticillata*, *Rhododendron groenlandicum*, *C. calyculata*, and *T. occidentalis*. Prevalent in the herbaceous understory were *C. lasiocarpa*, *Carex interior*, *Carex aquatilis*, *Carex trisperma*, and *Maianthemum trifolium*.

Farther landward, the 13 wetlands from S29 to S64 (Fig. 4) had 13 species in common with at least 11 swales, having *A. incana*, *R. groenlandicum*, and *T. occidentalis* as shrub dominants in S29 to S40; however, much of the *I. verticillatus* was gone, as were herbaceous understory *M. trifolium* and *Carex* species other than *C. trisperma*. New dominants were *Abies balsamea*, *Acer rubrum*, *Osmunda regalis*, and *Trientalis borealis*. The eight wetlands from S45 to S64 were dominated by shrubs and small trees, including *T. occidentalis*, *A. incana*, *I. verticillatus*, *A. balsamea*, and *A. rubrum*. In many swales, the herbaceous understory was dominated by *O. regalis*.

The four wetlands from S71 to S78 (Fig. 4) had 12 species in common with at least three swales. They plotted apart from other swales, with a floating mat of *C. calyculata* dominant in all and *C. lasiocarpa* sampled in all but S71. Wetlands S81 to S84 were dominated by shrubs and small trees: *A. incana* and *C. calyculata*, but also *L. laricina* in S81 and *Betula papyrifera* in S82, and *Salix exigua* and *Cornus sericea* in S84. The herbaceous understory was dominated by *C. stricta* and *Carex lacustris*.

Discussion

Successional and Hydrological Processes

Many classic plant-community studies in chronosequences of sites strived to demonstrate succession. In one of the earliest studies describing autogenic succession, Cowles (1899, 1901) worked on dunes along the south shore of Lake Michigan in Indiana that increased in age with distance from the lake. He suggested a plant-community sequence from annuals to sand-binding dune grasses to cottonwoods, pines, and oak. As described by Johnson and Miyanishi (2008), several arguments

Table 1 Number of trees having dbh ≥ 5 cm per meter swale width on the Manistique/Thompson strandplain

Taxa	Swale Number																								
	S9	S10	S11	S13	S17	S18	S23	S24	S28	S29	S30	S31	S37	S40	S45	S49	S54	S55	S59	S61	S63	S64	S81	S82	S84
<i>Abies balsamea</i>	0.1	0	0	0	0	0	0	0	0	0	0.2	0.1	1.3	0	0.4	0.1	0	0	0.3	0	0.3	0	0	0	0.2
<i>Acer rubrum</i>	0	0	0	0	0	0.1	0	0.1	0.3	0.2	0.1	0.1	0	0	0	0	0	0.1	0	0.2	0.3	0.4	0	0.1	0.7
<i>Alnus incana</i>	0.1	0	0	0	0.4	0	0	1.1	0.2	0.6	0.4	0.4	0.8	0	0.1	0	0	0	0	0	0.3	0.1	0	0.5	0.2
<i>Betula alleghaniensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Betula papyrifera</i>	0	0	0	0	0	0	0	0.2	0.2	0.2	0.1	0.2	0.3	0.2	0.1	0	0	0	0	0	0	0.3	0	0.4	0.1
<i>Fraxinus nigra</i>	0	0.3	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.1	0.1	0	0	0
<i>Larix laricina</i>	2	0.2	0.3	1.5	0.4	0.3	0.6	1.6	1	0.5	0.1	0	0	0	1.2	0.1	0	0	0	0	0	0	1.1	0.2	0.8
<i>Nenopanthus</i> sp.	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Picea mariana</i>	0	0.2	0	0.2	0.1	0.4	0	0.1	1	0.2	0.1	0.2	0.2	0.1	0	0	0	0	0	0	0.1	0.1	0	0	0.1
<i>Pinus strobus</i>	0	0.1	0	0.1	0.3	0.2	0.1	0.4	0	0.2	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0.1
<i>Populus tremuloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
<i>Salix</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
<i>Thuja occidentalis</i>	0.7	5.5	0.6	2.7	7.5	1.6	0.9	8.6	0.1	3.4	3.4	3.3	7.2	1.6	2.5	0.8	0.3	0.2	0.2	0.7	2.3	1.8	0.2	0.1	0.3
<i>Tsuga canadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.3	0.1	0	0	0

