Ecological Classification and Analysis of Swamp Forests Along the Lake Michigan and Lake Huron Shorelines




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ABSTRACT

Great Lakes coastal wetland research and efforts to restore coastal wetlands have focused primarily on herbaceous meadows and marshes. Although swamp forests typically occur immediately inland of these wetlands, a detailed understanding of their physiography, hydrologic regime, soil properties, vegetation, and factors that account for the regional distribution of different swamp types is lacking. Because swamp forests along the Great Lakes shorelines are an integral part of the coastal wetland complex, such an understanding would be a substantial contribution to coastal wetland restoration. Therefore, a landscape ecosystem approach was applied to classify swamp forests along the Lake Michigan and Lake Huron shorelines. Physiography, hydrology, soil, and vegetation was sampled in 447 plots in 42 swamps.

A three-level, hierarchical classification was developed based on integration of plot data, field reconnaissance, aerial photo interpretation, and GIS analyses. Two Major Shoreline Segments were identified based on the occurrence of swamp forests in different landforms–former embayments along Lake Huron and northern Lake Michigan, and drowned river mouths along eastern Lake Michigan. Each major shoreline segment was divided into a northern and southern Minor Shoreline Segment based on climatic and physiographic characteristics. Two or three Ecosystem Types, nine ecosystems in all, were nested within each minor shoreline segment. Ecosystem types were distinguished based on position in relative to the lake, and the corresponding physiography, hydrology, soil, and vegetation. Along each minor shoreline segment, ecosystem types located closest to shore were characterized by inundation of the soil surface, a substrate of mineral soil, and the forest canopy was dominated by hardwoods, primarily red ash and silver maple. Ecosystems located further from shore were characterized by soil saturation, a substrate of organic soil, and the forest canopy was dominated by conifers, primarily northern white-cedar.

Distinctness of the ecosystem types was supported by detrended correspondence analysis (DCA). The ecosystem classification was further corroborated, and interrelationships among physical environmental variables and species composition were determined by canonical correspondence analysis (CCA). Hydrologic and soil variables were more important in explaining variation among ecosystems than stand structure variables.

Analysis of historical and present land cover assisted in prioritizing restoration efforts among ecosystem types. Although southern shorelines historically contained both hardwood- and conifer-dominated swamp, practically all of the conifer-dominated swamp has been eliminated. Therefore, restoration of saturated, conifer-dominated ecosystems is a high priority along southern shorelines. Along northern Lake Michigan and Lake Huron, the historical abundance of conifer-dominated swamp was markedly greater than that of hardwood-dominated swamp. Although substantial areas of conifer-dominated swamp remain, the remaining area is markedly less than its historical abundance. Thus, restoration of saturated, conifer-dominated ecosystems also is a high priority along northern shorelines. Drowned river-mouth valleys of northwestern Lower Michigan were historically dominated by approximately equal proportions of hardwood- and conifer-dominated swamp, and nearly equal proportions of each type have been lost. Therefore, restoration in northwestern Lower Michigan should focus on sites with the best landscape context, or those that can be restored at the lowest cost.

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INTRODUCTION

Because Great Lakes coastal wetland research has focused primarily on herbaceous meadows and marshes (Keddy and Reznicek 1986; Albert et al. 1988, 1989; Bedford 1992; Heath 1992; Herdendorf 1992; Minc 1997), most efforts to protect and restore coastal wetlands have been directed toward herbaceous wetlands (Chow-Fraser 1998, Mitsch and Bouchard 1998, Wilcox and Whillans 1999, Kowalski and Wilcox 1999). However, within most former embayments and drowned river mouths along the Great Lakes shorelines, swamp forests occur inland of the open meadows and marshes, often less than two m above the lake. Although swamp forests are generally restricted to elevations above the maximum lake level (Keddy and Reznicek 1986, Edsall et al. 1988), their hydrologic regime may be determined, at least indirectly, by the Great Lakes. For example, in a beach ridge and swale complex along southwestern Lake Michigan, Visocky (1977) demonstrated that water-table fluctuation in swales at a higher elevation than Lake Michigan paralleled water-level fluctuation in the lake itself. Furthermore, whereas lake-level gauges indicate water-level fluctuation of less than 1 m about the mean over the last 150 years, longer-term fluctuation up to 2 m about the mean and lasting approximately 150 years was common throughout the late Holocene and may be continuing to the present (Larsen 1985; Thompson 1992; Thompson and Beadke 1995, 1997). Although herbaceous wetlands predominate within the narrow range of water-level fluctuation over the last 150 years, swamp forests are well represented in the wider range of water-level fluctuation indicated in the geologic record.

Due to substantial losses and degradation of coastal wetlands, the important role of such wetlands in the maintenance of regional biodiversity, and the high importance of wetlands to Michigan residents, restoration of coastal wetlands is a high priority. Approximately 60% of the Great Lakes coastal wetlands have been lost over the last 200 years, with losses as high as 90% in some areas (USFWS 1994, Mitsch and Bouchard 1998). The marked loss of Great Lakes coastal wetlands includes substantial amounts of swamp forest that have been either drained or converted to other wetland types. For example, comparison of land cover based on recent aerial photography to historical vegetation based on General Land Office (GLO) survey records reveals that 40% of the swamp forest within 1 km of the Lake Huron shoreline, from Saginaw Bay to the eastern Upper Peninsula, has been lost (Tepley et al. 2003). Recent surveys indicate that 73–87% of Michigan residents viewed wetland services including wildlife habitat, fish habitat, flood control, wildflower habitat, and water filtration as extremely important (Kaplowitz and Kerr 2003). Because both herbaceous wetlands and adjacent swamp forests provide such services, and both types have been severely degraded, restoration efforts should be directed toward both wetland types.

For the purposes of restoration and management, swamp forests along the Great Lakes shorelines should be considered an integral part of the coastal wetland complex. Due to their characteristic location, at the interface between upland ecosystems and herbaceous wetlands that extend into the lake, coastal swamp forests may provide refuge for numerous plants and animals, and they may buffer the effects of upland land use on the Great Lakes. Furthermore, vegetation composition and successional dynamics may, at least indirectly, be regulated by Great Lakes water levels through their influence on local groundwater hydrology (Visocky 1977). However, despite the widespread distribution of swamp forests along the Great Lakes shorelines and their spatial and functional linkages between upland and aquatic systems, only a few studies have systematically characterized them (Comer and Albert 1993, Tepley et al. 2003). A detailed understanding of swamp forests along the Great Lakes shorelines, including their hydrologic regime, soil properties, vegetation composition and structure, and the factors that affect the geographic distribution of different swamp types would contribute substantially to the success of coastal wetland restoration.

Conceptual Approach

Prioritization of limited resources toward restoration of degraded coastal wetlands depends on an understanding of the historical distribution of various wetland types and regional patterns of degradation. After such regional considerations have identified high-priority targets for restoration, a set of goals, or reference conditions, is necessary to guide restoration practices at the local level.

Although descriptions of vegetation composition and structure are essential to the development of restoration goals, such information provides little guidance in areas where an array of plant communities may occur within a small spatial scale (Palik et al. 2000). Along the Great Lakes shorelines, where small differences in elevation above the lake result in marked differences in hydrology, soil, and vegetation (Keddy and Reznicek 1986), land managers must determine which set of reference conditions apply to a specific site. Also, they must recognize characteristic patterns of species and communities along gradients of hydrologic regime and soil properties extending inland from the shore. Thus, identification of reference conditions is contingent upon a fundamental understanding of the factors that regulate ecological processes and species composition (Keough et al. 1999). Because topographic features and their associated parent material, hydrologic regime, and soil properties change more slowly than vegetation, reference conditions can be determined based on an understanding of physical site characteristics and their interrelationships with vegetation (Allen and Wilson 1991, Palik et al. 2000).

A landscape ecosystem approach, where ecosystems are identified within their regional landscape context based on integration of physical site factors (specific landform, slope, microclimate, hydrology, parent material, and soil properties) and species composition and abundances, provides the insight necessary to develop restoration goals. Under this approach, a landscape ecosystem is recognized as a single, perceptible topographic unit–a volume of land and air plus organisms extended areally over a particular part of Earth's surface for a certain time (Rowe 1961). By integrating geology, physiography, hydrology, climate, soil, vegetation, and historical factors, ecosystems may be identified, classified, and described within a multiple scale, hierarchical framework (Barnes 1996, Barnes et al. 1998 p.321-326). Through the process of classification, natural ecological units are grouped logically, emphasizing similarities and interrelationships. Thus, land managers and researchers can work at an appropriate scale for their problem or objectives.

Regional landscape ecosystems of Michigan (Albert et al. 1986, Albert 1995) provide the regional framework for classification of finer-scale local ecosystems (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985). Other examinations of forest ecosystems within such a framework have illustrated differences among ecosystem types in functional processes, such as nutrient cycling and succession (Zak et al. 1989, Host et al. 1988), and they have facilitated assessment of both biological and ecological diversity at multiple spatial scales (Pearsall 1995, Lapin and Barnes 1995, Baker and Barnes 1998). Management applications include the development of a framework to monitor the endangered Kirtland's warbler and identify areas best suited to sustain warbler populations (Kashian and Barnes 2000, Kashian et al. 2001, Walker et al. 2001).

Objectives

Our primary objective was to provide land managers with a detailed understanding of the major types of swamp forest that occur along the Great Lakes shoreline and the physical site factors that account for their spatial distribution. Specific objectives were to: (1) apply a landscape ecosystem approach to identify, classify, and describe swamp forest ecosystems along the Lake Michigan and Lake Huron shorelines, (2) identify the major hydrologic and soil variables that account for differences in vegetation composition and structure among major swamp ecosystem types, and (3) develop restoration priorities among swamp ecosystems based on estimates of their historical abundance, present distribution, and current level of degradation.

Although the mapping of local ecosystems is an important component of the landscape ecosystem approach as previously applied in Michigan (Barnes et al. 1982, Pretigzer and Barnes 1984, Spies and Barnes 1985), mapping all swamp ecosystems along the shorelines was beyond the scope of our study. Instead, our objective was to identify the major swamp types and provide a detailed understanding of physical site characteristics needed to distinguish among them on the ground, regardless of the current vegetation. Also, we were focusing on one generic type of ecosystem, coastal swamp forests, rather than identifying and mapping all ecosystems along the shoreline. Furthermore, whereas the landscape ecosystem approach, as applied to inland landscapes, proceeds from regional ecosystems of Section, Subsection, and Sub-subsection to local ecosystems of Physiographic System, Landform-Level Ecosystem, and Landscape Ecosystem Type

(Kashian et al. 2001, Walker et al. 2001), the hierarchy was modified somewhat to classify coastal swamp ecosystems. Classification of coastal swamp forests proceeded in a top-down manner by dividing the shoreline into major and minor shoreline segments that were progressively more homogeneous in physiography and climate, until local ecosystem types recurred within a shoreline segment, reflecting underlying fine-scale patterns of physiography, hydrology, soil, and vegetation.

STUDY AREA

Geological Context

Because Lake Michigan and Lake Huron are connected by the Straits of Mackinac, a channel 37 m deep and 5.8–8 km wide, hydrologically they may be considered two lobes of the same lake. Over the last 2,500 years mean water level in both basins has been adjusted to channel depth of the St. Clair River at Port Huron, with climatically-driven fluctuation about the mean (Larsen 1985). From 1860, when a systematic program of daily measurement was initiated, to 1985, mean annual water level has ranged from 175.5 to 177.1 m, with a mean annual level of 176.4 m (Bishop 1990). Seasonal water-level fluctuation over the same period averaged 0.33 m (Quinn 2002). Although an annual mean of 177.6 m was recorded in 1838, Bishop (1990) adjusted the maximum annual mean to 177.1 m to account for permanent lowering of water levels due to dredging in the St. Clair River (Brunk 1961, Lawhead 1961, Derecki 1985, Quinn and Sellinger 1990). Other notable high water levels were recorded for the intervals 1853–1862, 1882–1887, 1928–1931, 1943–1955, the early 1970s, and the mid 1980s (Larson and Schaetzl 2001). Low water levels were observed in 1926, 1934, 1964, and 1999–2003.

Development of the Great Lakes and their associated shoreline features was regulated by a complex history of water-level fluctuation following retreat of the Wisconsinan Glacier. Approximately 11,000 B.P., glacial retreat permitted water flow across the Straits of Mackinac and the Indian River lowland in the northern Lower Peninsula, and Glacial Lake Algonquin formed a confluent lake in the Huron and Michigan basins (Hansel et al. 1985). Shortly afterward, further glacial retreat across southern Ontario exposed isostatically depressed, lower outlets, causing water levels to fall to approximately 106 m, 70 m below modern levels (Larson and Schaetzl 2001). The opening of lower outlets resulted in a series of short-lived, lower lakes, represented by Lake Chippewa in the Michigan basin (Hough 1963, Hansel et al. 1985) and Lake Stanley in the Huron basin (Eschman and Karrow 1985).

After the low levels of Lakes Chippewa and Stanley, uplift of the North Bay region raised the northern outlet, causing a gradual rise in water level to the altitude of pre-existing outlets at Port Huron and Chicago. Following the rise in water level, three distinct middle to late Holocene lake events are recognized: Nipissing (5,500–3,800 B.P.), Algoma (3,800–2,500 B.P.), and modern Lakes Michigan and Huron (2,500 B.P. to present) (Hansel et al. 1985, Larsen 1985). The Nipissing and Algoma phases were previously thought to correspond to relatively stable lake levels, at 184.5 and 181.5 m, respectively, controlled by outlet elevation (Hough 1963). However, more recent research suggests that the Nipissing and Algoma phases were short-lived, high-water events within a fluctuating system, characterized by climatically-driven water-level fluctuation lasting 200–300 years (Larsen 1985, Hansel et al. 1985, Thompson and Beadke 1997).

Although the last 2,500 years is generally thought to be a period of relative stability, with water-level fluctuation of less than 1 m about the annual mean, radiocarbon-dated samples along Lake Michigan suggest that broader, climatically-driven fluctuation characteristic of the Nipissing and Algoma phases, may be continuing to the present (Larsen 1985; Thompson 1992; Thompson and Beadke 1995, 1997). High-water levels up to 2 m above the modern annual mean at 400, 900, 1,500, and 2,300 B.P. suggested by the study of a beach ridge complex along the southwestern Lake Michigan shoreline (Larsen 1985) are in general agreement with the timing of high water levels indicated by studies of numerous beach ridge complexes along Lake Michigan (Thompson 1992; Thompson and Beadke 1995, 1997).

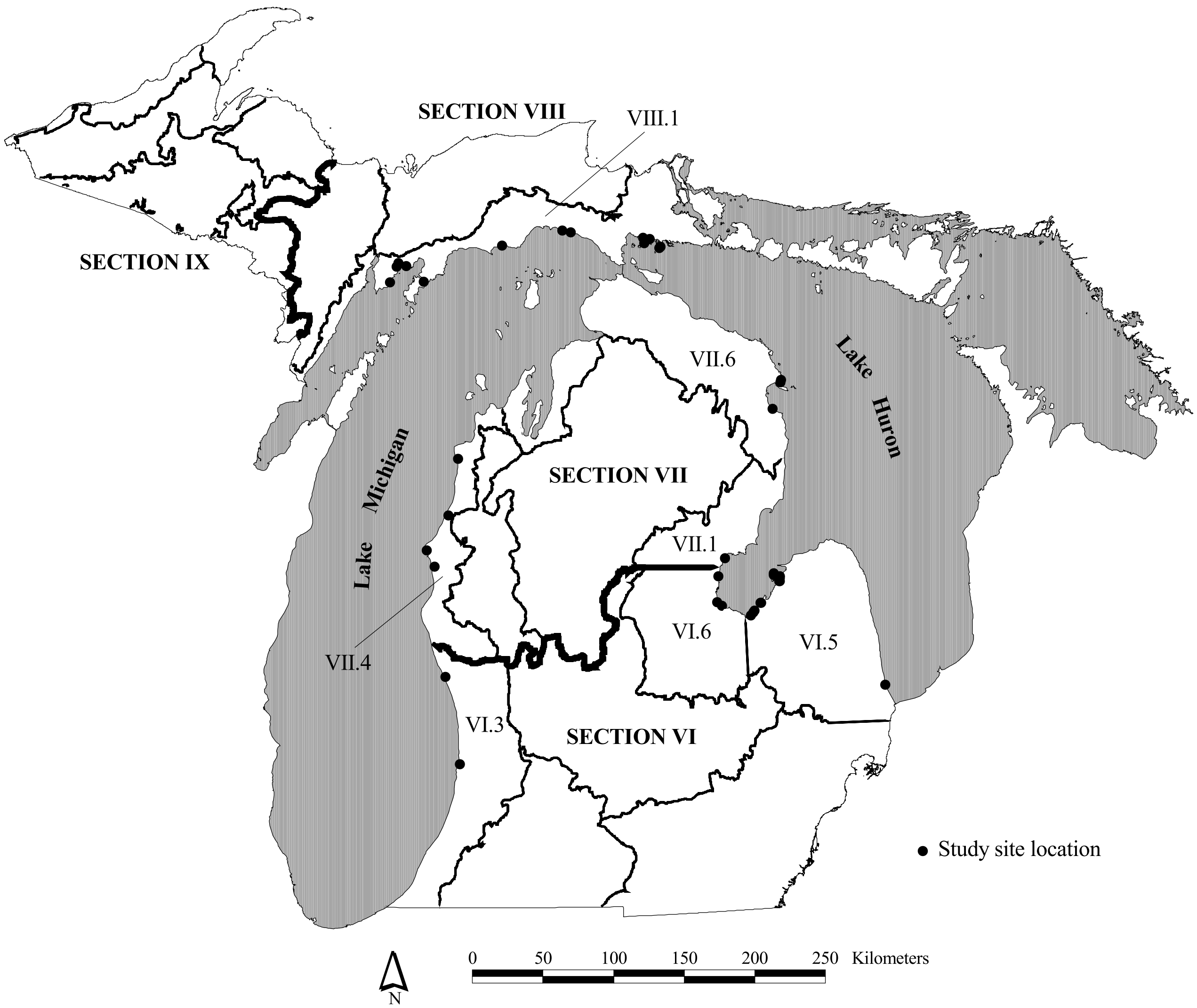

Figure 1. Location of 42 swamp forests sampled along the Lake Michigan and Lake Huron shorelines in relation to regional ecosystem boundaries (ecoregion map follows Albert 1995, thick lines delineate sections, thin lines delineate subsections).

Study Sites

A total of 42 swamp forests were sampled along the Lake Michigan and Lake Huron shorelines (Figure 1). All study sites were located within the elevational range of 177–179 m, less than 3 m above the modern annual mean water level of 176.4 m (Bishop 1990). In Upper Michigan, five sites were sampled along Lake Huron and eight along Lake Michigan (Subsection VIII.1). In Lower Michigan, 21 sites were sampled along Lake Huron: 3 along the northern shoreline (Subsection VII.6), 17 along Saginaw Bay (Subsections VI.6, VI.5, and VII.1), and 1 adjacent to the St. Clair River (Subsection VI.5). Along the eastern Lake Michigan shoreline, six sites were sampled at mouths of the Betsie, Manistee, Big Sable, and Pere Marquette Rivers in northwestern Lower Michigan (Subsection VII.4). Due to heterogeneity of rivermouth valleys of the Betsie and Manistee Rivers, two sites were sampled at each of these valleys. Two sites were sampled in southwestern Lower Michigan (Subsection VI.3), at mouths of the Muskegon and Kalamazoo Rivers (Figure 1).