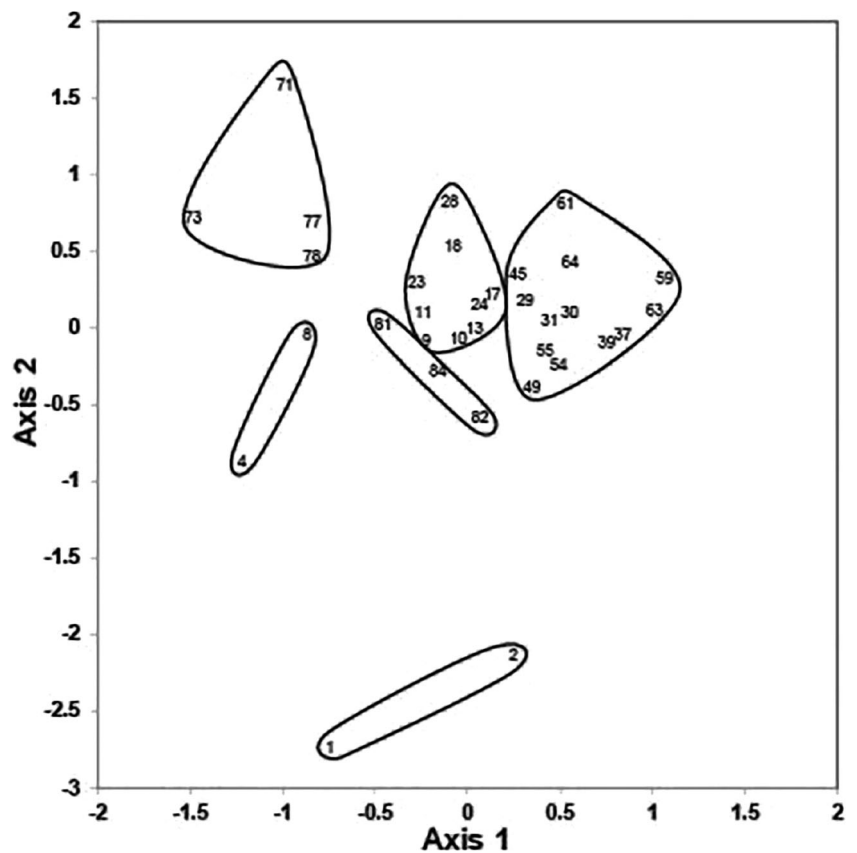
can be made to refute Cowles' conclusions. Other often-cited studies have used chronosequences to study hydrarch succession (e.g., Transeau 1903; Pearsall 1920), glacial till succession (e.g., Cooper 1923a, 1923b), and old-field succession (e.g., Oosting 1942). Again, the mistake of invoking successional processes for plant-community changes in these chronosequences was described by Johnson and Miyanishi (2008), with causation for apparent species-composition changes ranging from dynamics of sand transport, water-level change, and climatic variation to availability of initial colonizers and human disturbance. Walker et al. (2010) also noted cases in which chronosequences were inappropriate for studies of ecological succession but identified their value when there is evidence that sites of different ages follow the same trajectory. Neither review recognized groundwater influence as a reason to refute succession in chronosequences.

Adjacent to the Lake Michigan dunes of Cowles' fame lies a strandplain of low beach ridges with intervening swales similar in origin to those at Manistique; eolian sand transport has split many of them into rows of shallow dune ponds. Wilcox and Simonin (1987) showed that wetland plant communities changed across a chronosequence of five extant pond rows, with mostly submersed aquatic plants in the youngest ponds and increasing domination by emergent plants as pond rows increased in age. However, they noted the prevalence of human disturbance in the region. Jackson et al. (1988) demonstrated that plant-community change was very slow until the time of European settlement and discounted hydrarch succession. Although Doss (1993) studied groundwater flows at this site, he did not relate them to vegetation. In a recent resampling of the same dune ponds using the Wilcox and Simonin (1987) study design, Amatangelo et al. (2018) showed further changes in plant communities related to invasive species. Paleoeological studies from a much older (>10 K yrs) wetland in this strandplain concluded that major plant-community change during the Holocene resulted from hydrologic change forced by regional climate change (Singer et al. 1996). Although some of the changes were related to shallowing of the basin through autogenic sediment accumulation, hydrology was considered the mechanism of change.