Study sites extended over approximately 3.5º latitude, encompassing a broad range of climatic conditions. Growing season length ranged from 120 days along northern shorelines (Subsection VII.6), to 157 days along the southeastern Lake Michigan shoreline (VI.3) (Albert et al. 1986) (Table 1). Along the northern shorelines in Upper Michigan (VIII.1), growing season temperature averaged

Table 1. Mean climatic variables for subsections where sampling was conducted.[1]

	Northern Lake Michigan & Northern Lake Huron		Southern Lake Huron		Eastern Lake Michigan	
Variable	VIII.1	VII.6	VI.6	VI.5	VII.4	VI.3
Growing season length (days)	125	120	153	151	141	157
April–October heat sum (°C-days, base 7.2 °C)	1,860	2,020	2,500	2,410	2,300	2,560
Heat sum prior to last spring freeze (°C-days)	150	240	190	170	220	210
May–September potential evapotranspiration (mm)	460	470	520	520	500	530
July–August precip. to potential evapotranspiration ratio (%)	74	70	61	63	64	66
Total annual precipitation (mm)	800	770	740	760	840	900
May–September precipitation (mm)	420	400	360	360	380	410
Annual average temperature (°C)	5.2	6.2	8.6	8.2	7.8	9.4
May–September average temperature (°C)	14.9	15.9	17.8	18.1	17.2	18.7
Annual extreme minimum temperature (°C)	-29	-29	-24	-23	-22	-22

[1] Data taken from Table 2 of Albert et al. 1986

3.8ºC colder, and growing season heat sum and potential evapotranspiration averaged 700ºC-days and 70 mm lower, respectively, than in southwestern Lower Michigan (VI.3). Annual average temperature (5.2ºC) and extreme minimum temperature (-29ºC) were also lowest in Upper Michigan (VIII.1) and highest in southwestern Lower Michigan (9.4ºC and -22ºC, respectively) (VI.3). Total annual precipitation varied widely, from 900 mm along the eastern Lake Michigan shoreline in northwestern Lower Michigan (VII.4) to 740 mm along Saginaw Bay (VI.6). However, a large portion of precipitation along the eastern Lake Michigan shoreline is lake-effect snowfall. Growing season precipitation along the eastern Lake Michigan shoreline (380 and 410 mm in Subsections VII.4 and VI.3, respectively) was only slightly greater than that of Saginaw Bay (360 mm in both VI.6 and VI.5) (Table 1).

METHODS

Field Methods

Field work was conducted in two field seasons: summer 2002 and 2003. Sampling was conducted in 447, 200-m^2 sample plots located in 42 coastal swamp forests. In 2002, a total of 235 plots were sampled in 15 sites along Lake Huron (Tepley et al. 2003). The number of plots per site ranged from 8 to 20 (average 16) depending on site size and heterogeneity. In 2003, a total of 212 plots were sampled in 27 sites: 11 along Lake Huron and 16 along Lake Michigan. An average of 8 plots were sampled per site.

A systematic random method was used to locate sample plots. Plots were randomly located along a transect oriented parallel to the gradient in hydrologic and soil characteristics. At sites that were either small in size or relatively homogeneous

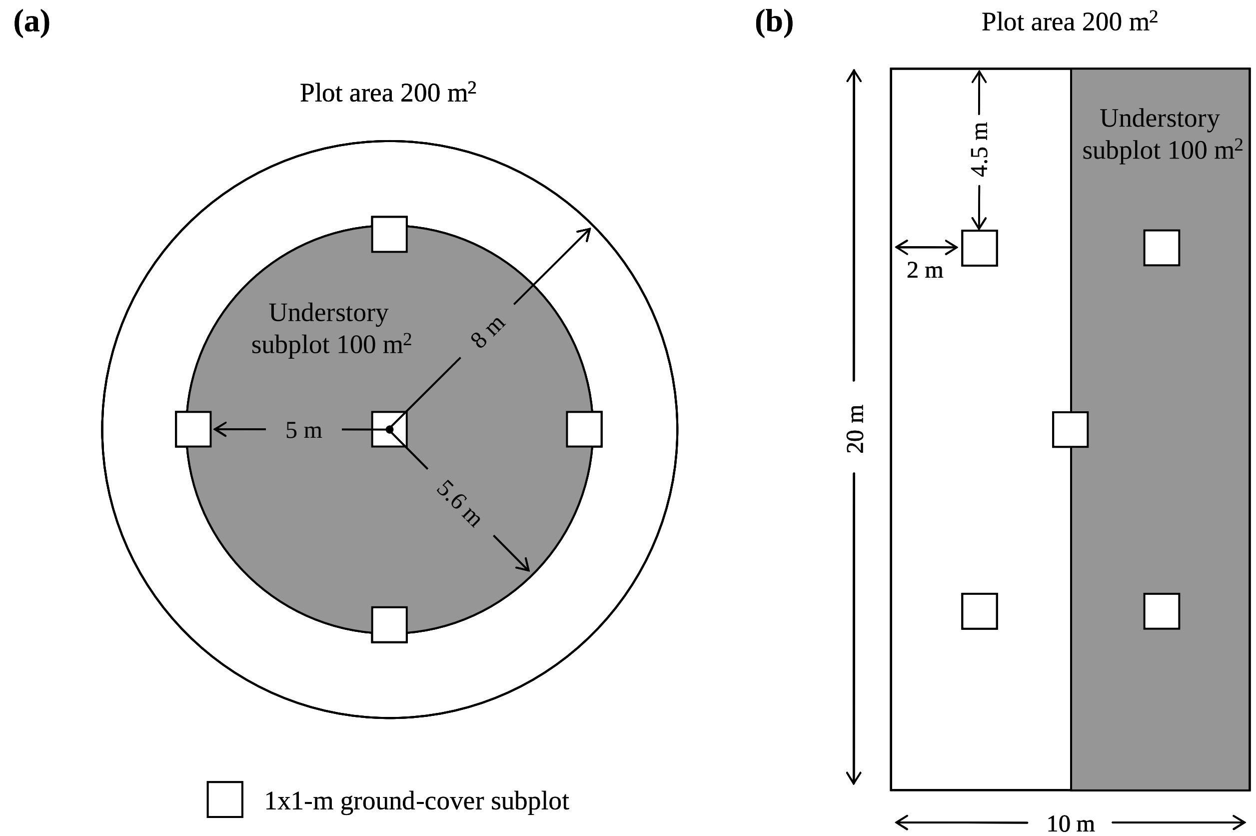

Figure 2. Diagram of (a) circular and (b) rectangular sample plots, illustrating the location and relative size of understory and ground-cover subplots.

in hydrology and soil, transects were established to permit the greatest transect length with the least influence of upland edge conditions. A random number generator was used to determine distance, in number of 20-m chains, from the start of the transect to the center of each sample plot. Plots were separated by a distance of at least two chains, except at the smallest sites, where one-chain spacing was used. Multiple transects were established at large or heterogeneous sites. Because drowned river-mouth valleys often extended several km upstream, transects were separated by a distance of more than 1 km at several sites. A Gramin® XL12 Global Positioning System (GPS) receiver was used to record the location of each plot.

Overstory, understory, and ground-cover vegetation was sampled in 200-m^2 sample plots. In the first field season (2002), sampling was conducted in circular sample plots, 16 m in diameter (Figure 2a). The species and diameter at breast height (dbh) to the nearest 0.1 cm was recorded for all live and standing dead overstory trees (dbh > 9.0 cm) over the entire plot. A DISTO Basic hand-held laser meter was used to determine whether or not trees were located within the plot boundary. Understory vegetation (woody plants taller than 50 cm and up to 9.0 cm dbh) was sampled in a 100-m^2 subplot (11.1 m in diameter) centered within the plot. Understory vegetation was subdivided into two size classes: large understory (1.5–9.0 cm dbh) and small understory (taller than 50 cm and up to 1.5 cm dbh), and the number of stems in each size class was tallied by species. For shrub species (species that do not typically reach overstory size), in addition to stem counts, aereal coverage was estimated to the nearest percent. Ground-cover vegetation (all herbaceous species and woody plants shorter than 50 cm) was sampled in a 1-m^2 subplot, located at the plot center. Aereal coverage of all ground-cover species, as well as water and coarse woody debris (> 9.0 cm in diameter) was estimated to the nearest percent. Ground-cover subplot boundaries were delineated with a 1x1-m wooden sampling frame. To standardize coverage estimates, species coverage within the subplot was compared to a sheet of notebook paper (21.6 x 27.9 cm) representing 6% of

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Photo 1. High-water marks on a red ash tree in the drowned rivermouth valley of the Kalamazoo River, Allegan Co., Michigan.

subplot area. Where standing water was present, water depth was measured to the nearest cm. Where high-water marks were present on the boles of trees (discolored bark on the lower bole resulting from inundation), height of the high-water mark above the soil surface was measured to the nearest cm (Photo 1).

Following analysis of 2002 data, sampling procedures were modified slightly for the second field season. Each site sampled in 2002 was characterized by relatively low variability among plots in overstory composition, but considerably higher variability in ground-cover vegetation. Therefore, in the second field season, a lower number of plots were sampled per site, but the number of ground-cover subplots was increased to five per plot. In addition to the subplot located at the plot center, four ground-cover subplots were located five m from the plot center in each cardinal direction (Figure 2a). Because sampling along Saginaw Bay in 2003 was conducted to be compatible with data collected in a project to analyze disturbance in swamp forests of southern Lower Michigan, sampling procedures were further modified. Sampling was conducted in 200-m^2, rectangular plots (10x20 m), with the 20-m plot lines oriented north-to-south (Figure 2b). Overstory vegetation was sampled over the entire plot. Understory vegetation was sampled in a 100-m^2 subplot, either the east or west half of the plot, chosen randomly by spinning a compass in the field. Ground-cover vegetation was sampled in 5, 1-m^2 subplots, one located at the plot center, and four centered within each quadrant (Figure 2b). Other than reducing the number of plots per site, increasing the number of ground-cover subplots, and using rectangular rather than circular plots along Saginaw Bay, sampling procedures followed those of the 2002 field season.

Soil was sampled within the plot boundary of at least one out of every five plots. Soil was sampled with a 100-cm long core in 2002 and a 200-cm long bucket auger in 2003. Data recorded in each auger boring include substrate type, depth, and pH, and depth to water table and bedrock. Soil textural and pH analyses were conducted in the field. Mineral soil texture was determined following the texture-by-feel flow chart of Thien (1979). For sand soil, sand particle size was estimated by visual comparison to samples of very fine, fine, medium, coarse, and very coarse sand. For organic soil, organic matter type was classified as sapric (< 17% fibers), hemic (17–75 % fibers), or fibric (> 75% fibers); fiber content was estimated by rubbing (USDA 1999). A Hellige-Truogg soil reaction/pH kit was used to measure soil pH. Soil pH was recorded at the soil surface and at depths of 50 and 100 cm in 2002. In 2003, additional soil pH values were recorded at 150 and 200 cm.

The age of one or two dominant overstory trees was recorded at one out of every five plots. An increment borer with a 44-cm long shaft was used to core trees at breast height (137 cm). Cores were read in the field, and four years were added to the age determined from the core to approximate growth before reaching breast height.

Data Analyses

The study sites were classified into 8 ecosystem types based on qualitative analyses of physiography, hydrology, soil, and vegetation data. A ninth ecosystem type (ecosystem 9) was identified based on field reconnaissance and aerial photo interpretation, but field sampling was not conducted in it. Quantitative analyses were conducted to evaluate the distinctness of the ecosystem types and analyze interrelationships among physical site factors and vegetation. Physiogrpahy, hydrology, soil, and vegetation data, collected by sample plot, were averaged for each site. Although ground-cover vegetation was sampled in a larger number of subplots per sample plot in the second field season than the first, the total number of ground-cover subplots per site was similar between field seasons, and data were analyzed together. Two ecosystem types, ecosystems 4 and 9, were excluded from quantitative analyses because only one plot was sampled in ecosystem 4, and field sampling was not conducted in ecosystem 9.

The ecosystem classification and the identification of characteristic ground-cover species of each type were evaluated with two-way indicator species analysis (TWINSPAN; Hill 1979) conducted in PC-ORD (McCune and Mefford 1999). Mean percentage cover values for each ground-cover species at each site were entered into the analysis, excluding plants not identified to species. Because a large number of ground-cover species were sampled, many of which were present at a low number of sites, species occurring at fewer than five sites were excluded from the analysis. Such removal of infrequent species is likely to reduce random variation due to chance presence or absence while removing little information from the data set (Gauch 1982).

Distinctness of the ecosystem types was further evaluated, and identification of characteristic ground-cover species of each type was further supported by detrended correspondence analysis (DCA; Hill and Gauch 1980) conducted in CANOCO (ter Braak and Šmilauer 1998). DCA was conducted with the data set containing mean percentage cover values for each ground-cover species at each site, excluding plants not identified to species level and species occurring at fewer than five sites. Distinctness of each ecosystem type with respect to ground-cover species composition was evaluated by plotting site scores along the first two DCA axes, where site scores represent the weighted mean of species scores present at each site.

The influence of environmental and stand structure variables on the ordination of ecosystem types with respect to ground-cover species composition was examined using canonical correspondence analysis (CCA; ter Braak 1986), conducted in CANOCO (ter Braak and Šmilauer 1998). The data set containing mean percentage cover values for each ground-cover species at each site (used in TWINSPAN and DCA) was constrained with a set of eight environmental and stand structure variables suspected to have the strongest effect upon ground-cover species composition. The following variables were entered into the analysis: depth of organic soil (cm), range of soil surface pH, height of the high water mark (cm), overstory density (stems/ha), overstory basal area (m^2/ha), large understory stem density (stems/ha), small understory tree density (seedlings/ha), and coverage of shrubs (%). The variable, 'range of soil surface pH,' was used rather than average soil surface pH because many sites were characterized by pit-and-mound microtopography with very strongly acid soil on hummocks and circumneutral soil between hummocks (Boelter and Verry 1977). Because certain ground-cover species were restricted to acid hummocks and others were common in hollows between hummocks, the range of soil surface pH was suspected to more accurately account for variation among sites than average pH. Site scores, derived from species coverage and constrained by environmental and stand structure variables, were examined in the ordination space of the first two CCA axes. The significance of the first two axes and that of each variable to the analysis was determined using a stepwise Monte Carlo procedure with 199 permutations and $\alpha = 0.05$ (ter Braak and Šmilauer 1998).

Land-Cover Analysis

To assist in prioritizing restoration efforts among ecosystem types, historical and present land cover along the Lake Michigan and Lake Huron shorelines was analyzed in a Geographical Information System (GIS). A Digital Elevation Model (DEM) with 90-m resolution (USGS 1984–1992) was used to identify all 90-m pixels at elevations lower than 180 m and contiguous to the shoreline. For land lower than 180 m and contiguous to the shoreline, historical vegetation was determined based on the Circa 1800 data set of Comer et al. (1995a). Circa 1800 land cover is a statewide data set, with 30-m resolution, developed based on interpretation of the original General Land Office (GLO) surveys of Michigan (Comer et al. 1995b). For land lower than 180 m, contiguous to the shoreline, and identified as swamp forest in the Circa 1800 data set, present land cover was determined based on IFMAP/GAP Michigan 2000 land cover (MDNR 2001). The 2000 land cover data set was developed from Landsat Thematic Mapper (TM) imagery from spring, summer, and fall 1997–2001. Supervised classification was used to classify land cover into 35 classes modified from level 2 of Andersen et al. (1976). All GIS analyses were conducted in ArcView 3.2 (ESRI 2000).

RESULTS AND DISCUSSION

Ecological Classification

Major and Minor Shoreline Segments

A three-level, hierarchical classification was developed for swamp forests along the Lake Michigan and Lake Huron shorelines. At the highest level of classification, the shorelines were divided into two Major Shoreline Segments: (I) Lake Huron and the northern Lake Michigan, and (II) eastern Lake Michigan (Table 2). Subdivision of major shoreline segments was based on gross physiographic characteristics that result in the occurrence of swamp forests in a different generic landform along each segment: former embayments along Lake Huron and northern Lake Michigan, and drowned river mouths along eastern Lake Michigan.

Along the Lake Huron and northern Lake Michigan shorelines, former embayments of various size are situated between moraines, areas of thin till over bedrock, or dunes (Figures 3–5). Within such embayments, fluctuation in lake level through the late Holocene resulted in the formation of a nearly flat plain just above the high water level, characterized by numerous beach ridges (typically less than 5 m high and 10–30 m wide) and intervening swales (often less than 30 m wide) oriented parallel to the shoreline (Comer and Albert 1993, Thompson and Beadke 1997). Each beach ridge was formed when lake levels fell from a previous higher Great Lakes water level (Olson 1958). Swamp forests occur in the inter-ridge swales and depressions, and in gently sloping groundwater seepages along the margin of the embayment. The regular patterning of ridges and swales is not always apparent along Saginaw Bay due to the large size of the embayment, small amounts of sand available to be reworked as lake levels receded, and past modifications of the landscape for agricultural management.

In contrast to the low beach ridges and swales within former embayments along Lake Huron and northern Lake Michigan, prevailing westerly winds led to the formation of large dunes (up to 60 m high) along the eastern Lake Michigan shoreline. Swamps are restricted to broad valleys at the mouths of Lake Michigan tributaries. During Chippewa low water levels, the river mouths were located far to the west and lower than the modern shoreline, within present Lake Michigan. The rise in water level following isostatic uplift of the northern outlet forced the river mouths inland of the modern shoreline. Later, as water levels receded, river mouths were partially closed by growth of sand spits and baymouth bars, resulting in the formation of shallow, inland lakes at the same elevation as Lake Michigan, and connected to it by a short, narrow channel (Figure 6, Appendices A1–A6). Large dunes, most likely related to Nipissing high water levels were formed on top of the sand spits and baymouth bars, increasing constriction of the river mouth (Dorr and Eschman 1970 p.194-195).

Each Major Shoreline Segment was further divided into two Minor Shoreline Segments– northern and southern, on the basis of climatic and physiographic characteristics (Table 2). Subsections of the regional ecosystem classification of Albert (1995) were used to delineate boundaries of the Minor Shoreline Segments (Figure 7). Colder climate of the northern segments (A and C) resulted in a shorter growing season and slower rates of organic matter decomposition than along southern segments (B and D). Differences between wetlands along northern and southern parts of the shoreline also may reflect different historical development of the wetlands due to a greater rate of isostatic uplift in the north than the south (Larsen 1985, 1994). In addition, the geographic range of many plant species is restricted to either the northern or southern part of the state, though some may extend their range southward along the lakeshore (Denton and Barnes 1987).

Ecosystem Types

At the finest level of classification, a total of nine Ecosystem Types were identified (Table 2, Appendix B). Within each minor shoreline segment, two or three ecosystem types recur in a mosaic, reflecting underlying patterns of fine-scale physiographic features, hydrology, and soil. Ecosystem types of each minor shoreline segment are distinguished from each other by their position in relation to the shoreline and the resulting effect of groundwater hydrology, as influenced by shoreline configuration and Great Lakes water levels, on their hydrologic regime, soil, and vegetation (Table 2) (a detailed description of each ecosystem type is included in Appendix C).

Table 2. Ecological classification of swamp forests along the Lake Michigan and Lake Huron shorelines.

Classification			Physiography	Hydrology	Soil		Vegetation	
Major Shoreline Segment	Minor Shoreline Segment (Subsection)	Eco-system Type	Landform	Regime Modifier[1]	Substrate[2]	pH[3]	Canopy Dominants	Ground Cover[4]
(I) Lake Huron & northern Lake Michigan (embayments)	**(A)** Northern Lake Huron & northern Lake Michigan (VIII.1 & VII.6)	**1**	swales, depressions, & seepages	Saturated	SM over FS	7.1 (4.4)	Northern white-cedar	*Coptis trifolia, Mitella nuda*
		2	swales & depressions	Semipermanently inundated	SM over FS	7.3	Red ash	*Carex stricta*
	(B) Southern Lake Huron (VI.6 & VI.5)	**3**	swales & depressions	Seasonally inundated	FS over C	7.2	Silver maple, red ash, American elm	*Glyceria striata, Boehmeria*
		4	swales, depressions, & seepages	Saturated	FS, or SM over FS	7.0	Northern white-cedar, tamarack	*Smilacina stellata, Solidago gigantea*
		5	broad, flat terrain on islands	Intermittently inundated	FS over R	7.2	Red ash	*Carex stricta, Calamagrostis canadensis*
(II) Eastern Lake Michigan (drowned river mouths)	**(C)** Eastern Lake Michigan shoreline, northern Lower Michigan (VII.4)	**6**	valley floor	Seasonally inundated	L-SiCL over FS	7.3	Red ash, silver maple, American elm	*Carex lacustris*
		7	seepages along valley margin	Saturated	SM & HM over Ma	7.5 (4.2)	Northern white-cedar, eastern hemlcok, yellow birch, black ash, red maple	*Osmunda cinnamomea*
	(D) Eastern Lake Michigan shoreline, southern Lower Michigan (VI.3)	**8**	valley floor	Seasonally inundated	L-SiCL over FS	7.2	Silver maple, red ash, American elm	*Saururus cernuus, Peltandra virginica*
		9	seepages along valley margin	Saturated	SM & HM over Ma	7.2 (4.5)	Northern white-cedar, tamarack, eastern hemlock, yellow birch, black ash, red maple	*Osmunda cinnamomea*

[1] Hydrologic regime modifiers follow Cowardin et al. 1979
[2] SM = sapric muck, FS = fine sand, C = clay, R = limestone bedrock, L = loam, SiCl = silty clay loam, HM = hemic muck, Ma = Marl
[3] minimum soil pH recorded on hummocks is in parentheses
[4] one or two of the most characteristic species are listed

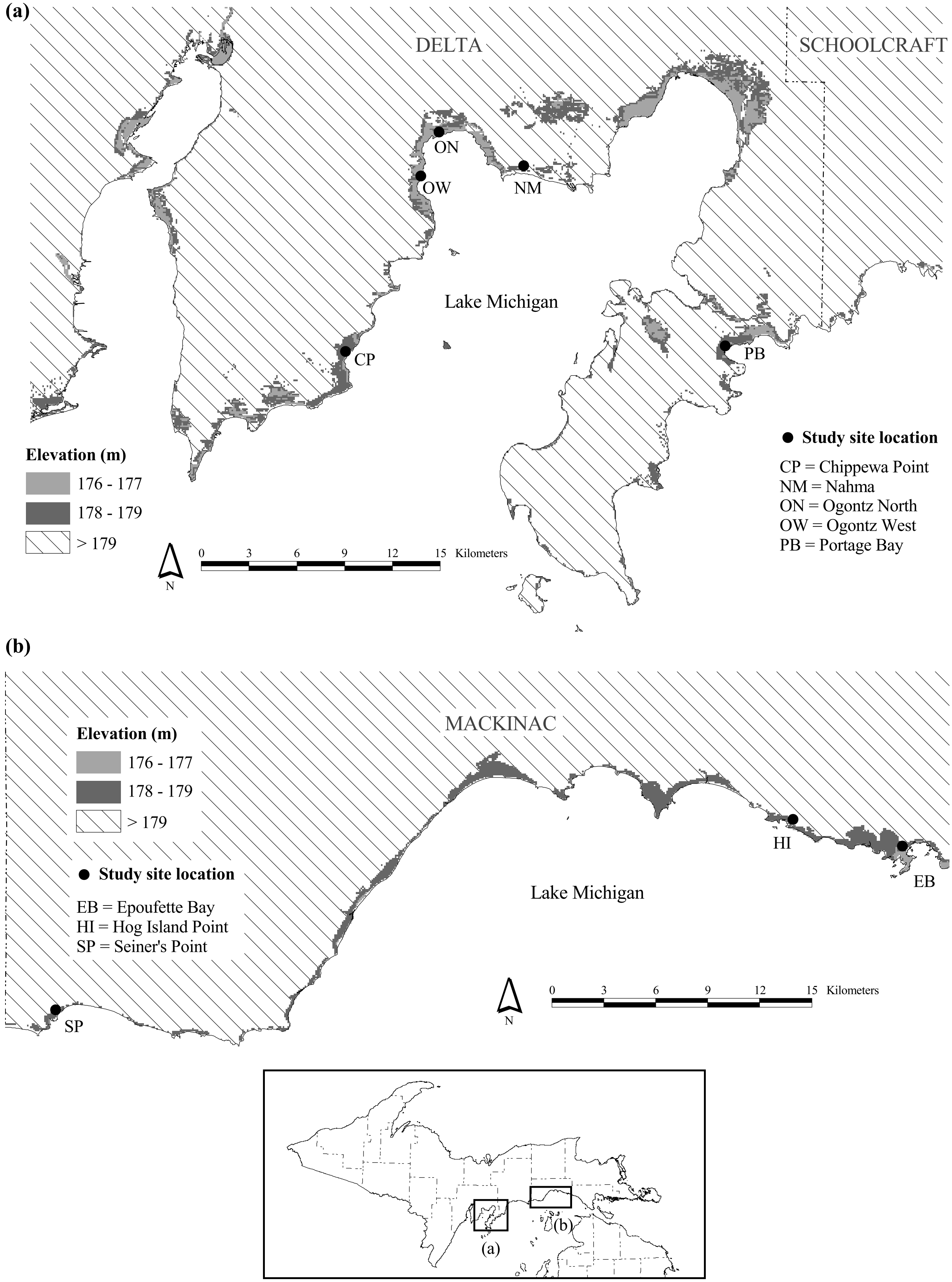


Figure 3. Location of (a) five study sites in Delta County and (b) three study sites in Mackinac County within former embayments along the northern Lake Michigan shoreline.

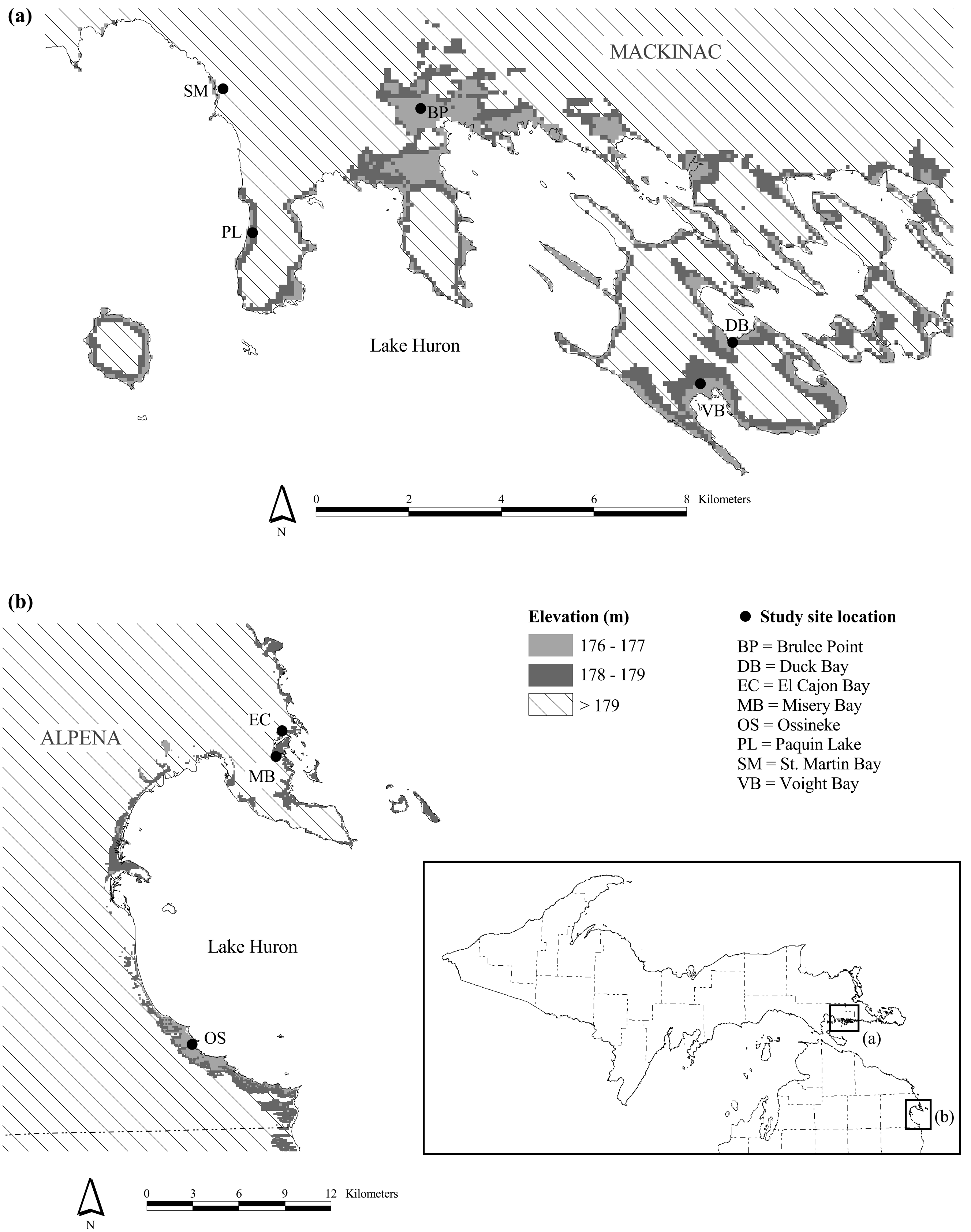


Figure 4. Location of (a) five study sites in southeastern Upper Michigan and (b) three study sites in northeastern Lower Michigan within former embayments along the northern Lake Huron shoreline.

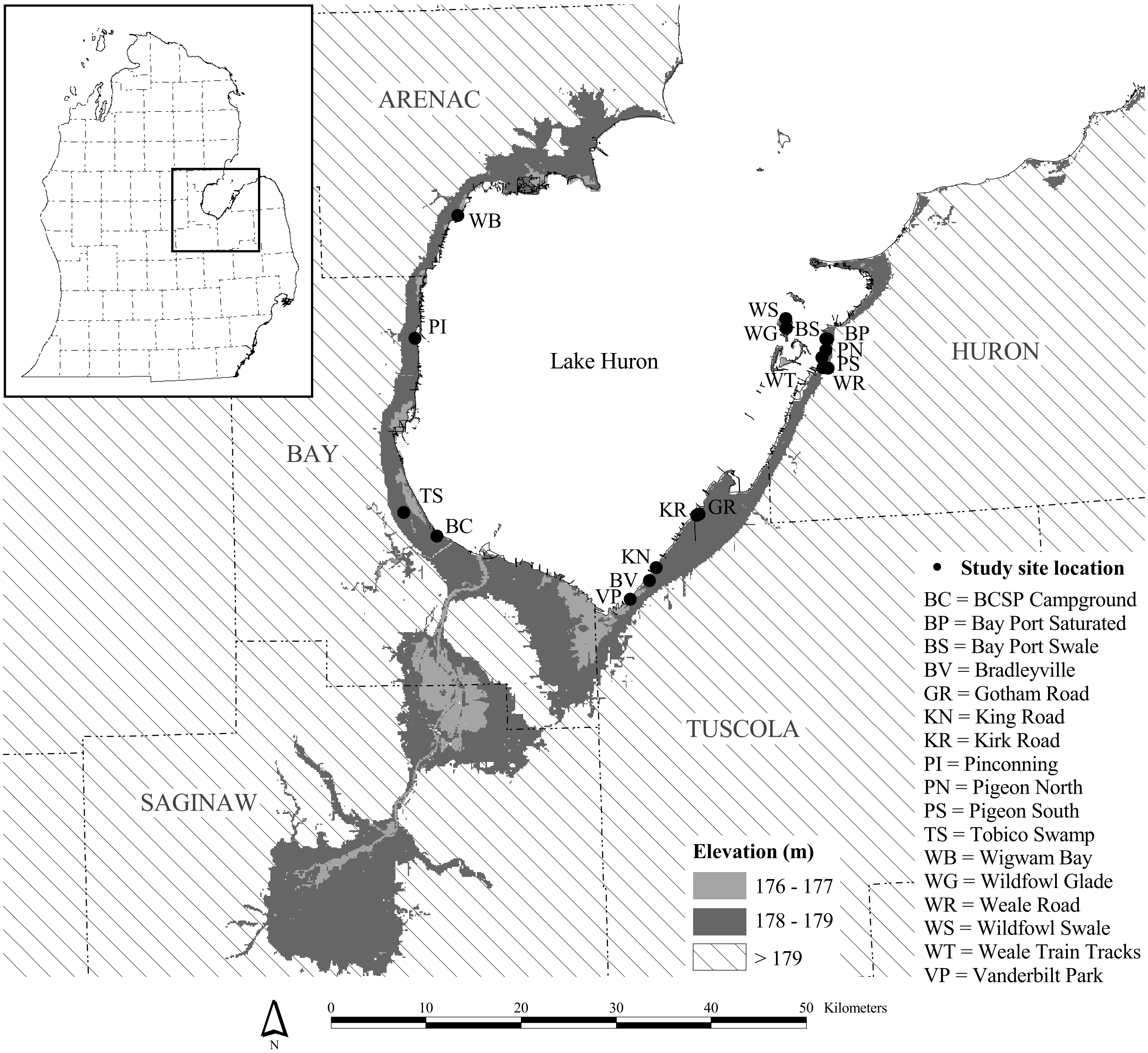


Figure 5. Location of 17 study sites along the Saginaw Bay shoreline, east-central Lower Michigan, in relation to elevation.

Each minor shoreline segment contains one or two ecosystem types located close to the shoreline, at an elevation within or slightly higher than the range of lake-level fluctuation (ecosystems 2, 3, 5, 6, and 8), and another ecosystem located further inland and at a higher elevation (ecosystems 1, 4, 7, and 9) (Figures 8–11). Whereas the ecosystem types located close to the shore (ecosystems 2, 3, 5, 6, and 8) are characterized by periodic soil surface inundation during the growing season, those located further inland (ecosystems 1, 4, 7, and 9) are characterized by saturated soil resulting from groundwater influence (Table 2).

In the inundated ecosystem types, the timing and duration of inundation is either directly regulated by the Great Lakes, or indirectly regulated by the lakes through their influence on local groundwater hydrology (Visocky 1977). Because the elevation of ecosystems 2 and 5 is approximately equal to the maximum annual mean lake level of 177.1 m (Bishop 1990), water-level fluctuation in the Great Lakes has a direct influence on their hydrologic regime (Figures 8 and 10). During periodic high lake levels, the soil surface may remain inundated throughout the growing season, resulting in mortality of most, if not all, tree

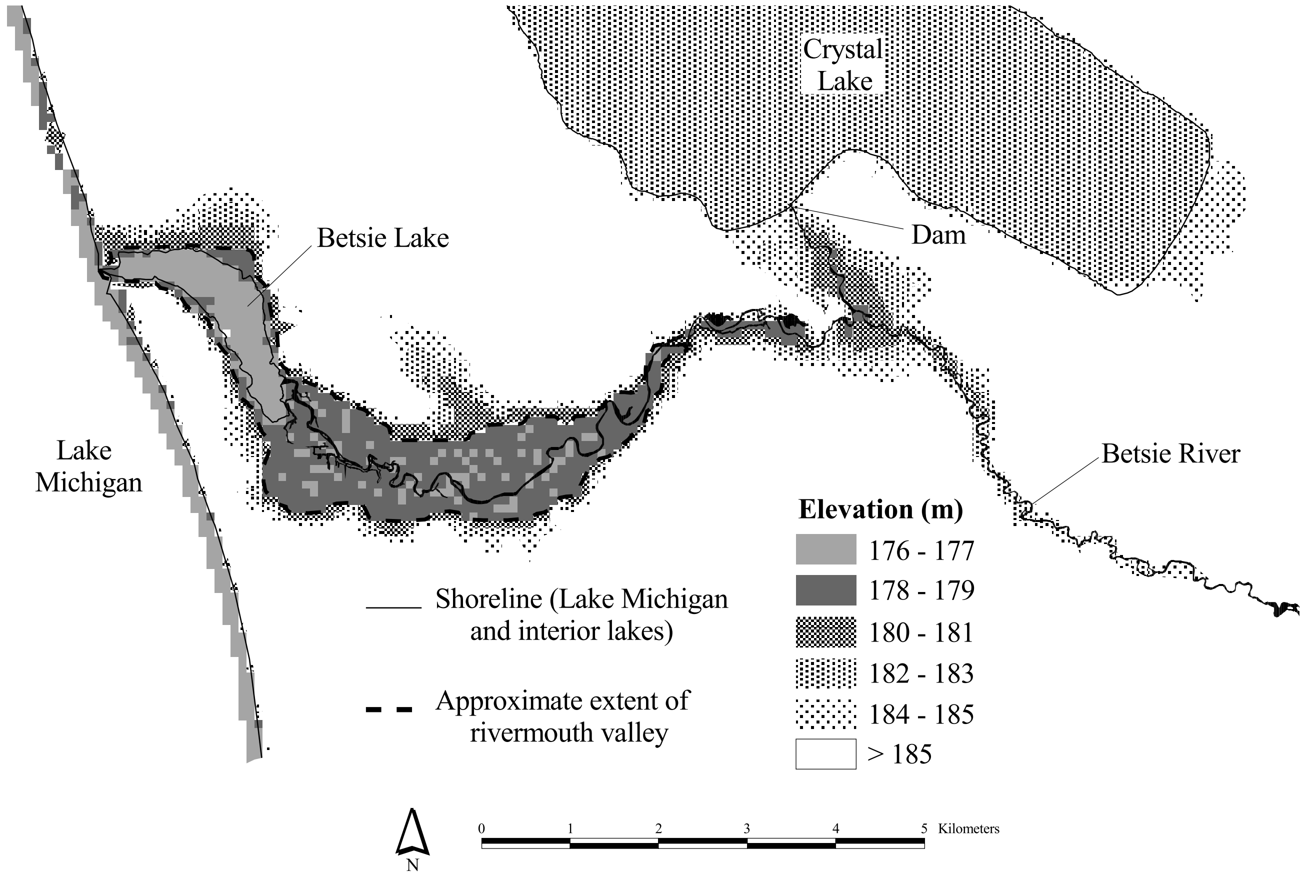


Figure 6. Comparison of the broad, flat drowned river-mouth valley of the Betsie River, northwestern Lower Michigan, to the narrow, steeper valley upstream.

seedlings and saplings. If water levels remain high for several consecutive years, mature trees also would be killed (Hook 1984).