Influence of Groundwater on Vegetation

As the swales at Manistique increase in age across the strandplain, plant communities change from being dominated by moist soil/shallow water emergents to floating sedge mats to shrubs to northern white cedars, which might be construed as a successional sequence. However, domination of older swales then reverts to floating sedge mats before progressing to swamp with mixed vegetation, including hardwood trees. The nature of these plant communities and the changes across the strandplain suggested influence from groundwater and resulted in follow-up hydrologic studies (Wilcox et al. 2020).

Fig. 4 Non-metric multidimensional scaling (NMS) ordination of understory vegetation sampled along four 1-m-wide belt transects placed in a stratified random design across each of 33 wetlands near Manistique, Michigan. Sampling data using the Braun-Blanquet scale were converted to the van der Maarel scale for use in the ordination. The numbers shown in the ordination represent wetland number from youngest (1) to oldest (84) across the chronosequence. [autopilot on; Sorensen distance; no species weighting; final stress = 13.60; final stability = 0.00001; number of iterations = 64]



The relations between groundwater and plant communities at Manistique are striking and may help in understanding plant-community/hydrology relations at these and other strandplains.

As water generally flows downslope, influence of the groundwater flow system on plant-community change at Manistique can best be described starting at the older, most-landward swales and relating vegetation to hydrology as determined by Wilcox et al. (2020). Ridge R73 formed at the peak of the Nipissing stage of Lake Michigan (Baedke and Thompson 2000) and creates a surface-water and groundwater divide near the oldest part of the strandplain (Figs. 2 and 5). Chemically dilute, shallow groundwater supplied by local recharge (specific conductance ≤ 63 $\mu\text{S}/\text{cm}$) flows both landward and lakeward from this ridge (Wilcox et al. 2020). On the landward side, S73 to S78 were dominated by mat-forming *C. calyculata* and *C. lasiocarpa* (Table 2), with no large trees, suggesting previously ponded conditions (Hipp 2008; Voss and Reznicek 2012; Smith 2018). Farther landward, *C. calyculata* was still dominant in the shrub/herbaceous layer in S81, but *L. laricina* and *A. balsamea* ≥ 5 cm dbh, characteristic of poorly drained swamps and peatlands (Chadde 2012; Voss and Reznicek 2012), were found in S82 and S84 (Table 1). Other prominent understory species in S81, S82, and S84 (*A. incana*, *C. stricta*, *C. lacustris*, and *Calamagrostis canadensis*) (Table 2) are

often common to marsh conditions (Swink and Wilhelm 1979; Hipp 2008; Chadde 2012; Voss and Reznicek 2012; Smith 2018). Conversion of plant communities sampled in S73–S78 to those in S81–S84 was likely related to succession.

Lakeward from R73, dilute groundwater flows from swale to swale until S65. Discovery of a flowing spring in S59 led to piezometer studies that identified a groundwater divide at S60 (Wilcox et al. 2020). A clay confining layer underlies the older swales and terminates in the vicinity of S60, releasing upward discharge (Fig. 5). Most flow from the S60 divide moves lakeward, but the landward back-flow meets with groundwater moving lakeward from upslope flow-through swales and causes ponding in S71, where a buoyant *C. calyculata* floating mat with no trees remained.

Wetlands S64, S63, S61, and S59 are greatly affected by the calcareous groundwater discharging at S60 (228 $\mu\text{S}/\text{cm}$, $\text{HCO}_3 = 96$ mg/L, $\text{Ca} = 20$ mg/L, $\text{Mg} = 12$ mg/L) (Wilcox et al. 2020). The presence of *T. occidentalis* as trees ≥ 5 cm dbh (Table 1) and dominance as small trees (Table 2) coincides with hydrologic/hydrochemical conditions typical of northern white cedars (Swink and Wilhelm 1979; Wilcox et al. 1986; Voss and Reznicek 2012). Also common in the shrub/herbaceous layer were cedar-swamp species *C. trisperma*, *Coptis trifolia*, and *T. borealis* (Hipp 2008; Chadde 2012; Voss and Reznicek 2012). Lakeward flow of calcareous groundwater from the S60 divide (Fig. 4) also

Table 2 (continued)