The other inundated ecosystem types (ecosystems 3, 6, and 8) are typically located at elevations above the maximum lake level, and the Great Lakes have an indirect effect on their hydrologic regime. Thus, ecosystem types 3, 6, and 8 are characterized by seasonal inundation of the soil surface, where surface water may persist through mid-July, corresponding to seasonal high lake levels (Quinn 2002). However, the water table often falls more than 100 cm below the soil surface later in the growing season. Periodic inundation of the soil surface followed by soil aeration when surface water recedes enables high rates of decomposition, thereby preventing accumulation of organic soil. As a result, all inundated ecosystem types are characterized by a substrate of mineral soil. However, in ecosystem 2, where the water table remains close to the soil surface after surface water recedes, the substrate is a shallow layer of sapric muck (< 20 cm deep) over mineral soil (Figure 8, Appendix C).

Ecosystems located further from the shore and at a higher elevation than the inundated ecosystems are characterized by saturated soil and a substrate of organic soil (Table 2). Differences in hydrologic regime between saturated ecosystems located in former embayments (ecosystems 1 and 4) and those located in drowned river mouths (ecosystems 7 and 9) result in marked differences in substrate. Ecosystems 1 and 4 are characterized by a shallow layer of sapric muck (typically less than 30 cm deep) over sand (Table 2, Figures 8 and 9). Due to convergence of groundwater flow in embayments (Cherkauer and McKereghan 1991), combined with shallow depth to impervious clay, and the influence of local topographic features on groundwater flow, the water table is slightly higher than the sand surface early in the growing season, and the overlying organic soil is saturated by capillary water. Later in the growing season, the water table falls below the sand surface, but water is maintained

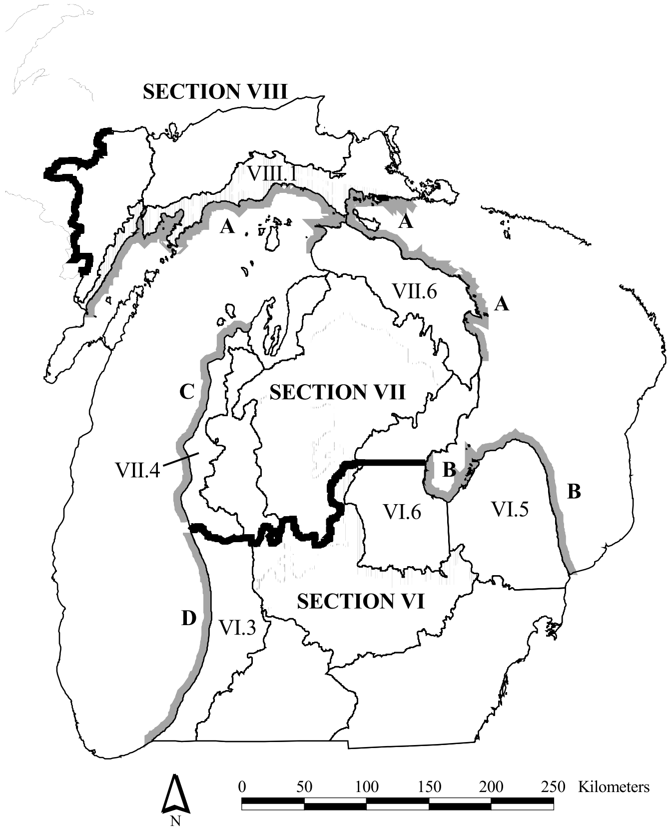


Figure 7. Minor Shoreline Segments of the Lake Michigan and Lake Huron shorelines in relation to subsections of Albert (1995) (letters A-D correspond to Table 2).

in the small pores of the sapric muck, and near saturated conditions are maintained (Boelter and Verry 1977). In contrast, due to the location of ecosystems 7 and 9 at the base of steep slopes along the margin of rivermouth valleys, groundwater seepage is continuous and the water table is maintained close to the soil surface throughout the growing season. Continuous groundwater seepage facilitates deep accumulations of sapric and hemic muck (average depth > 150 cm) (Figure 11, Appendix C). In all saturated ecosystems (ecosystems 1, 4, 7, and 9), shallow rooting in the organic soil in combination with strong winds coming off the lakes results in a high frequency of windthrow and well developed pit and mound microtopography (Figures 8, 9 and 11). In addition to tip-up mounds, hummocks are often built up at the bases of trees, and they are often covered by sphagnum mosses.

Differences among ecosystem types in hydrology and soil, as influenced by their position in relation to the shoreline, result in marked differences in forest composition and structure (Table 3, Appendices D1–D2; comparison of forest composition and structure among sites within each ecosystem type are included in Appendices E1–E3, F1–F4, G1–G4, H1–H4, I1–I4, and J1–J4). Whereas the inundated ecosystem types (ecosystems 2, 3, 5, 6, and 8) are dominated by hardwoods, saturated ecosystems (ecosystems 1, 4, 7, and 9) are dominated primarily by conifers (Table 3). In all minor shoreline segments, total overstory stem density of the inundated ecosystem type averages 47–57% lower, and basal area averages 39–62% lower than that of the saturated ecosystem type (Table 3). Overstory basal area is lowest in ecosystems 2 and 5 (21.3 and 22.3 m^2/ha, respectively), which are located closest to the shore and at the lowest elevation. These ecosystems are characterized by widely-spaced, small trees, and a continuous, graminoid-dominated ground-cover layer (Figures 8 and 10, Photos 2 and 3). Red ash (*Fraxinus pennsylvanica* Marsh.) accounts for 81 and 90% of the overstory basal area in ecosystems 2 and 5, respectively, and it is practically the only tree species capable of surviving prolonged inundation of the soil surface when lake levels are high. Tree species other than red ash are primarily restricted to high microsites near the upper boundary of the ecosystem (Figure 8).

Inundated ecosystem types 3, 6, and 8, which are located further from the shore and at a slightly higher elevation than ecosystems 2 and 5, are dominated by silver maple (*Acer saccharinum* L.) in addition to red ash, and their total overstory basal area (28.7–45.1 m^2/ha) is substantially greater than that of ecosystems 2 and 5 (Table 3). Variation in microtopography in ecosystem 3 results in the occasional occurrence of eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) and swamp white oak (*Quercus bicolor* Willd.) on low rises. Greater water depth and a lack of such microtopography account, in part, for the absence of these species in ecosystems 6 and 8 (Table 3, Figure 10). Small American elm (*Ulmus americana* L.) trees are common in the understory of ecosystem types 3, 6, and 8 (Appendix D1–D2), indicating that American elm was likely also a canopy dominant prior to the introduction of Dutch elm disease (Figure 8) (Barnes 1976). In ecosystem 3, the combination of inundation of the soil surface, often through mid July, and relatively dense tree canopy coverage result in a sparse, patchy distribution of ground-cover vegetation and low diversity and coverage of shrub species (Photo 4). Compared to ecosystem 3, deeper inundation and lower tree

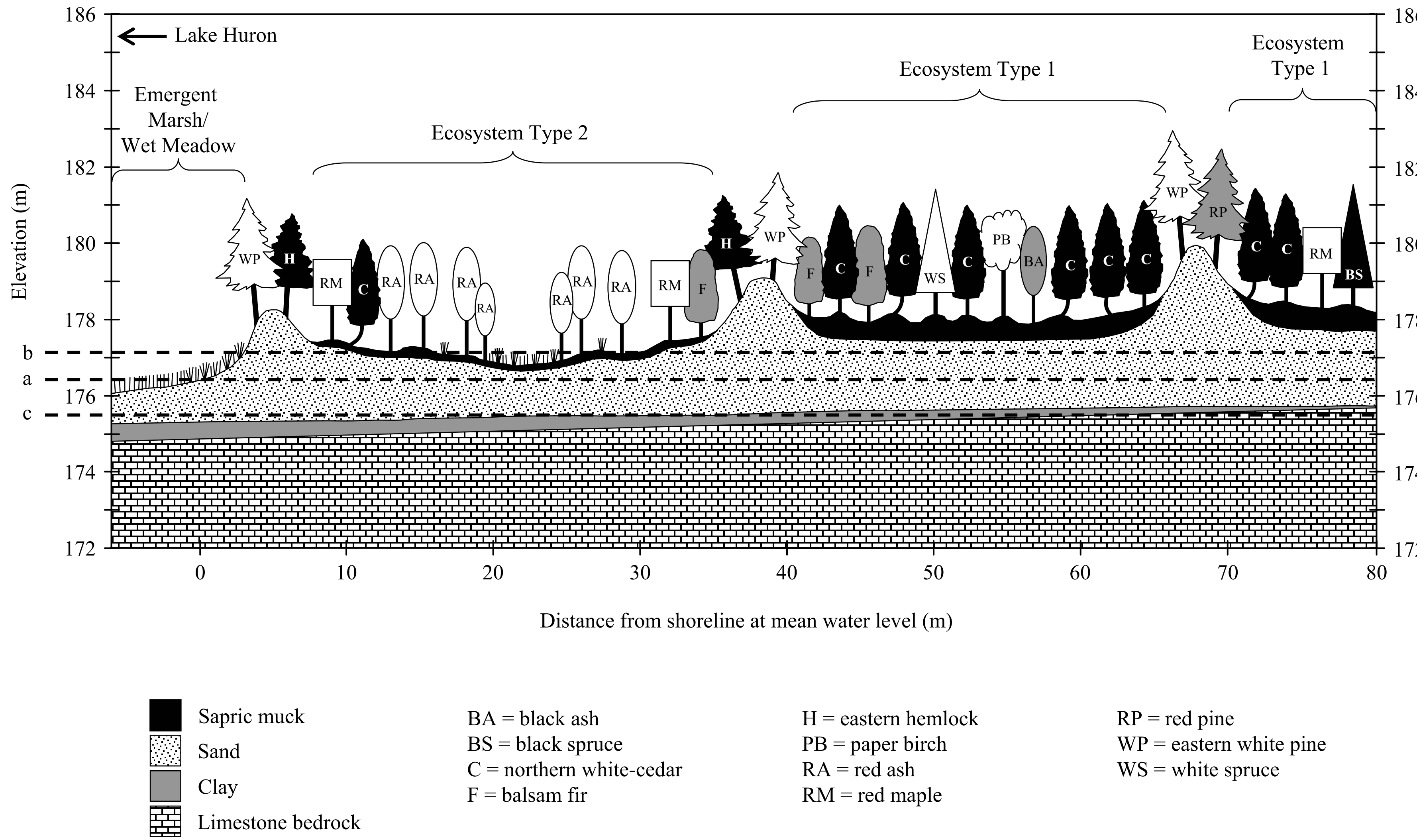


Figure 8. Comparison of the location, substrate, and overstory species composition of ecosystem types 1 and 2 along an idealized cross-section of a transect across a beach ridge and swale complex of the northern Lake Huron shoreline. Mean (176.4 m), maximum (177.1 m), and minimum (175.5 m) annual lake level is indicated by a, b, and c, respectively (Bishop 1990) (trees are not drawn to scale).

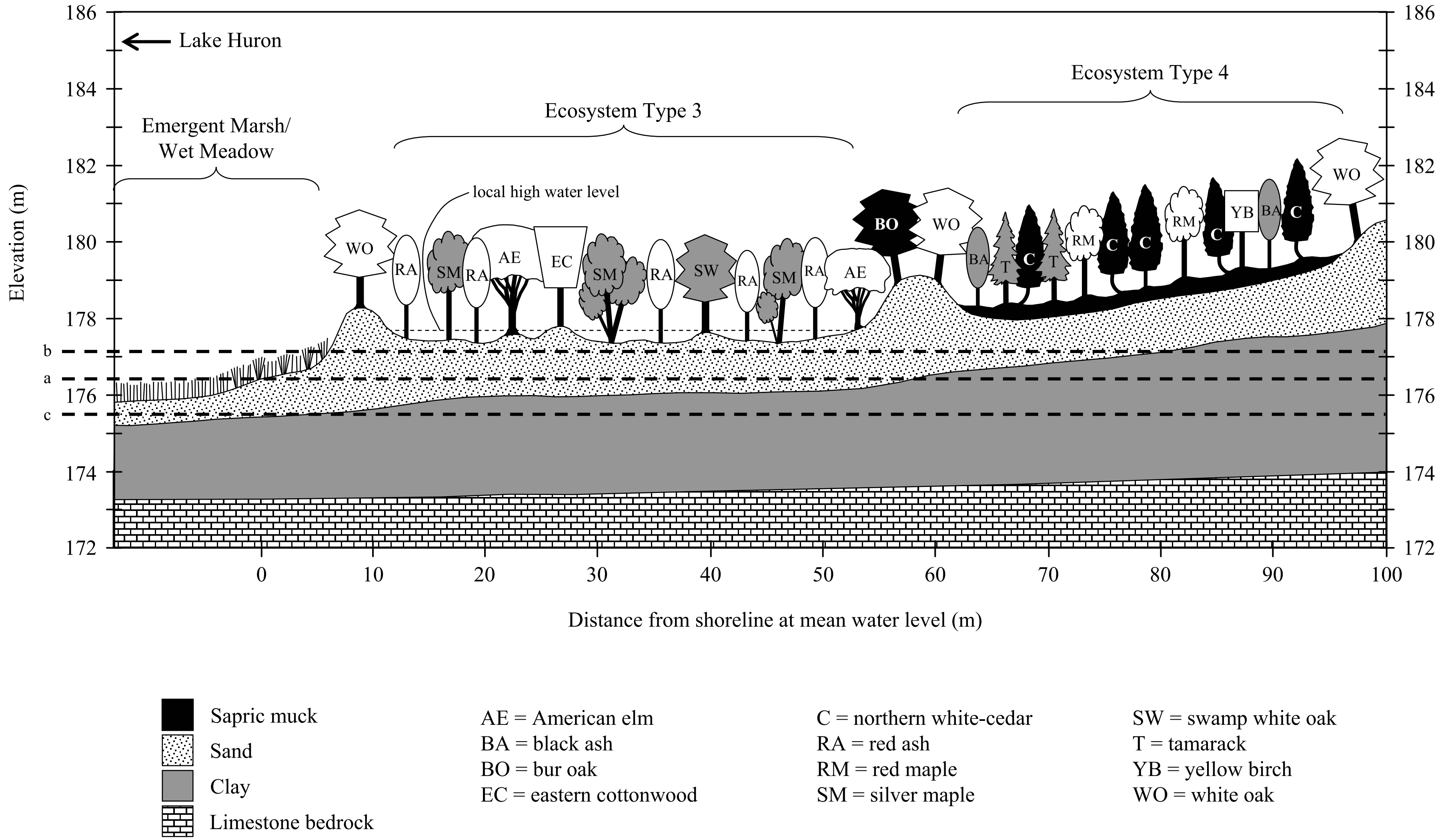


Figure 9. Comparison of the location, substrate, and overstory species composition of ecosystem types 3 and 4 along an idealized cross-section of a transect across a beach ridge and swale complex of the southern Lake Huron shoreline. Mean (176.4 m), maximum (177.1 m), and minimum (175.5 m) annual lake level is indicated by a, b, and c, respectively (Bishop 1990) (trees are not drawn to scale).

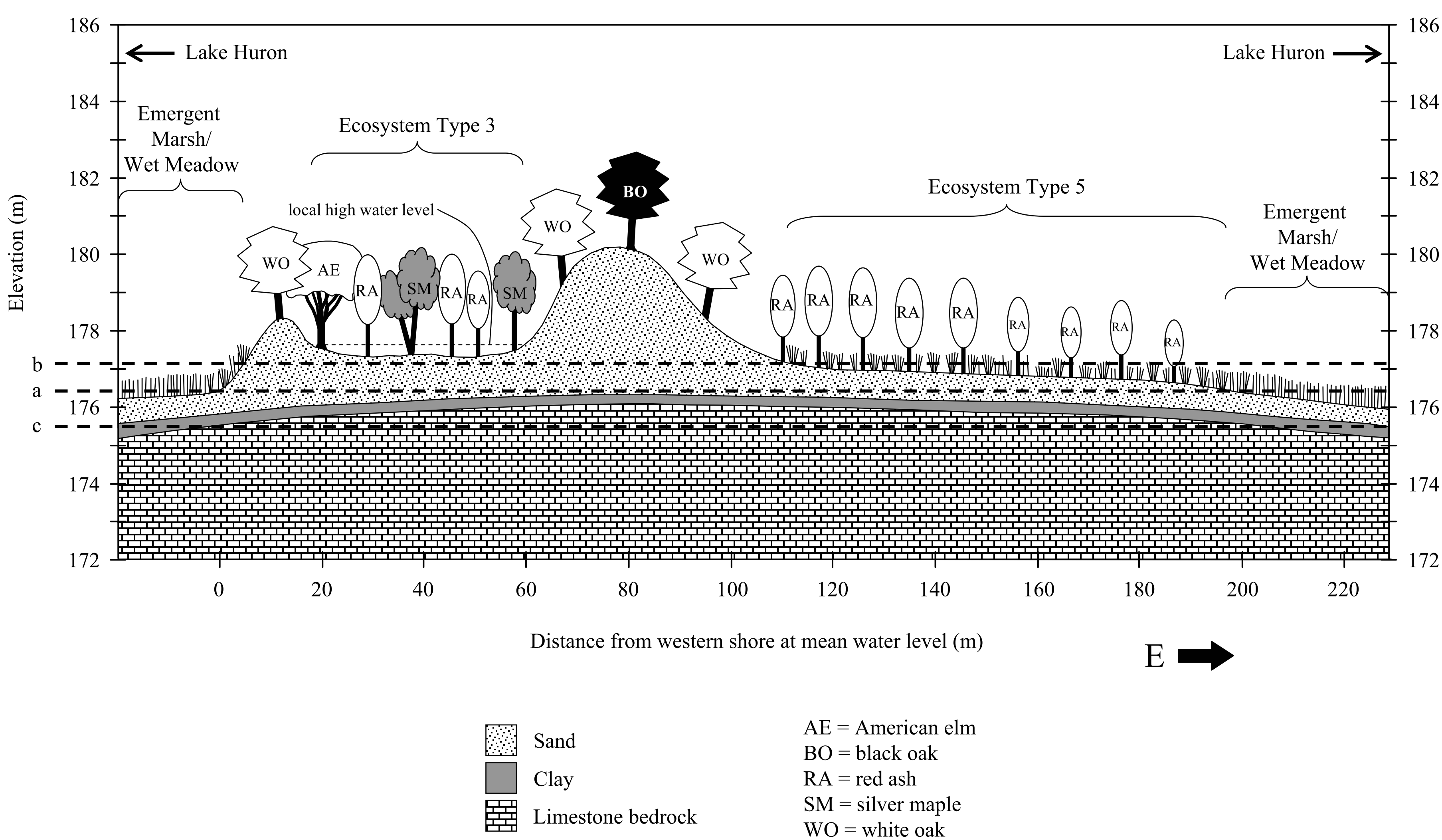


Figure 10. Comparison of the location, substrate, and overstory species composition of ecosystem types 3 and 5 along an idealized cross-section of a transect across Heisterman Island of southern Lake Huron. Mean (176.4 m), maximum (177.1 m), and minimum (175.5 m) annual lake level is indicated by a, b, and c, respectively (Bishop 1990) (trees are not drawn to scale).

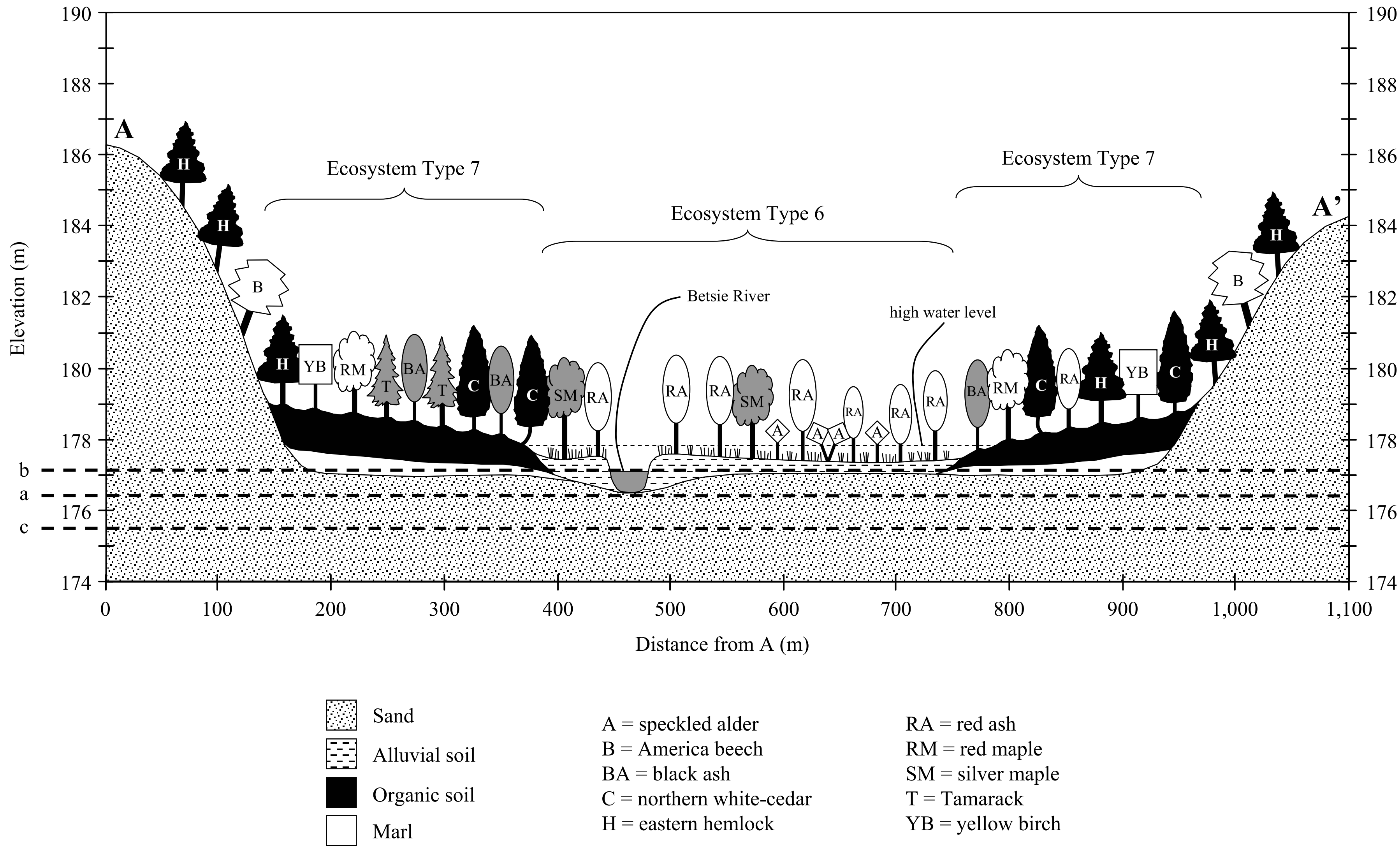
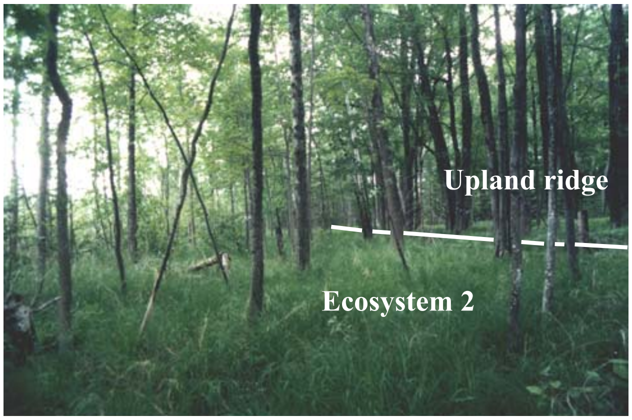


Figure 11. Comparison of the location, substrate, and overstory species composition of ecosystem types 6 and 7 along an idealized cross-section of a transect across the drowned rivermouth valley of the Betsie River, northwestern Lower Michigan. Mean (176.4 m), maximum (177.1 m), and minimum (175.5 m) annual lake level is indicated by a, b, and c, respectively (Bishop 1990) (trees are not drawn to scale).

Table 3. Comparison of overstory composition among eight swamp ecosystems along the Lake Michigan and Lake Huron shorelines.[1]

	Lake Huron and norhtern Lake Michigan Shorlelines					Eastern Lake Michign Shoreline		
	Northern Shoreline		Southern Shoreline			Northern Shoreline		Southern Shoreline
Species	1	2	3	4	5	6	7	8
Thuja occidentalis	46.7 (81)	0.3 (2)	--	61.0 (94)	--	0.1 (0)	23.2 (58)	--
Betula papyrifera	2.3 (4)	0.7 (3)	0.0 (0)	--	--	--	0.6 (1)	--
Picea glauca	1.3 (2)	--	--	--	--	--	--	--
Picea mariana	0.9 (2)	0.1 (0)	--	--	--	--	--	--
Abies balsamea	1.1 (2)	0.3 (1)	--	--	--	--	--	--
Tsuga canadensis	0.0 (0)	--	--	--	--	--	7.3 (14)	--
Larix laricina	0.2 (1)	0.4 (3)	--	1.7 (3)	--	--	1.0 (2)	--
Fraxinus nigra	1.5 (3)	0.5 (2)	0.0 (0)	--	0.0 (0)	0.9 (4)	3.6 (8)	--
Acer rubrum	0.3 (1)	1.6 (7)	--	--	--	--	4.4 (9)	--
Betula alleghaniensis	0.1 (0)	--	--	--	--	0.0 (0)	1.8 (4)	--
Fraxinus pennsylvanica	0.1 (0)	17.1 (81)	13.3 (41)	--	20.0 (90)	15.1 (62)	1.3 (4)	7.8 (21)
Acer saccharinum	--	0.2 (0)	14.5 (35)	--	1.5 (7)	10.0 (33)	--	36.4 (76)
Ulmus americana	--	--	0.9 (4)	--	0.5 (2)	0.1 (0)	0.1 (0)	0.9 (2)
Populus deltoides	--	--	7.1 (14)	--	--	--	--	--
Quercus bicolor	--	--	0.8 (5)	--	--	--	--	--
Other Species	2.2 (4)	0.1 (1)	0.7 (2)	1.9 (3)	0.3 (1)	2.5 (0)	4.2 (0)	--
Total Basal Area (m^2/ha)	56.8	21.3	37.4	64.6	22.3	28.7	47.4	45.1
Total Density (stems/ha)	2,145	913	812	1,800	808	699	1,321	530

[1] Values are average basal area (m^2/ha), average percentage of total basal area is in parentheses



J. Cohen

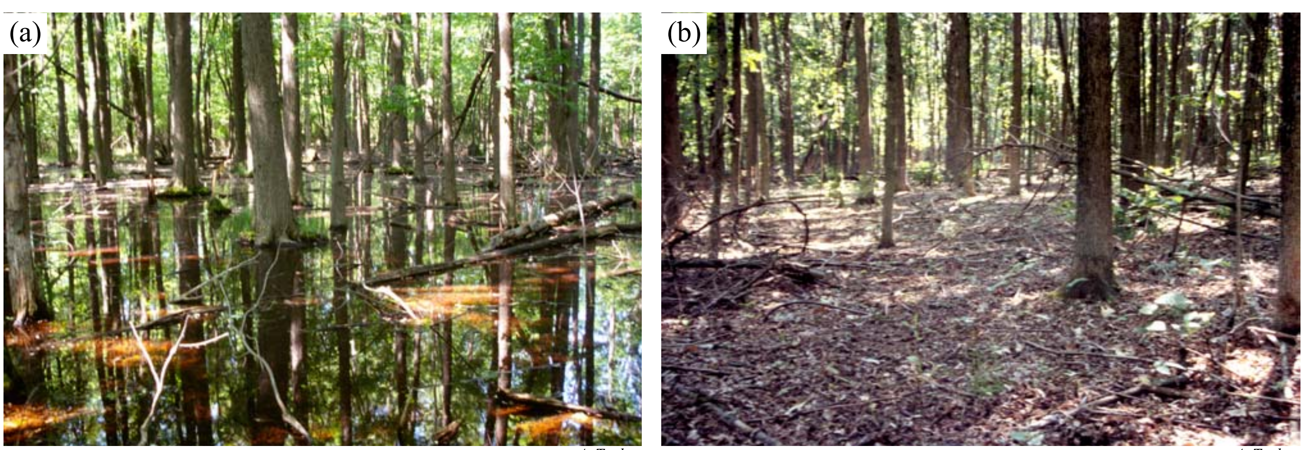
Photo 2. Ecosystem 2 at Ossineke, Alpena Co., Michigan, illustrating the low density of small trees and continuous, graminoid-dominated ground-cover vegetation. Trees are larger and denser on the adjacent upland ridge.

J. Cohen

Photo 3. Ecosystem 5 on Heisterman Island, Huron Co., Michigan, illustrating the low density of small trees, absence of shrubs, and graminoid-dominated ground cover.

canopy coverage in ecosystems 6 and 8 favor a more continuous, graminoid-dominated ground cover (Figure 11, Photos 5 and 6).

In contrast to the hardwood-dominated forests of the inundated ecosystem types, coniferous trees are dominant in ecosystems characterized by saturated, organic soil (ecosytems 1, 4, 7, and 9) (Table 3, Figures 8, 9, and 11). Northern white-cedar (*Thuja occidentalis* L.) is the dominant overstory species of all saturated ecosystems. In ecosystem 1, northern white-cedar accounts for 81% of the overstory basal area, and low numbers of species such as paper birch (*Betula papyrifera* Marsh.), black ash (*Fraxinus nigra* Marsh.), black spruce (*Picea mariana* (P. Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) P. Mill.) are often present (Figure 8, Photo 7, Appendix E1). The overstory of ecosystem 4 is dominated by northern white-cedar (94% of overstory basal area) with a low number of tamarack (*Larix laricina* (Du Roi) K. Koch) trees (Table 3). However, only one site was sampled, and additional species such as black ash, yellow birch (*Betula alleghaniensis* Britt.), and red maple (*Acer rubrum* L.) are also likely to occur within this ecosystem. Due to poor drainage and deep organic soil of ecosystem 7, the overstory basal area of northern white-cedar (23.2 m^2/ha) is only half that of ecosystem 1 (46.7 m^2/ha), and basal area of moderately tolerant species such as black ash,



A. Tepley *A. Tepley*

Photo 4. Comparison of water level of ecosystem 3 in (a) mid June and (b) late July. Shrub layer is virtually absent and ground-cover vegetation is patchy with low species diversity due largely to the combined influence of soil surface inundation in the growing season and relatively high tree canopy coverage.

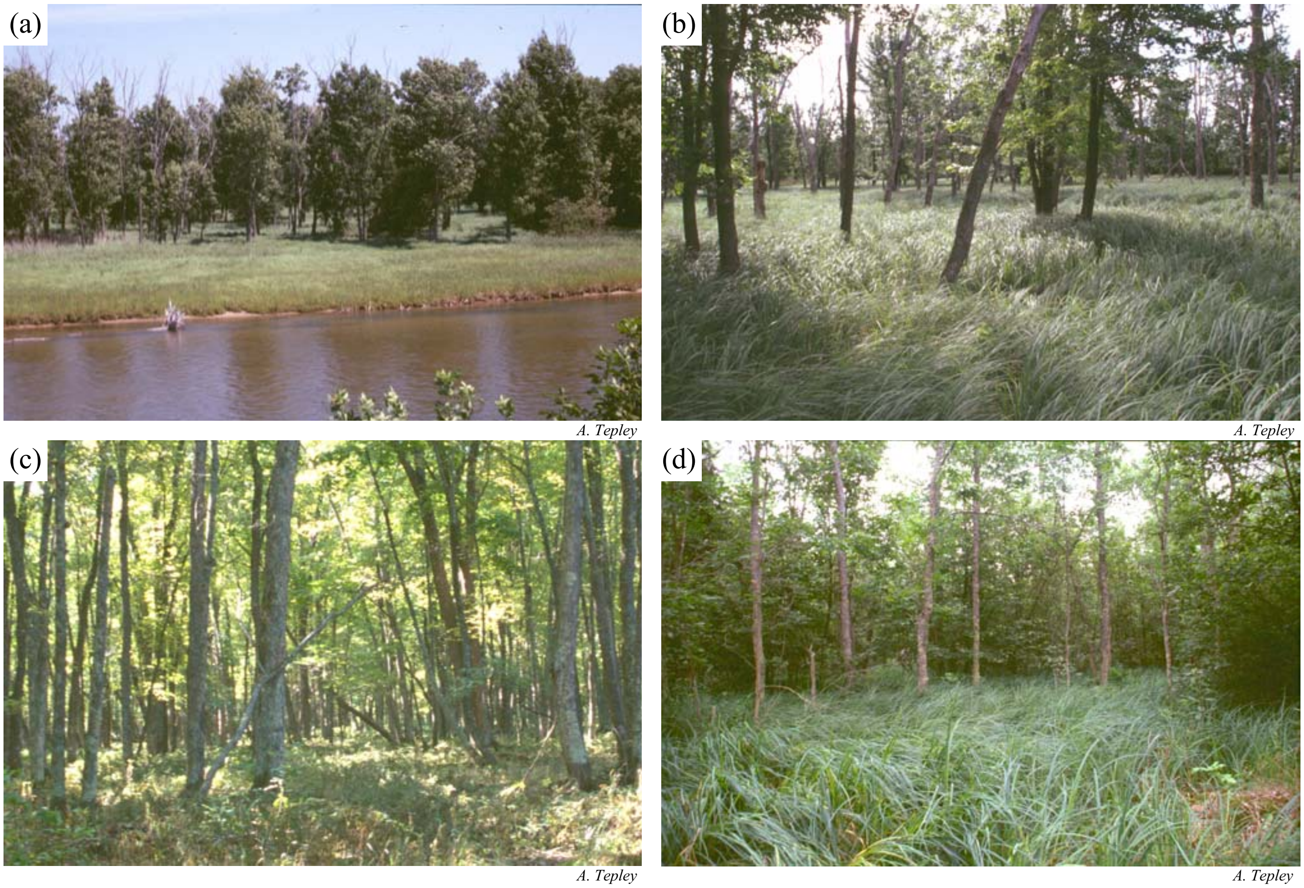


Photo 5. Comparison of ecosystem 6 in the drowned rivermouth valley of the Manistee River, northwestern Lower Michigan, to the first bottom of the Manistee River floodplain upstream, illustrating the lack of a natural levee, widely scattered trees, numerous standing dead trees, and sedge-dominated ground-cover in the rivermouth valley (a and b), and higher tree density with forb- and graminoid-dominated ground cover upstream (c). In the drowned rivermouth valley of the Betsie River, ecosystem 6 is characterized by widely scattered red ash trees are interspersed with dense clumps of speckled alder and sedge-dominated openings (d).

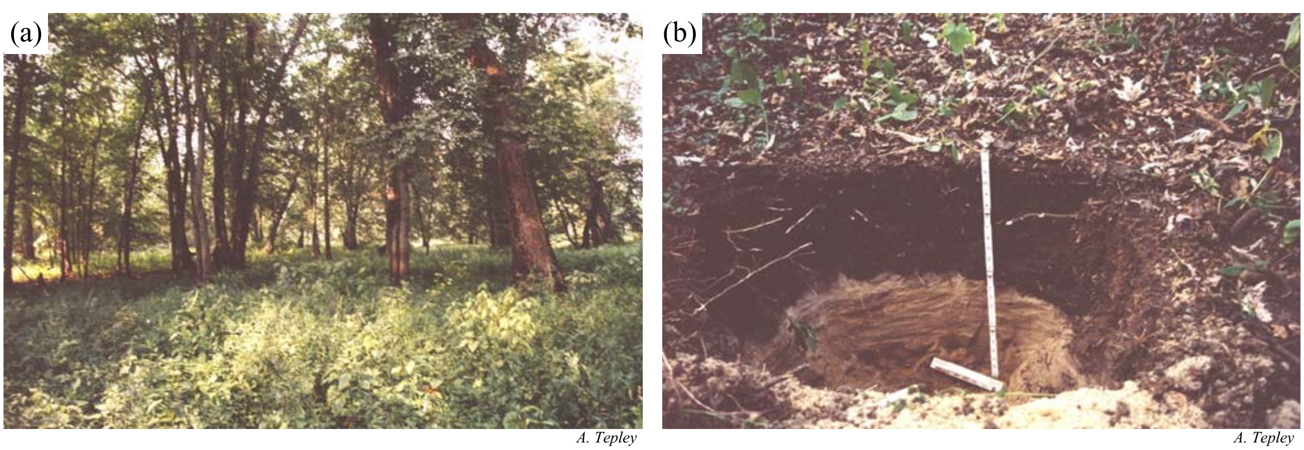


Photo 6. Ecosystem 8 in the drowned rivermouth valley of the Kalamazoo River, southwestern Lower Michigan, illustrating (a) low tree density and the absence of a shrub layer, and (b) a typical soil profile, with a shallow layer of fine textured alluvial soil over sand.