Taxa	Swale Number																																				
	S1	S2	S4	S8	S9	S10	S11	S13	S17	S18	S23	S24	S28	S29	S30	S31	S37	S40	S45	S49	S54	S55	S59	S61	S63	S64	S71	S73	S77	S78	S81	S82	S84				
<i>Lysimachia thyrsiflora</i>	0	0	4	6	10	8	8	8	8	0	4	8	0	0	4	1	6	6	6	1	12	1	7	0	0	0	4	0	0	0	2	2	9	8			
<i>Maianthemum trifolium</i>	0	0	0	0	0	8	5	15	14	12	8	11	18	0	10	7	9	7	2	20	12	2	1	0	0	0	0	0	0	0	3	0	2	2			
<i>Myrica gale</i>	0	10	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Nuphar lutea</i>	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Osmunda cinnamomea</i>	0	0	0	0	0	0	0	3	2	3	9	0	0	0	0	0	0	0	10	0	0	3	4	0	14	8	0	0	0	0	0	0	0	0	0		
<i>Osmunda regalis</i>	0	0	0	0	1	2	3	3	9	0	0	0	3	22	24	20	22	27	28	16	18	22	2	0	0	4	0	0	2	2	0	4	0	0			
<i>Parnassia glauca</i>	2	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Persicaria amphibia</i>	0	0	0	0	0	0	2	3	0	12	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8		
<i>Potamogeton pusillus</i>	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Quercus rubra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	10	8	0	0	0	0	0	0	0	0	0		
<i>Rhododendron groenlandicum</i>	0	0	0	6	18	14	9	10	12	16	8	14	20	10	16	10	10	10	24	7	8	7	0	4	5	16	0	3	10	9	10	0	6	0	6		
<i>Rhynchospora capillacea</i>	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rubus pubescens</i>	0	0	0	3	8	10	9	7	11	0	6	12	0	10	6	11	8	6	16	20	9	6	0	2	0	0	0	0	0	0	4	8	20	16	0		
<i>Salix candida</i>	0	0	0	12	9	0	5	2	2	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	
<i>Salix exigua</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Salix petiolaris</i>	0	0	0	12	6	3	4	6	8	4	12	4	0	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	7	12	16	0	5	28		
<i>Salix petiolaris</i>	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	
<i>Sarracenia purpurea</i>	0	0	0	0	2	6	2	6	8	8	7	4	11	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Schoenoplectus pungens</i>	20	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Solidago rugosa</i>	0	0	2	0	0	0	0	2	2	0	0	2	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Solidago uliginosa</i>	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Symphytotrichum puniceum</i>	0	0	0	0	0	1	7	6	6	0	0	8	0	2	0	0	5	4	1	10	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thuja occidentalis</i>	0	15	0	10	6	11	13	16	26	11	16	14	0	16	11	5	17	16	32	28	22	24	15	22	32	28	0	0	1	0	7	6	9	0	0	0	
<i>Torreya chlora pallida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	6	15	0	0	0	0	0	0	0	0	0	
<i>Trientalis borealis</i>	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Triantha glutinosa</i>	0	0	0	2	6	8	6	8	9	9	4	8	4	9	11	12	10	8	20	8	10	6	11	5	11	9	0	0	2	2	4	6	6	6	6	6	
<i>Trientalis borealis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	13	5	19	17	0	0	0	0	0	0	0	0	0	0	
<i>Tsuga canadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium angustifolium</i>	0	0	0	0	6	0	5	4	8	0	2	6	0	8	2	0	0	0	7	0	0	11	10	0	2	5	13	0	0	9	10	11	4	8	8	8	
<i>Vaccinium macrocarpon</i>	0	0	0	4	10	12	8	9	8	6	8	6	4	8	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium myrtilloides</i>	0	0	0	2	2	8	4	6	6	10	4	6	6	6	9	4	9	2	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Viburnum nudum</i>	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	4	2	0	0	10	3	7	5	2	5	2	2	

resulted in domination of shrub vegetation by *T. occidentalis* in the four wetlands from S55 to S45, as well as downslope S37, S31, and S30 (Table 2), with trees ≥ 5 cm dbh very dominant in S49, S45, S37, S31, and S30 (Table 1). Herbaceous vegetation was overwhelmingly dominated by *O. regalis*, which is often found in peatland habitats (Swink and Wilhelm 1979; Chadde 2012). Also common were *C. canadensis*, *C. trisperma*, *T. borealis*, *C. canescens*, and *R. groenlandicum*, the latter two species common to coniferous swamps (Chadde 2012; Voss and Reznicek 2012; Smith 2018).