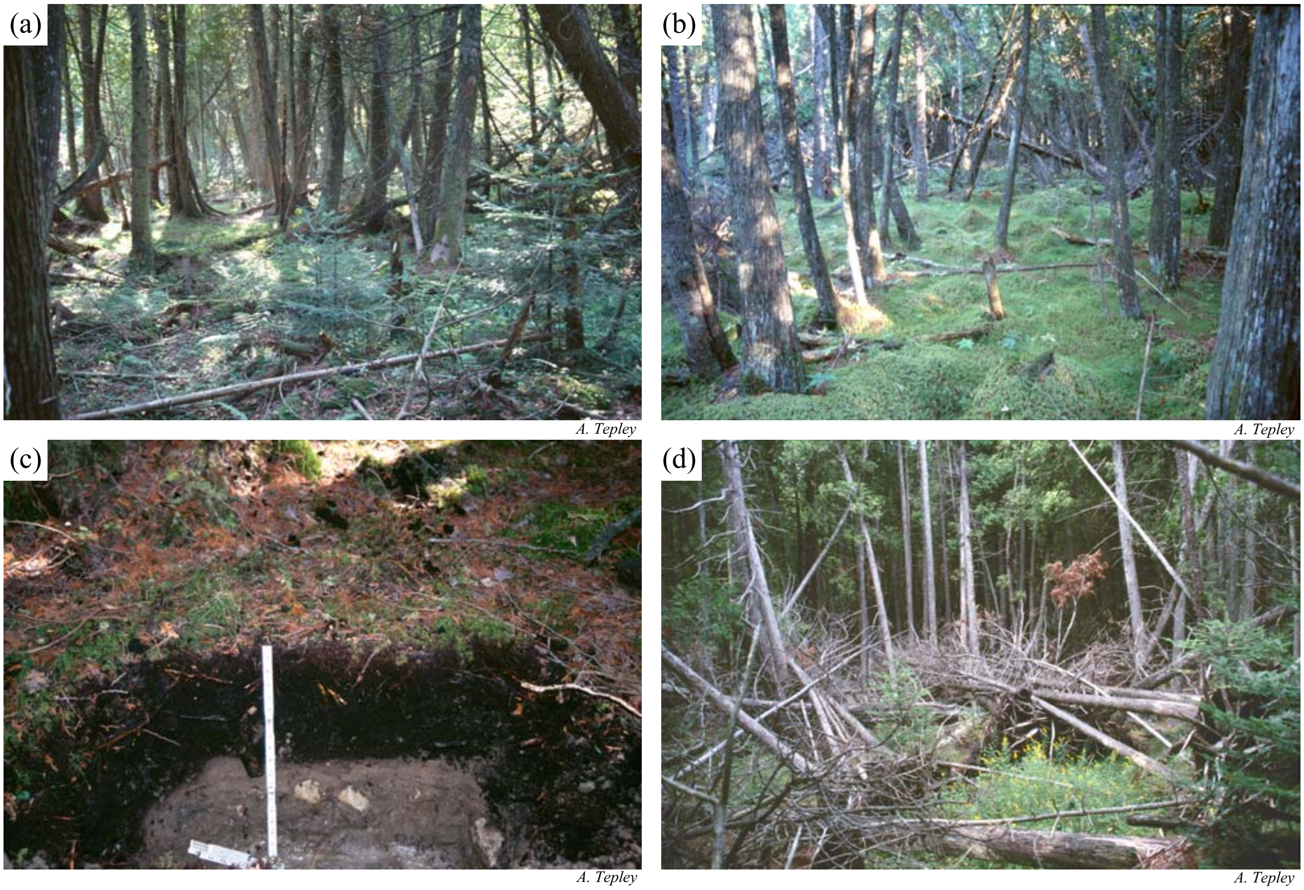


Photo 7. Ecosystem 1 illustrating (a) high tree density and dominance by northern white-cedar at Ogontz North, Delta Co., Michigan, (b) sphagnum hummocks at Seiner's Point, Mackinac Co., (c) a typical soil profile, with a shallow layer of sapric muck over fine sand with limestone cobbles at Portage Bay, Delta Co., and (d) multiple tree blowdown at Seiner's Point.

yellow birch, and red maple, is greater than that of ecosystem 1 (Table 3, Appendix E3). All saturated ecosystem types are characterized by a continuous ground-cover layer, with high species richness (Appendices F4, G4, and J4).

Analysis of Ecosystem Types

Ground-Cover Species Composition

Distinctness of the ecosystem types was supported by detrended correspondence analysis (DCA). Ecosystem types were well distinguished in the ordination space of the first two DCA axes (Figure 12). The first two axes account for 20.5% of the variation among sites in ground-cover species abundances. Strong within-ecosystem clustering of sites and clear separation of clusters in the ordination supports the ecosystem classification. The ordination was corroborated by TWINSPAN, which yields a similar grouping of sites and similar associations between sites and species.

The first DCA axis accounts for 13.7% of the variation among sites in ground-cover species composition, and it represents a hydrologic gradient. Ecosystems characterized by inundation of the soil surface are represented by scores greater than 3 on the first axis, and those characterized by saturated soil are represented by scores less than 3 (Figure 12). Sites of ecosystems 6 and 8, where height of high-water marks averages 82 and 121 cm, respectively, generally have higher first axis scores than those of ecosystems 2 and 3, where high-water marks average 36 and 26 cm, respectively (Appendix C). High site scores within ecosystems 6 and 8 are associated with high scores of species tolerant of deep inundation during part of the growing season, such as common lake sedge (*Carex lacustris* Willd.), Virginia wild rye (*Elymus virginicus* L.), cut grass (*Leersia oryzoides* (L.) Sw.), and wood nettle (*Laportea canadensis* (L.)

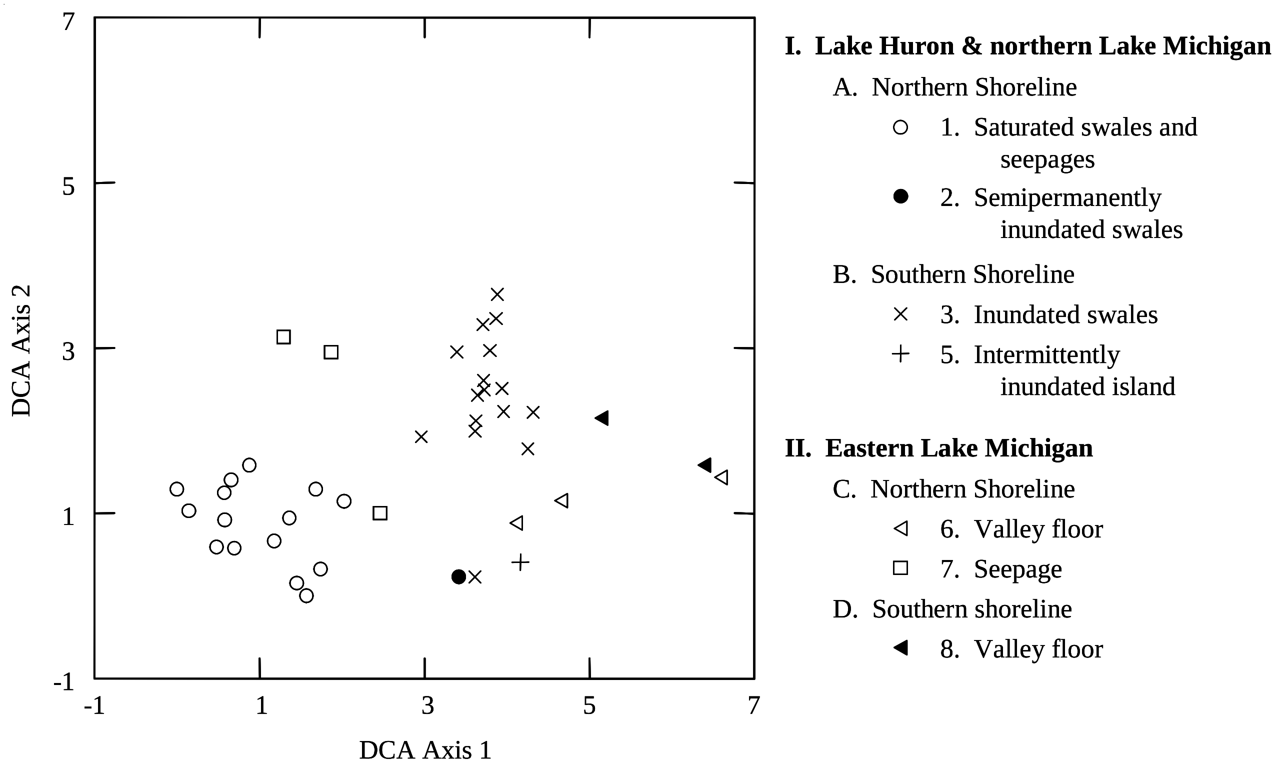


Figure 12. Ordination of 41 Lake Michigan and Lake Huron coastal swamp forests of 7 ecosystem types along the first 2 axes of detrended correspondence analysis of 98 ground-cover species.

Wedd.). Ecosystems 2, 3, and 5 encompass a narrow range along the first axis, corresponding to scores of species tolerant of shallow inundation for a large portion of the growing season, including fowl manna grass (*Glyceria striata* (Lam.) Hitchc.), tufted loosestrife (*Lysimachia thyrsiflora* L.), mad dog skullcap (*Scutellaria lateriflora* L.), blue joint grass (*Calamagrostis canadensis* (Michaux) Beauv.), and tussock sedge (*Carex stricta* Lam.). Low first axis scores of numerous species that often occur in wet but not inundated sites, including starflower (*Trientalis borealis* Raf.), Canada mayflower (*Maianthemum canadense* Desf.), oak fern (*Gymnocarpium dryopteris* (L.) Newm.), dwarf bishop's cap (*Mitella nuda* L.), and goldthread (*Coptis trifolia* (L.) Salisb.) clearly distinguish ecosystems 1 and 7 from ecosystems 2, 3, 5, 6, and 8 along the first axis (Figure 12).

The second DCA axis accounts for 6.8% of the variation among sites in ground-cover species abundances. It represents a general north-south gradient, where sites located along southern shorelines generally have higher scores than those located further north. Although sites representing ecosystems 1 and 7 were not separated from each other along the first axis, they are reasonably separated along the second axis due to high scores of cinnamon fern (*Osmunda cinnamomea* L.) and spicebush (*Lindera benzoin* (L.) Blume) associated with ecosystem 7 (Photo 8), and low scores of numerous species, including twinflower (*Linnaea borealis* L.), creeping snowberry (*Gaultheria hispidula* (L.) Bigelow), and gay wings (*Polygala paucifolia* Willd.) associated with ecosystem 1 (Figure 12). Ecosystems 6 and 8 also are reasonably separated along the second axis due to high scores of wood nettle, false nettle (*Boehmeria cylindrica* (L.) Sw.), and reed canary grass (*Phalaris arundinacea* L.) associated with ecosystem 8, and low scores of common lake sedge and sensitive fern (*Onoclea sensibilis* L.) associated with ecosystem 6. Although ecosystems 2, 3, and 5 were not clearly distinguished from each other along the first axis, a low score of tussock sedge separates ecosystem 2 from ecosystem 3 along the second axis. Low scores of species characteristic of open meadows, such as tussock sedge, blue joint grass, marsh skullcap (*Scutellaria galericulata* L.), and wild mint (*Mentha arvensis* L.), separate ecosystem 5 from ecosystem 3 along the second axis (Figure 12).

A. Tepley

Photo 8. Ecosystem 7 along the Big Sable River, Mason Co., Michigan, illustrating high tree density and the abundance of cinnamon fern in the ground cover.

Vegetation–Environment Relationships

Canonical correspondence analysis (CCA) revealed interrelationships among environmental and stand structure variables and ground-cover species composition that further corroborate the ecosystem classification. The first two CCA axes account for 53.5% of the ground-cover species-environmental and stand structure variation, and the F ratios of both axes are significant ($P < 0.01$) (Table 4). The stepwise Monte Carlo procedure reveals that variables relating to hydrology and soil are more important in explaining variation among sites in ground-cover species composition than stand structure variables. As determined by the stepwise Monte Carlo procedure, the four most important variables, in order of decreasing significance, are: range of surface soil pH, height of the high-water mark, depth of organic soil, and coverage of shrubs. Although the first four variables are significant ($P < 0.05$), overstory basal area, large understory stem density, and overstory density are not significant ($P > 0.1$). The variable, density of tree seedlings taller than 50 cm, is of borderline significance ($P = 0.05$) (Table 4).

The first axis represents a gradient relating primarily to degree of soil inundation and within-site variability of soil surface pH. Height of the high-water mark has a strong positive correlation with the first axis, and range of soil surface pH has a strong negative correlation (Table 4). The opposite influence of these variables (as indicated by arrows in Figure 13) illustrates the importance of relationships between hydrologic regime and microtopographic relief in regulating soil surface pH and species distribution (Vitt et al. 1975, Boelter and Verry 1977, Huenneke and Sharitz 1986, Titus 1990). As indicated by positive site scores for all inundated ecosystem types, periodic inundation of the entire soil surface by calcareous groundwater results in a uniform, high soil surface pH (7.2–7.3 in ecosystems 2, 3, 5, 6, and 8) (Table 2, Appendix

Table 4. Eigenvalues and weighted inter-set correlations for the fist two axes of canonical correspondence analysis of 98 ground-cover species of 41 Lake Michigan and Lake Huron coastal swamp forests, constrained by 8 environmental and stand structure variables. Variables are listed in decreasing order of significance, as determined by Monte Carlo permutation (α = 0.05).

	CCA Axis 1	CCA Axis 2
Eigenvalue	0.793	0.445
Species-environment correlation	0.978	0.928
Cumulative % variance of species	12.4	19.3
Cumulative % variance of species-environment relation	34.2	53.5
Correlations		
pH range at the soil surface (pH-RANGE)	-0.906	0.007
Average height of high-water mark, cm (HWM)	0.799	-0.189
Depth of organic soil, cm (MUCKD)	-0.493	0.549
Coverage of shrubs, % (SHRUB)	0.204	0.409
Density of tree seedlings taller than 50 cm, seedlings/ha (TSEED)	-0.313	-0.183
Overstory basal area, m^2/ha (OBA)	-0.734	-0.355
Large understory density, stems/ha (UDEN)	-0.170	0.080
Overstory tree density, stems/ha (ODEN)	-0.889	-0.187

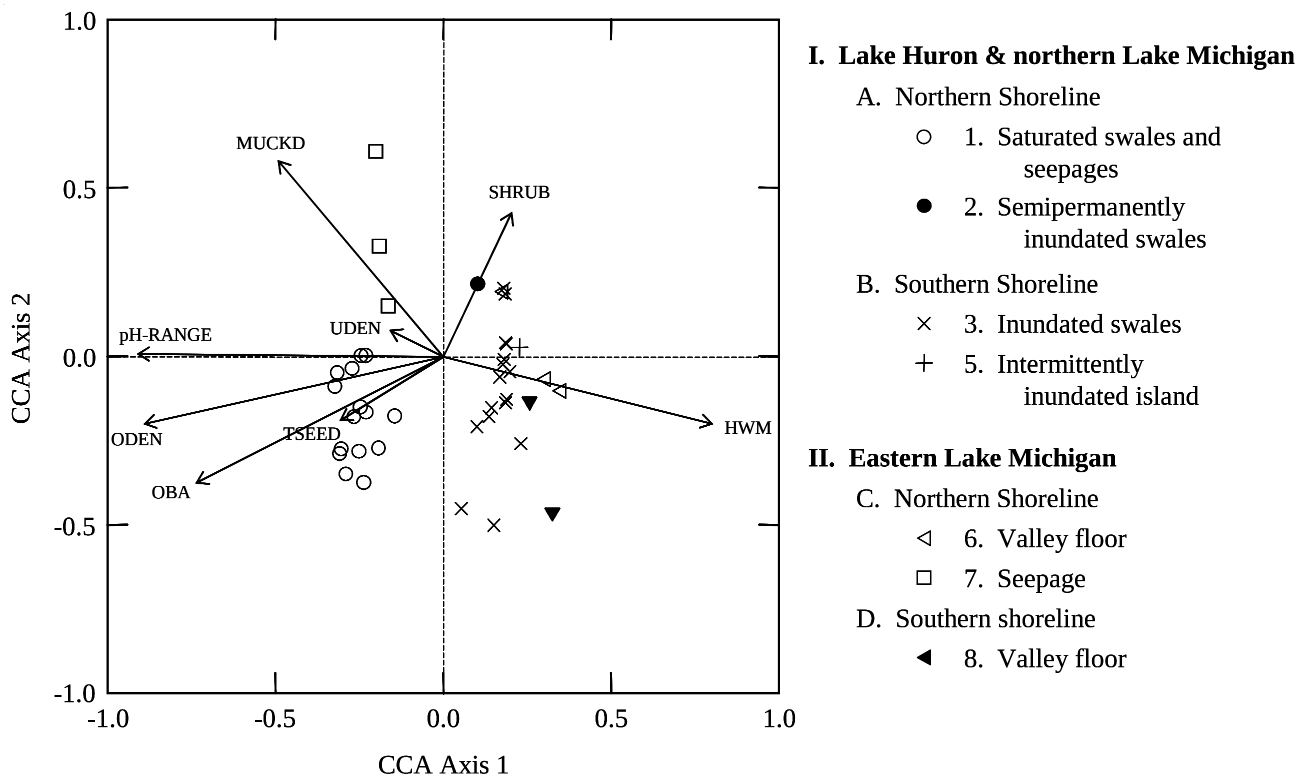


Figure 13. Ordination of 41 Lake Michigan and Lake Huron coastal swamp forests of 7 ecosystem types derived from canonical correspondence analysis of 98 ground-cover species and 8 environmental and stand structure variables (arrows indicate the direction and magnitude of the influence of environmental and stand structure variables; variable codes are the same as those listed in Table 4).

C). In contrast, a wide range of soil surface pH occurs in ecosystems 1 and 7 (4.4–7.1 and 4.2–7.5, respectively), where the organic soil remains saturated throughout the growing season, but numerous tip-up mounds and hummocks stand higher than the maximum water level. As a result of the wide range of soil surface pH, species characteristic of acid conditions, such as creeping snowberry, sedge (*Carex trisperma* Dewey), twinflower, and Canada mayflower, occur adjacent to species characteristic of calcareous soil, such as alder-leaved buckthorn (*Rhamnus alnifolia* L'Her.) and sedge (*Carex eburnea* Boott). Thus, negative first axis scores of numerous acidifiles, and several calcifiles that do not usually grow under inundated conditions distinguish saturated from inundated ecosystems along the first axis (Figure 13).

Variables that have a strong influence on the separation of ecosystems along the second axis include depth of organic soil, shrub coverage, and overstory tree density (Table 4). The opposite influences of organic soil depth and overstory tree density clearly separate sites of ecosystem 7 from those of ecosystem 1 along the second axis. In ecosystem 7, the constant influx of groundwater due to the location at the base of steep slopes results in a deep accumulation of sapric and hemic muck (average depth >150 cm) that supports a markedly lower overstory tree density (1,321/ha) than that of ecosystem 1 (2,145/ha), where the substrate is shallow sapric muck (average depth 27 cm). The resulting lower tree canopy coverage of ecosystem 7 favors a greater abundance of light-demanding species, such as cinnamon fern, spotted joe-pye weed (*Eupatorium maculatum* L.), and marsh fern (*Thelypteris palustris* Schott), whose positive second axis scores distinguish ecosystem 7 from negative scores of ecosystem 1 (Figure 13).

Inundated ecosystem types are reasonably separated from each other along a gradient relating to shrub coverage and overstory tree density on the second axis. Low tree density and high shrub coverage of ecosystem type 2 distinguish it from ecosystem 3 along the second axis (Figure 13). Due to the low elevation of ecosystem 2 in relation to lake levels, tree density is low, and coverage of shrubs including speckled alder (*Alnus rugosa* (Duroi) Sprengel), bog birch (*Betula pumila* L.), and meadowsweet (*Spiraea alba* Duroi) is high. Likewise, a low tree density in ecosystem 5, due to its elevation below the maximum lake level, results in its distinction from ecosystem 3 due to high second axis scores of species characteristic of open meadows, including wild mint, marsh skullcap, and blue joint grass (Figure 13).

Land-Cover Analysis

Because each minor shoreline segment contains two ecosystem types–one dominated by conifers and the other by hardwoods, analysis of Circa 1800 land cover (Comer et al. 1995a), where land cover can easily be classified as conifer- of hardwood-dominated swamp, provides a reasonable estimate of the abundance of each ecosystem type prior to European settlement. Analysis of IFMAP/GAP Michigan 2000 land cover (MDNR 2001) within areas identified as hardwood- and conifer-dominated swamp in the Circa 1800 data set approximates the amount of each type that has been lost. Although the southern Lake Huron shoreline contains three ecosystem types–two dominated by hardwoods and one by conifers, one of the hardwood-dominated ecosystems (ecosystem 5) is restricted to Heisterman and Maisou Islands, where limestone bedrock is within 100 cm of the soil surface. We assume that the spatial distribution of ecosystem 5 was always highly limited, and it has minimal contribution to the total area of hardwood-dominated swamp along the southern Lake Huron shoreline in either land-cover data set.

Conifer-dominated swamp was historically abundant along the northern Lake Michigan and Lake Huron shorelines (minor shoreline segment A), and a substantial portion of the Circa 1800 conifer-dominated swamp remains largely unchanged today. At the time of the GLO surveys, 56% of the land along northern shorelines at an elevation below 180 m was identified as wetland: 47% forested and 9% non-forested (Figure 14). Whereas conifer-dominated swamp (an approximation of ecosystem 1) accounted for 97% of the forested wetland, hardwood-dominated swamp (an approximation of ecosystem 2) accounted for only 3%. Although 36% of the Circa 1800 conifer-dominated swamp

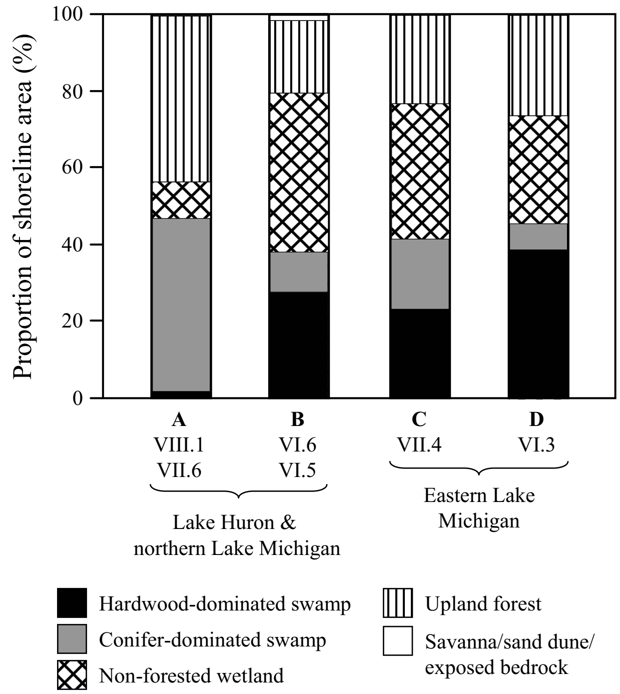


Figure 14. Comparison of historical land cover (Comer et al. 1995a) among four minor shoreline segments (minor shoreline segment letters correspond to Table 2 and Figure 7; land cover was calculated for all land at elevations below 180 m and contiguous to the shore).

remained in the 2000 data set, only 1% of the hardwood-dominated swamp remained (Figure 15). Conversion of both types was primarily to non-forested wetland. Twenty-five percent of the Circa 1800 conifer-dominated swamp and 56% of the hardwood-dominated swamp were classified as non-forested wetland in the 2000 data set (Figure 15).

In contrast to northern shorelines, hardwood-dominated swamp was historically more abundant than conifer-dominated swamp along the southern Lake Huron shoreline (minor shoreline segment B). Over the last 200 years, the majority of both types has been converted to agricultural land cover. In the Circa 1800 data set, 79% of the southern Lake Huron shoreline at an elevation below 180 m was classified as wetland: 38% forested and 41% non-forested (Figure 14). Hardwood-dominated swamp (an approximation of ecosystem 3) accounted for 73% of the forested wetland and conifer-dominated swamp (an approximation of ecosystem 4) accounted for 27%. By 2000, only 11% of the Circa 1800 hardwood-dominated swamp and 7% of the conifer-dominated swamp remained (Figure 15).

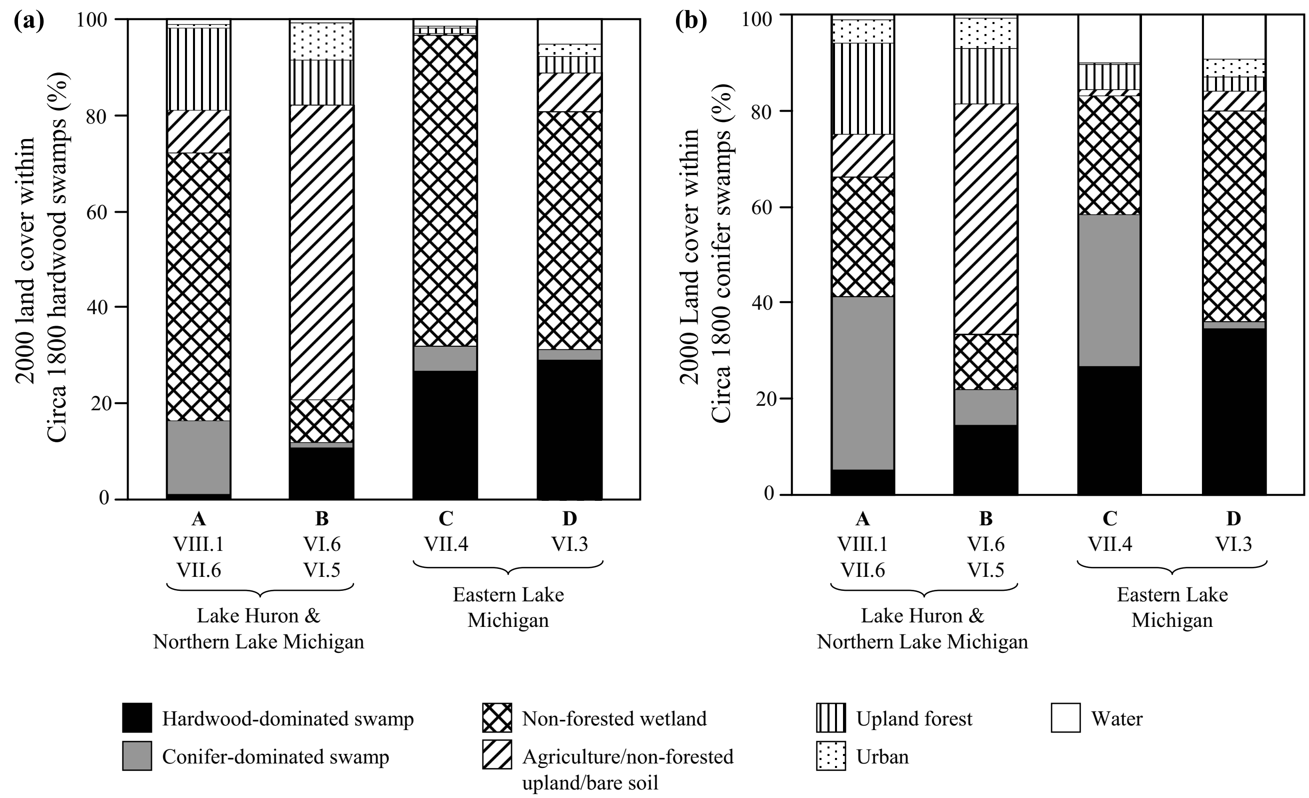


Figure 15. Comparison of present land cover (MDNR 2001) within areas identified as (a) hardwood- and (b) conifer-dominated swamp in GLO survey records (Comer et al. 1995a) among four minor shoreline segments of the Lake Huron and Lake Michigan shorelines (minor shoreline segment letters correspond to Table 2 and Figure 7; land cover analysis was conducted for land at elevations below 180 m and contiguous to the shore).

Because both types were converted primarily to agricultural land cover (62% of the hardwood-dominated swamp and 48% of the conifer-dominated swamp) (Figure 15), restoration likely involves re-establishment of natural hydrologic regimes, soil, and vegetation.

Historically, drowned river-mouth valleys of northwestern Lower Michigan (minor shoreline segment C) contained approximately equal proportions of hardwood- and conifer-dominated swamp. Substantial portions of both types remained largely unchanged in 2000. At the time of the GLO surveys, forested wetland accounted for 41% of the land at an elevation below 180 m in the drowned river-mouth valleys (Figure 14). Fifty-six percent of the forested wetland was dominated by hardwoods (an approximation of ecosystem 6) and 44% by conifers (an approximation of ecosystem 7). By 2000, 27 and 32% of the hardwood- and conifer-dominated swamp, respectively, remained (Figure 15). Whereas conversion of hardwood-dominated swamp was primarily to non-forested wetland (65%), conifer-dominated swamp was converted to approximately equal proportions of hardwood-dominated swamp (27%) and non-forested wetland (25%) (Figure 15).

In contrast to northwestern Lower Michigan, hardwood-dominated swamp was considerably more abundant than conifer-dominated swamp in drowned river-mouth valleys of southwestern Lower Michigan (minor shoreline segment D). At the time of the GLO surveys, hardwood-dominated swamp (an approximation of ecosystem 8) accounted for 85% of the forested wetland, and conifer-dominated swamp (an approximation of ecosystem 9) accounted for 15% (Figure 14). Whereas a substantial portion of the historical hardwood-dominated swamp (29%) remained by 2000, conifer-dominated swamp was virtually eliminated (only 2% remained) (Figure 15). Conversion of both types was primarily to non-forested wetland: 65% of the Circa 1800 hardwood-dominated swamp and 44% of the conifer-dominated swamp (Figure 15).

GENERAL DISCUSSION

Ecosystem Classification

The ecological classification of swamp forests along the Lake Michigan and Lake Huron shorelines illustrates the broad diversity of coastal swamp forests in Michigan. Classification of coastal swamp forests was conducted in a top-down manner by dividing the shorelines into major and minor shoreline segments that were progressively more homogeneous in physiography and climate until several local ecosystem types recurred within each minor shoreline segment, reflecting underlying patterns of physiography, hydrology, soil, and vegetation. Two Major Shoreline Segments, four Minor Shoreline Segments, and nine Ecosystem Types were identified and described. Major shoreline segments were distinguished based primarily on the generic landform where swamp forests occur–former embayments along Lake Huron and northern Lake Michigan, and drowned river mouths along eastern Lake Michigan (Table 2, Figures 3–6). Each major shoreline segment was divided into a northern and southern Minor Shoreline Segment on the basis of gross climatic and physiographic characteristics influencing hydrologic regime, soil properties, and species distribution (Table 2, Figure 7, Appendix B).

At the finest level of classification, two or three ecosystems types (nine ecosystems in all) were nested within each minor shoreline segment (Table 2, Appendices B and C). Ecosystem types of each minor shoreline segment were distinguished based on their position relative to the shoreline, and the corresponding physiography, hydrology, soil, and vegetation (Figures 8–11). Ecosystems located at a low elevation and close to shore (ecosystems 2, 3, 5, 6, and 8) were characterized by periodic inundation, mineral soil (or shallow sapric muck in ecosystem 2), and a forest canopy dominated by hardwoods. Ecosystem types located further from shore and at a higher elevation (ecosystems 1, 4, 7, and 9) were characterized by saturated organic soil and a conifer-dominated forest canopy (Tables 2 and 3).

Whereas the classification of coastal swamp forests was developed by first dividing the shorelines geographically based on gross physiographic and climatic characteristics, then identifying local ecosystem types on the basis of fine-scale physiography, hydrology, soil, and vegetation, other classifications of Great Lakes coastal wetlands have focused primarily on hydrogeomorphic characteristics (Minc and Albert 1998, Keough et al. 1999). Due to strong emphasis on physiography in developing both types of classification, they are largely compatible. For example, Major Shoreline I (Lake Huron and northern Lake Michigan), where swamp forests occur in swales and depressions within former embayments (Table 2, Figures 3–5), corresponds to the Protected Wetland Type of Keough et al. (1999) and the Protected Embayment Site Type of Minc and Albert (1998). Similarly, Major Shoreline Segment II (eastern Lake Michigan), where swamp forests are restricted to valleys at the mouths of Lake Michigan tributaries (Table 2, Figure 6, Appendices A1–A6), corresponds to the Drowned River Mouth and Flooded Wetland Type of Keough et al. (1999) and Lake Michigan Lacustrine Estuaries of Minc and Albert (1998).

Compared to our classification, classifications based primarily on hydrogeomorphology have the advantage of more direct application to the entire shorelines of all Great Lakes. However, climatically-driven regional differences among ecosystem types represented in our classification are not represented in such classifications. For example, Keough et al. (1999) developed a classification where all Great Lakes wetlands can be classified as one of the following three types: open coastal wetland, drowned river mouth and flooded delta wetlands, and protected wetlands. Although this classification establishes a framework where biotic characteristics of each hydrogeomorphic type can be compared along climatic gradients or among the Great Lakes, it does not account for characteristic groupings of coastal wetland types along a given stretch of shoreline due to the influence of surrounding upland features or bedrock type. Nor does it account for marked biotic differences between similar physiographic features along different parts of the shoreline reflecting climatic characteristics or differences in the historical development of the wetland due to differential rates of post-glacial uplift. However, the issue of identifying broad climatic regions was addressed by Minc (1997) and Minc and Albert (1998) through cluster analysis of vegetation data for the entire Great Lakes shorelines. They also addressed development of broader physiographic map units with repeated occurrences of geomorphic wetland types in their description of *ecoreaches* (Minc 1997, Minc and Albert 1998, Chow-Fraser and Albert 1998). Such broad physiographic map units closely correspond to major and minor shoreline segments of our classification.

Because the classification of coastal swamp forests was developed for the Lake Michigan and Lake Huron shorelines in Michigan, applying it to the entire shorelines of all Great Lakes would likely require revision of the hierarchical organization of ecosystems and description of additional ecosystem types. However, because geographic divisions of the coastal swamp classification reflect gross physiographic and climatic factors that have a strong influence on the spatial distribution of swamp ecosystems, the classification provides a sound basis to interpret geographic patterns of coastal swamp ecosystems at multiple spatial scales. At a broad scale, each minor shoreline segment is characterized by a different group of ecosystem types (Table 2, Appendix B). The pattern of local ecosystem types within each minor shoreline segment reflects underlying fine-scale patterns of physiography, hydrology, soil, and vegetation (Figures 8–11). Although additional research is required before this classification can be applied to the remaining Great Lakes shorelines, broad and fine-scale differences in the geographic distribution of coastal swamp ecosystems reflecting climatic and physiographic characteristics of the shorelines are represented. Likewise, the coastal wetland classification of Minc and Albert (1998) incorporates climatic factors and regional land-use patterns to account for factors in addition to hydrogeomorphology that influence vegetative composition of Great Lakes coastal wetlands.

Regional Comparisons

Substantial differences between swamp types located within similar landforms but in a different regional context are illustrated by comparing ecosystem types 1 and 3. Ecosystems 1 and 3 occupy swales and depressions situated between beach ridges within former embayments along northern Lake Huron and Lake Michigan (Minor Shoreline Segment A) and southern Lake Huron (Minor Shoreline Segment B), respectively (Table 2, Figures 8 and 9). Although these ecosystems occur within a similar elevational range and at a similar distance from shore, marked differences between them in hydrology, soil, and vegetation reflect differences in climate, as well as differences in long-term successional development of the swamps due to greater rates of isostatic uplift along northern than southern shorelines (Larsen 1985, 1994). Whereas the substrate of ecosystem 1 (northern shorelines) is sapric muck over sand and it remains saturated throughout the growing season, the substrate of ecosystem 3 (southern Lake Huron) is sand, and it lacks a layer of organic soil on top of it. The average depth of sapric muck in ecosystem 1 (27 cm) is almost identical to the average height of high water marks in ecosystem 3 (26 cm) (Appendix C). Thus, early in the growing season when the water table is close to the soil surface of ecosystem 1, the soil surface of ecosystem 3 is entirely inundated. Later in the growing season, the water table falls below the soil surface of both ecosystems. Because water is not easily drained from the small pores of sapric muck (Boelter and Verry 1977), near saturated conditions are maintained in ecosystem 1. In contrast, water drains readily from sand at the soil surface of ecosystem 3 after the water table recedes.

Differences between ecosystem types 1 and 3 in hydrology and soil result in marked differences in vegetation. Ecosystem 1 was dominated by northern white-cedar (Table 3), and the ground-cover layer was continuous and highly diverse. Seasonal inundation in ecosystem 3 favored dominance by silver maple and red ash, the major dominants of seasonally inundated bottoms of river floodplains in Michigan (Baker and Barnes 1998, Goforth et al. 2001). Ground-cover vegetation was sparse, and species diversity was low due to inundation by stagnant water throughout much of the growing season.

Another example of regional differences among ecosystem types located within a similar physiographic context is illustrated by comparing ecosystems of drowned river-mouth valleys along the eastern Lake Michigan shoreline. Ecosystems 6 and 8 occupy the flat valley floor of drowned river mouths in northwestern and southwestern Lower Michigan (Minor Shoreline Segments C and D, respectively) (Table 2, Figure 7). Although these ecosystems are similar in physiography and soil, total overstory basal area of ecosystem 6 (28.7 m^2/ha) was 36% lower than that of ecosystem 8 (45.1 m^2/ha) due primarily to the shorter growing season and colder temperatures (Table 3). In addition, several ground-cover species with a southerly range, such as lizard's tongue, sedge (*Carex grayi* Carey), and false dragonhead (*Physostegia virginiana* (L.) Bentham) were abundant in ecosystem 8, but absent from ecosystem 6 (Appendix J4).

Coastal Swamp Hydrology

Influence of Great Lakes Water Levels

Forest vegetation is generally considered restricted to elevations above the maximum lake level (Keddy and Reznicek 1986, Edsall et al. 1988). Nevertheless, 2 of the 42 study sites were located at an elevation below the maximum annual lake level of 177.1 m (Bishop 1990). The hydrologic regime at these sites, Ossineke (ecosystem 2) and Heisterman and Maisou Islands (ecosystem 5) was directly influenced by the lakes (Figures 8 and 10). However, because most sites were located at elevations above the maximum lake level, the influence of the Great Lakes on the hydrology of most coastal swamp forests is indirect, through the effects of lake level fluctuation on local groundwater elevation.

In contrast to sites located above the maximum lake level, the soil surface of ecosystems 2 and 5 likely remains inundated throughout the growing season when lake levels are high. Periodic persistence of surface water throughout the growing season results in marked differences in forest composition and structure from the other ecosystem types. Total overstory basal area of ecosystems 2 and 5 (21.3 and 22.3 m^2/ha, respectively) was substantially lower than that of the seasonally inundated ecosystem types located at a slightly higher elevation (37.4, 28.7, and 45.1 m^2/ha in ecosystems 3, 6, and 8, respectively (Table 3). Furthermore, whereas red ash dominated the overstory of ecosystems 2 and 5, accounting for 81–90% of the overstory basal area, seasonally inundated ecosystems 3, 6, and 8 located above the maximum lake level were dominated by both red ash and silver maple. The Kirk Road site of ecosystem 3, which was located closer to shore and at a lower elevation than the other sites of this ecosystem, was also dominated by red ash, and silver maple was absent (Appendix E2).