Groundwater chemistry data collected by Wilcox et al. (2020) in S40, as well as downslope S29, indicated that those swales were perched above the calcareous groundwater flows at the time when sampling was conducted (specific conductance ≤ 36 $\mu\text{S}/\text{cm}$, $\text{HCO}_3 \leq 10$ mg/L, $\text{Ca} \leq 1$ mg/L, $\text{Mg} \leq 3$ mg/L). Shrub and herbaceous vegetation in S40 and S29 was dominated by *O. regalis*, with *A. incana* and *T. occidentalis* prevalent (Table 2). Many *T. occidentalis* trees with ≥ 5 cm dbh were also found (Table 1), which belies the relation to calcareous groundwater. However, Wilcox et al. (2020) noted that glacial isostatic adjustment has been lifting the strandplain through time (Baedke and Thompson 2000), altering hydrologic boundary conditions and causing a redistribution of groundwater discharges. Thus, perched S40 and S29 may have had calcareous flows in the past that resulted in establishment of the existing northern white cedar swamp.

R26 is a very large amalgamated beach ridge that creates recharge conditions and a shallow groundwater divide, with landward discharge reaching at least S27 (Figs. 2 and 5) (Wilcox et al. 2020). Plant-community composition in S28 suggests that it is perched, like adjacent S29, but did not receive calcareous flows in the past. Although *T. occidentalis* is mostly lacking in S28, the species present (*C. calyculata*, *R. groenlandicum*, *M. trifolium*, *C. trisperma*; Table 2) are characteristic of cedar swamps (Hipp 2008; Chadde 2012; Voss and Reznicek 2012). Lakeward from R26, S24 receives groundwater discharge from the R26 divide (123 $\mu\text{S}/\text{cm}$) and had large numbers of *T. occidentalis* ≥ 5 cm dbh (Table 1). The understory was dominated by *A. incana*, *I. verticillata*, *T. occidentalis*, and *R. groenlandicum* (Table 2)—again indicative of cedar swamp.

Downslope S23 also has water chemistry indicating that it is perched above calcareous groundwater flows (36 $\mu\text{S}/\text{cm}$) (Wilcox et al. 2020). Dominant in the understory were *C. calyculata*, *A. incana*, and *Andromeda polifolia* var. *glaucophylla*. Also prevalent were *T. occidentalis*, *I. verticillata*, and *C. lasiocarpa* (Table 2). Trees included *T. occidentalis* and *L. laricina* (Table 1), which suggests that it may have received calcareous groundwater flows in the past.

Groundwater having chemistry similar to that at S60 also discharges at about S18 (236 $\mu\text{S}/\text{cm}$) (Figs. 2 and 5) (Wilcox

et al. 2020); *T. occidentalis* was prevalent as trees and shrubs in S18 and especially S17 (Tables 1 and 2). Other prominent shrubs included *A. incana*, *C. calyculata*, *I. verticillata*, and *R. groenlandicum*. Prominent herbaceous species included *M. trifolium* and *C. trisperma*. These cedar swamp species show the correlation with groundwater discharge.

Wilcox et al. (2020) concluded that S13 to S9 received flow-through groundwater from the S18/S17 discharge. Prominent trees in S13 were *T. occidentalis* and *L. laricina*; the latter was very prominent in S9. *Thuja occidentalis* was also found in S11, S10, and S9 (Table 1), and calcareous groundwater influence was thus suggested. Shrubs *A. incana*, *C. calyculata*, *R. groenlandicum*, *T. occidentalis*, and *Vaccinium macrocarpon* were prevalent in those swales, as was mat-forming *C. lasiocarpa* in S9 (Table 2). Another groundwater discharge site was noted at S5 (247 $\mu\text{S}/\text{cm}$) (Figs. 2 and 5). Similar to the S60 discharge, landward backflow meeting with groundwater moving lakeward from upslope flow-through swales may cause ponding in S9, as well as S8. Both swales had *C. lasiocarpa* floating mats but differed in other species, as S9 contained more trees and shrubs, indicative of successional change (Tables 1 and 2). Discharge at S5 also affected S4, which had many species in common with S8 but no floating mat and partial ponding by beavers.

A deep regional groundwater flow system discharges upward to Lake Michigan and supplies S2 and S1 at the beach (838 $\mu\text{S}/\text{cm}$) (Figs. 2 and 5) (Wilcox et al. 2020). Continuously wet sands receiving calcareous groundwater provide habitat for *Juncus arcticus*, *Schoenoplectus pungens*, *Dasiphora fruticosa*, *Juncus alpinoarticulatus*, and other species found there (Swink and Wilhelm 1979; Chadde 2012; Voss and Reznicek 2012) (Table 2).

Climate Change Signals

Paleoecological Trends

Groundwater flows may affect interpretation of paleoecological data regarding climatic change. Singer et al. (1996) found few similarities in plant macrofossil sequences in peat cores from S29 and S40, which are about 580 m apart, suggesting that there was no signal for regional hydroclimatic change. A pertinent example is the count of *C. lasiocarpa* achenes, which increased in S29 from about 1800 to 1100 ^{14}C years BP, while simultaneously declining and eventually disappearing from S40. Those swales are now perched above the groundwater flow system (Wilcox et al. 2020), but that may not have been the case long ago. Recharge from large, amalgamated ridge R26 creates a groundwater divide that now discharges mostly lakeward toward S24, but flows also go landward to at least S27 (Wilcox et al. 2020). During the post-Algoma stage of Lake Michigan from about 1800 to 1400 calendar years before 1950, lake levels rose to as high

as 178.6 m IGLD1985 (Fig. 3) and would have backed up against ridge R24. With a reduction in the head differential from R26 to the lake, landward discharge would have increased. Wetland S29 is only about 120 m from R26 and may have been ponded by this change in groundwater flow, resulting in establishment of a *C. lasiocarpa* floating mat. Wetland S40 is about 700 m from R26 and likely would not have been affected. When lake levels dropped after the post-Algoma stage, the count of *C. lasiocarpa* achenes declined rapidly at S29.

Water Availability

Changes in the water cycle are projected to occur globally with predicted climate warming (IPCC 2013). Buffering of climatic changes by groundwater varies based on the groundwater source and position in the hydrological landscape. Changes in temperature and associated precipitation patterns resulting from climate change may influence local and, eventually, regional groundwater patterns (Brooks 2009).

Winter (2000) noted that wetlands in hummocky glacial and dune landscapes may have complex groundwater flow systems, with some receiving no groundwater inflow, some receiving inflow from local groundwater flow systems, and others receiving inflow from large, regional flow systems (conditions also found at Manistique; Wilcox et al. 2020). He concluded that wetlands dependent on only precipitation

for their water supply are highly vulnerable to climate change, while those receiving water from regional flow systems are much less vulnerable. Havril et al. (2018) drew similar conclusions and stated that preservation of groundwater-dependent ecosystems would be challenging if flows were reduced in transient, local flow systems—some wetlands potentially disappearing. Studies of prairie potholes wetlands in the north-central United States found that wet and dry cycles may accompany climate change and that a warmer climate without increased precipitation would reduce wetland area (Fay et al. 2016; Johnson et al. 2016; Johnson and Poiani 2016).

In the North American midwest, warming has increased markedly since the 1990s (Horton et al. 2014). Warming has also been more rapid during winter, resulting in less ice cover in the Great Lakes. Hydrologic response to warming in recent decades has been shown in Lake Michigan-Huron by increased total water inputs during autumn and winter seasons, with an increase in winter runoff at the expense of spring runoff (Argyilan and Forman 2003). Future projections suggest increases in annual temperature, decreases in summer precipitation, increases in winter and spring precipitation, and increases in streamflows into Lake Michigan by the end of the century (Cherkauer and Sinha 2010; Hayhoe et al. 2010).

Increased temperatures and reductions in summer precipitation could have implications for wetland vegetation in some

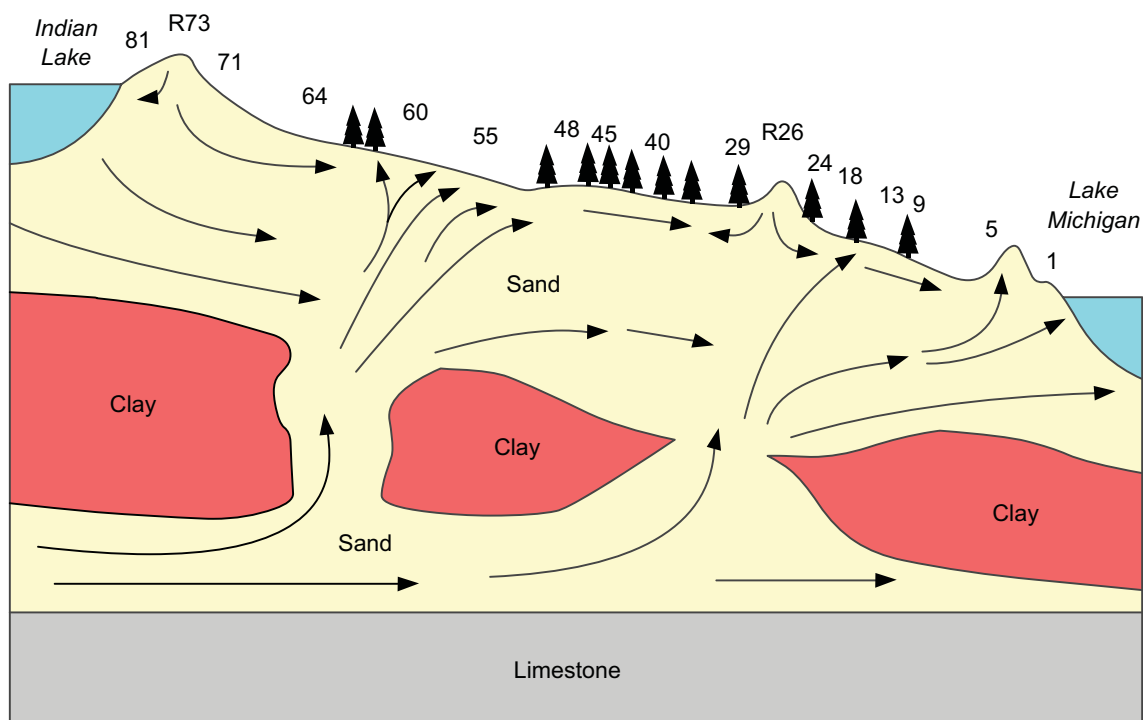


Fig. 5 Schematic cross-section of the Manistique strandplain with ridges R26 and R73 labeled, as are a series of swales across the strandplain, bedrock, clay confining layer, and groundwater flow paths in a deep regional aquifer, release from a confined aquifer at swale S60 and

potentially at S18 and S5, and surficial sands. Recharge from large R26 results in landward flows and a groundwater divide. Vertical exaggeration is approximately 1:140 (modified from Wilcox et al. (2020)

of the swales at Manistique. Indeed, Booth et al. (2006) identified six extreme droughts occurring across the western Great Lakes over the past 2000 years, several of which were tied to known climatic drivers that could recur. As suggested by Winter (2000) and Havril et al. (2018), the swales identified in this study and by Wilcox et al. (2020) having local flow systems (S71, S73, S77, S78, S81, S82, S84) and those perched above groundwater flows (S23, S28, S29, S40) could undergo changes in vegetation during an extreme drought. Wetlands S81–S84 could lose herbaceous wetland species and see more shrub invasion, including terrestrial species. Floating mat swales S71–S78 could dry down enough to allow wetland shrubs such as *A. incana* and *I. verticillata* to become more prevalent. Perched S23, S29, and S40 that already contain stands of larger *A. balsamea*, *A. incana*, *L. laricina*, or *T. occidentalis* and shrub-layer *A. incana* and *T. occidentalis* could also lose herbaceous wetland species. Wetland S28 currently has few trees or larger shrubs but could face shrub invasion. Most other swales have substantial groundwater flows and would likely continue on their current successional trajectories. Even though lengthy extreme droughts may reduce recharge of groundwater flow systems, those that discharge to the Manistique strandplain are likely recharged by deep regional systems or landward Indian Lake (Wilcox et al. 2020) and would not be affected.

Conclusions

Succession in plant communities has often been studied in chronosequences of sites. Johnson and Miyanishi (2008) and Walker et al. (2010) pointed out problems in doing so, but they did not address groundwater influences in wetlands. Our results suggest that although successional processes may result in vegetation changes in some wetlands, groundwater discharge and flows can have overriding effects in others. The use of wetland chronosequences to study temporal plant-community changes should, therefore, include hydrology studies. For these reasons, evaluations of the potential effects of climatic changes in wetland chronosequences should include groundwater studies, as should interpretation of paleoecological data. Managers must recognize the potential for groundwater influence to avoid taking management actions that would have a negative effect on resources under their care.

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Appendix

Table 3 Shrub and herbaceous species in swales on the Manistique/Thompson strandplain. Shown are van der Maarel values, narrowed to taxa identified to species level

Taxa	Swale Number																																		
	S1	S2	S4	S8	S9	S10	S11	S13	S17	S18	S23	S24	S28	S29	S30	S31	S37	S40	S45	S49	S54	S55	S59	S61	S63	S64	S71	S73	S77	S78	S81	S82	S84		
<i>Abies balsamea</i> (L.) Miller	3	0	0	0	8	8	1	7	7	0	0	4	0	0	10	13	18	16	0	26	6	6	3	12	0	21	24	0	0	0	0	2	14	14	
<i>Acer rubrum</i> L.	0	1	0	0	6	5	0	11	9	5	0	9	0	14	16	11	8	8	6	15	10	9	8	8	14	20	0	0	5	0	10	14	18		
<i>Alnus incana</i> (L.) Moench	0	2	5	11	26	20	18	22	15	20	20	24	5	24	18	20	12	15	28	28	16	18	3	7	10	20	0	0	10	8	24	34	24		
<i>Anelanchier laevis</i> Wieg.	0	0	0	0	2	2	0	3	4	6	0	4	0	2	6	2	0	0	7	4	0	0	0	0	0	0	0	0	2	0	2	0	0		
<i>Andromeda polifolia</i> L. var. <i>glaucophylla</i> (Link.) DC	0	0	0	11	8	4	0	6	6	8	18	6	10	0	0	1	0	0	3	0	0	0	0	0	0	0	0	9	2	0	0	0	0		
<i>Aralia nudicaulis</i> L.	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	
<i>Argentina anserina</i> (L.) Rydb.	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Aronia melanocarpa</i> (Michx.) Elliott	0	0	0	0	2	7	3	2	6	5	0	0	5	3	0	0	0	0	0	0	0	0	1	0	0	2	0	0	9	8	5	2	0	0	
<i>Betula papyrifera</i> Marshall	0	1	4	0	2	5	4	11	6	4	0	4	6	0	0	0	6	4	6	13	0	0	3	1	0	5	0	1	1	0	6	20	8	0	
<i>Betula pumila</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	15	11	15	3	15	0	
<i>Bolboschoenus flaviventris</i> (Torr.) Sojak (Michx.) P. Beauv.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i> (Michx.) P. Beauv.	0	2	11	6	10	13	8	10	4	6	9	4	5	7	6	6	0	0	9	20	11	5	0	4	0	0	0	2	4	6	16	28	12	0	

Table 3 (continued)

Taxa	Swale Number																																	
	S1	S2	S4	S8	S9	S10	S11	S13	S17	S18	S23	S24	S28	S29	S30	S31	S37	S40	S45	S49	S54	S55	S59	S61	S63	S64	S71	S73	S77	S78	S81	S82	S84	
<i>Tsuga canadensis</i> (L.) Carrière	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	13	5	19	17	0	0	0	0	0	0	0	
<i>Typha angustifolia</i> L.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	
<i>Typha latifolia</i> L.	0	0	0	7	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	
<i>Utricularia macrorhiza</i> Leconte	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Utricularia minor</i> L.	0	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Vaccinium angustifolium</i> Aiton	0	0	0	0	6	0	5	4	8	0	0	2	6	0	9	2	0	0	7	0	11	10	0	2	5	13	0	0	0	9	10	11	4	8
<i>Vaccinium macrocarpon</i> Aiton	0	0	0	4	10	12	8	9	8	6	8	6	4	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium myrtilloides</i> Michx.	0	0	0	2	2	8	4	6	6	10	4	6	6	6	4	9	2	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium oxycoccos</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> (L.) T. & G.	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	4	2	0	0	0	10	3	7	5	2

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