Dominance by red ash and the near absence of silver maple in ecosystems where surface water persists throughout the growing season during periodic high lake levels is probably due to a greater tolerance of red ash than silver maple to oxygen deficiency under prolonged soil inundation. Hook (1984) reported that mature silver maple trees died after two years of continuous inundation, but it took three to four years of inundation to kill mature red ash trees. Growth responses and physiological adaptations of red ash to oxygen deficiency, such as the ability to form adventitious roots (Photo 9) (Gomes and Kozlowski 1980), may contribute to the persistence of red ash in ecosystems 2 and 5, as well as low-elevation sites of ecosystem 3. However, because seedling establishment of silver maple may be dependent on the presence of bare mineral soil (Bell 1974), the near absence of silver maple from ecosystems 2 and 5 also may be related to a lack of sites for seedling establishment in these ecosystems, where the ground-cover is characterized by dense, continuous coverage of graminoids.

In contrast to ecosystem types 2 and 5, the hydrologic regime of ecosystems located above the maximum lake level was indirectly influenced by the lakes, through the influence of lake-level fluctuation on local groundwater elevation. Along Lake Huron and northern Lake Michigan, swamp forests are located within former embayments (Figures 3–5). Due to curvature of the shoreline, groundwater flow converges in such embayments, increasing flow by as much as 500% relative to straight shoreline stretches (Cherkauer and McKereghan 1991). As a result, water levels up to 2.4 m higher than the lake have been recorded in inter-ridge wetlands within former embayments (Thompson and Beadke 1997). Near the shore, groundwater head gradients are forced to adjust to lake-level fluctuation in order to maintain continuous flow. Because such adjustments affect local groundwater elevation, fluctuation in groundwater elevation of inter-ridge wetlands likely

A. Tepley

Photo 9. Adventitious roots on red ash trees in ecosystem 3 at Kirk Road, Tuscola Co., Michigan.

responds to lake-level fluctuation, even at elevations higher than the lake. Weekly water-level measurements in a beach ridge and swale complex along southwestern Lake Michigan revealed that water-level fluctuation in inter-ridge wetlands paralleled that of Lake Michigan, and the degree of correspondence to the lake increased with decreasing distance from shore (Visocky 1977). The effects of lake-level fluctuation on groundwater elevation may extend far inland along Saginaw Bay due to the long, gradual slope above the shore (Figure 5) and the shallow depth to impervious clay or bedrock (Figure 9). Likewise, the effect of lake-level fluctuation on groundwater in drowned river-mouth valleys along eastern Lake Michigan may extend several km inland (Figure 6, Appendices A1–A6) (Herdendorf 1990).

Soil Saturation vs. Inundation

Forest composition differed considerably between ecosystem types characterized by periodic soil inundation (ecosystems 2, 3, 5, 6, and 8) and those characterized by saturated soil (ecosystems 1, 4, 7, and 9). Whereas red ash, or silver maple and red ash, were the dominant overstory species of all inundated ecosystems, conifers including northern white-cedar, balsam fir, white spruce, black spruce, eastern hemlock, and tamarack were among the dominant overstory species of the saturated ecosystems (Table 3). Additional overstory species present in most saturated ecosystems, such as red maple, yellow birch, and black ash, were either absent, or present in low numbers, often on elevated microsites, in the inundated ecosystems (Figure 8).

The correspondence of silver maple and red ash to inundated ecosystem types, and affinity of conifers, yellow birch, black ash, and red maple to saturated ecosystems is similar to the distribution of tree species among saturated and inundated sites documented in other areas. In an Ontario swamp dominated by northern white-cedar, daily measurements with a soil tensiometer revealed that soil at depths of 15, 30, and 45 cm remained saturated throughout the growing season (Stephenson and Hodgson 1996). In New York, substantial differences in hydrology were useful in distinguishing swamps dominated by silver maple and red ash from those dominated by eastern hemlock, yellow birch, and red maple (Huenneke 1982). Hemlock-yellow birch-red maple swamps occurred on muck that remained moist, even in the driest summer months, and ground-cover species diversity was considerably greater than that of silver maple-red ash swamps. In contrast, the soil surface of silver maple-red ash swamps was dry late in the growing season, and low ground-cover species diversity combined with high abundance of species such as wood nettle and water hemlock (*Cicuta maculata* L.) suggest that the soil surface was inundated earlier in the growing season (Huenneke 1982). Inundated silver maple-dominated swamps also have been described along shores of numerous lakes in Canada, including Lake Huron, Lake Erie, and Lake Ontario (National Wetlands Working Group 1988). As in coastal swamp ecosystems of Michigan, silver maple-dominated swamps of Canada were characterized by seasonal inundation, where surface water persisted 12–105 days.

Differential growth responses and physiological adaptations of tree seedlings to oxygen deficiency under soil inundation likely account for the marked differences in species composition between saturated and inundated ecosystems. Seedlings of silver maple, a major dominant of inundated ecosystems, exhibited considerable tolerance to complete inundation in the greenhouse (Hosner 1960). All seedlings survived 30 days and exhibited rapid height-growth when water was drawn down. In contrast, seedlings of red maple, which was absent from most inundated ecosystems (Table 3), were all killed after 20 days of inundation. Red maple seedlings that survived 10 days of inundation exhibited poor height-growth when water was drawn down (Hosner 1960). However, when red maple seedlings were grown under saturated conditions, all seedlings survived 32 days and responded with rapid height-growth when water was drawn down (McDermott 1954). Similarly, tamarack was present in the overstory of saturated ecosystem types 1, 4, and 7, but it was absent from all inundated ecosystems, except ecosystem 2, where it was restricted to relatively high microsites along the margin of the swale (Table 3). Field observations in Minnesota suggest that complete inundation kills tamarack seedlings in 7–10 days, but submergence of only the roots (i.e., soil saturation) caused little if any mortality (Duncan 1954).

Hydrology and Microtopography

Interrelationships between microtopographic relief and hydrology played a strong role in determining species composition of coastal swamp ecosystems. In inundated ecosystem types (ecosystems 2, 3, 6, and 8), depth and duration of soil inundation were reduced on microsites elevated above the general ground level. Thus, seedling establishment and recruitment on such microsites largely account for the persistence of tree species that could not otherwise tolerate prolonged inundation. For example, in ecosystem 3, eastern cottonwood and swamp white oak were restricted to microsites elevated above the general ground level (Figure 9). Prior to the introduction of Dutch elm disease, American elm also probably reached canopy size on small rises in ecosystem 3 (Figure 9). The influence of elevated microsites on tree species distribution is also illustrated in ecosystem 2, where red ash was common in low parts of the swale, where high-water marks up to 50 cm above the soil surface were recorded on their boles. However, balsam fir, red maple, tamarack, and paper birch were restricted to higher microsites along the margins of the swale (Figure 8).

A similar correspondence of certain tree species to elevated microsites has been documented in inundated hardwood-dominated swamps of Florida (Titus 1990). Most tree seedlings were restricted to microsites 10 cm or more above a distinct moss line on the boles of trees that indicated the seasonal high water level. Likewise, numerous studies have documented microtopography as a major factor determining species distribution in inundated riparian forests (Hupp and Osterkamp 1985, Huenneke and Sharitz 1986, Jones et al. 1996, Williams et al. 1999, Dixon et al. 2002).

In addition to providing sites for seedling establishment and recruitment in inundated ecosystems, elevated microsites have a strong influence on soil surface pH and ground-cover species diversity in saturated ecosystems. Numerous studies have demonstrated substantial differences in soil pH among wetland types, such as bogs and fens (Schwintzer and Tomberlin 1982, Siegel and Glaser 1987). To a large extent, factors that account for differences in pH among wetland types also operate at a small scale, resulting in considerable differences in pH among microsites within a wetland (Vitt et al. 1975, Boelter and Verry 1977). Whereas wetlands that receive base cations and bicarbonate from groundwater have a soil pH higher than 5.6, the soil surface pH of wetlands that receive water solely from the atmosphere is generally lower than 4.4 due to the effects of organic acids (Swanson and Grigal 1989). Bicarbonate-rich groundwater in wetland complexes along Lake Michigan and Lake Huron maintains a high soil surface pH (Hiebert et al. 1986, Wilcox and Simonin 1987). However, because mounds and hummocks of the saturated ecosystems stand higher than groundwater elevation, their soil surface was probably more strongly influenced by rain water than ground water. Thus, saturated ecosystems are characterized by a high soil surface pH in hollows between hummocks (7.1, 7.5, and 7.2 in ecosystems 1, 7, and 9, respectively), but the soil surface pH on mounds and hummocks is very strongly acid (4.4, 4.2, and 4.5 in ecosystems 1, 7, and 9, respectively) (Table 2). Similarly, depressions in sandy outwash plains, where peat deposits have not built up enough to isolate surface water from ground water are characterized by a high soil surface pH, except on sphagnum hummocks, where the soil is acid (Boelter and Verry 1977). Likewise, Vitt et al. (1975) reported a difference of 1.0 to 1.5 pH units from the top to the bottom of hummocks in bogs of northern Lower Michigan.

As determined by canonical correspondence analysis and stepwise Monte Carlo procedures, range of soil surface pH was the most significant environmental factor accounting for variation among sites in ground-cover species composition (Table 4, Figure 13). In inundated ecosystems, periodic inundation by groundwater rich in base cations and bicarbonate maintains a uniform, circumneutral soil surface pH, thereby resulting in the absence of acidifiles in the ground cover. In contrast, acidifiles such as creeping snowberry, sedge (*Carex trisperma* Dewey), and goldthread occurred adjacent to calcifiles including alder-leaved buckthorn and sedge (*Carex eburnea* Boott), in the saturated ecosystems due to local acid and circumneutral conditions on hummocks and hollows, respectively. Although acid soil was only found within a few cm of the soil surface, the depth of acid soil corresponds to the rooting depth of many ground-cover species.

Similar occurrence of acidifiles adjacent to calcifiles has been documented at other swamps characterized by pit and mound microtopography. In a hardwood-conifer swamp in central New York, putative calcifiles such as Canada mayflower, partridge berry (*Mitchella repens* L.), goldthread, starflower, and bluebead-lily (*Clintonia borealis* (Aiton) Raf.) were restricted to mounds, and species that do not exhibit a strong affinity to acid soil, including jewelweed (*Impatiens capensis* Meerb.), sensitive fern (*Onoclea sensibilis* L.), and bugleweed (*Lycopus uniflorus* Michx.) were located primarily in depressions (Paratley and Fahey 1986). Likewise, in a northern hardwood forest characterized by well developed pit and mound microtopography, Beatty (1985) found a lower pH on mounds than in adjacent pits. As a result, presumed acidifiles, such as Canada mayflower, were common on mounds, and species characteristic of moist, rich conditions, such as blue cohosh (*Caulophyllum thalictroides* (L.) Michx.) and two-leaved toothwort (*Dentaria diphylla* (Michx.) Wood), were restricted to pits (Beatty 1985).

Restoration Priorities

Regional Considerations

The ecological classification organizes coastal swamp ecosystems within a geographical hierarchy, thereby facilitating designation of restoration priorities among ecosystem types due to their regional distribution and differential degrees of degradation among them relating to regional land-use patterns. Each minor shoreline segment contains one ecosystem type dominated by conifers and another ecosystem dominated by hardwoods (or one conifer-dominated ecosystem and two hardwood-dominated ecosystems along the southern Lake Huron shoreline) (Tables 2 and 3). Because hardwood- and conifer-dominated swamp can easily be distinguished from GLO survey records, Circa 1800 land cover (Comer et al. 1995a) provides a reasonable approximation of the historical distribution of each ecosystem type (Figure 14). Analysis of present land cover within areas identified as Circa 1800 swamp forest provides a reasonable estimate of the portion of the historical swamp that remains (Figure 15). High conservation benefits can be achieved by restoration of ecosystems types where the historical distribution has been markedly reduced (Palik et al. 2000). In addition, conservation benefits can be enhanced by prioritizing restoration efforts to ensure that the present representation of each ecosystem type is proportional to its historical abundance along its respective shoreline segment. Furthermore, focusing restoration efforts on sites that require the least restoration effort will increase conservation benefits.

Because swamp forests occur in a different generic type of landform along each major shoreline segment, each shoreline segment is characterized by a different type of land-use history. The location of swamp forests within former embayments along the Lake Huron and northern Lake Michigan shorelines (Major Shoreline Segment I) facilitated drainage to allow for urban and agricultural development. Because local groundwater hydrology has a strong influence on hydrologic regimes of such swamps, excavation of drainage ditches could cause sufficient lowering of the water table to enable urban or agricultural development. Such drainage was most apparent along the southern Lake Huron shoreline (Minor Shoreline Segment B), where 43% of the Circa 1800 hardwood-dominated swamp and 54% of the conifer-dominated swamp had been converted to urban or agricultural land cover (Figure 15). Drainage of conifer-dominated swamps and burning of their organic soil to allow for agricultural land use was documented in early soil surveys of Tuscola and Saginaw Counties (Deeter and Matthews 1926, Moon et al. 1938).

The location of swamp forests in drowned river-mouth valleys along the eastern Lake Michigan shoreline (Major Shoreline Segment II) largely prohibited drainage for urban and agricultural development. Because drowned river-mouth valleys are the outlets of large watersheds, drainage could not substantially be altered without drastic changes to the entire watershed. Thus, by 2000, only 8% of the Circa 1800 hardwood-dominated swamp and 11% of the conifer-dominated swamp had been converted to urban or agricultural land cover along eastern Lake Michigan in southwestern Lower Michigan (Minor Shoreline Segment D) (Figure 15). Conversion to urban and agricultural land cover was less common in northwestern Lower Michigan (Minor Shoreline Segment C).

Within each major shoreline segment, substantial differences between northern and southern minor shoreline segments in the historical abundance of hardwood- and conifer-dominated swamp, are essential in prioritizing restoration efforts. Also, marked regional differences in the degree of loss of conifer- and hardwood-dominated swamp are instrumental in assigning restoration priorities among ecosystems. Along the northern Lake Michigan and Lake Huron shorelines (Minor Shoreline Segment A), conifer-dominated swamp historically accounted for 97% of the forested wetland and hardwood-dominated swamp accounted for 3% (Figure 14). By 2000, a substantial area of conifer-dominated swamp remained (36%), but hardwood-dominated swamp was practically eliminated (only 1% remained) (Figure 15). Despite the near elimination of hardwood-dominated swamp along this shoreline segment, restoration of ecosystem 1 should be a higher priority than that of ecosystem 2 due to the markedly greater historical abundance of conifer-dominated swamp. Because both the historical and present distribution of hardwood-dominated swamp are notably limited, efforts to restore ecosystem 2 should be limited to the low number of inundated swales near the shore where the duration of inundation is not too long to prevent trees from attaining a size large enough to survive inundation throughout the growing season. Identification of such sites would require long-term monitoring of water levels within swales.

In contrast to the northern shorelines, hardwood-dominated swamp historically accounted for a considerably greater portion (73%) of the forested wetland along southern Lake Huron (Minor Shoreline Segment B) than conifer-dominated swamp (27%) (Figure 14). By 2000, only 11% of the hardwood-dominated swamp and 7% of the conifer-dominated swamp remained (Figure 15). Because conifer-dominated swamp has been nearly eliminated, restoration efforts along this shoreline segment should focus primarily on ecosystem 4. However, because substantial portions of the historical conifer-dominated swamp undoubtedly have been drained and converted to agricultural land cover, restoration efforts should focus on sites such as Bay Port (Appendix B), where hydrology and soil have not been markedly altered, and small numbers of coniferous trees are present. Also, restoration of ecosystem 3 is a high priority due to the small area that remains relative to its extensive historical abundance.

Trends in the historical abundance and loss of hardwood- and conifer-dominated swamp along eastern Lake Michigan are generally similar to those along Lake Huron and northern Lake Michigan. Historically, conifer-dominated swamp accounted for a substantially greater portion of the coastal swamp forest of northwestern than southwestern Lower Michigan (Minor Shoreline Segments C and D, respectively) (Figure 14). Similar to the Lake Huron and northern Lake Michigan shorelines, the loss of conifer-dominated swamp along the eastern Lake Michigan shoreline was considerably greater in the northern than southern minor shoreline segment. Drowned river-mouth valleys of northwestern Lower Michigan historically supported similar proportions of hardwood- and conifer-dominated swamp (56 and 44% of the Circa 1800 forested wetland, respectively) (Figure 14). Because a similar portion of both types remains (27% of the historical hardwood-dominated swamp and 32% of the conifer-dominated swamp) (Figure 15), restoration effort should be divided equally between ecosystem types 6 and 7, focusing on sites that could be restored at the lowest cost.

In southwestern Lower Michigan, hardwood-dominated swamp historically accounted for 85% of the forested wetland, and conifer-dominated swamp accounted for 15% (Figure 14). By 2000, although a substantial portion of the historical hardwood-dominated swamp remained (29%), conifer-dominated swamp was virtually eliminated (2% remained) (Figure 15). Thus, restoration of ecosystem 9 is the highest priority in southwestern Lower Michigan. However, restoration of ecosystem 8 also should be a high priority due to its markedly greater historical abundance, and substantial losses to this ecosystem over the last 200 years (Figure 15).

Additional Considerations

Although analysis of the Circa 1800 and 2000 data sets within each minor shoreline segments provides a reasonable approximation of the historical distribution of each coastal swamp ecosystem, and the proportion of its historical abundance that has been lost, inaccuracies in both data sets should not be overlooked in assigning restoration priorities. For example, the substantial portion of Circa 1800 swamp forest that was identified as non-forested wetland in the 2000 data set (Figure 15) may be related to the different types of data used to develop each data set rather than actual conversion to non-forested wetland. Because Circa 1800 land cover was developed from GLO survey records, it is based on data recorded exclusively along section lines (Comer et al. 1995b). Thus, land-cover values were assigned to areas not located along section lines based on comparison to land cover in similar topographic locations along nearby section lines. However, because small differences in elevation near the Great Lakes often result in marked differences in vegetation, much of the land classified as Circa 1800 swamp forest may include non-forested wetland. In contrast to Circa 1800 land cover, supervised classification of satellite imagery was used to assign land-cover values to each 30-m pixel of the 2000 land cover (MDNR 2001). Thus, small areas of non-forested wetland that were likely classified as swamp forest in the Circa 1800 data set, were identified as non-forested wetland in the 2000 data set. Such differences in land-cover classification due to differences in data resolution likely gave the false appearance of substantial conversion to non-forested wetland (Figure 15). Although the resolution of data used to develop 2000 land cover was finer than that of Circa 1800 land cover, satellite imagery was not always accurate in distinguishing between upland and wetland, especially in the relatively flat terrain of former embayments, where narrow ridges and swales rarely align with 30-m pixels.

In addition to assigning restoration priorities based on the historical distribution of each ecosystem and the portion of its historical distribution that has been lost, the specific type of disturbance must be considered. Although land-cover data can be used to determine whether or not the generic overstory vegetation (hardwood or conifer) is present, it does not provide information on other factors that influence the restoration potential. For example, the cost of restoration generally increases with increasing abundance of non-native species. However, the need for stewardship activity increases with increasing abundance of non-native species, especially in ecosystems where a large portion of the historical abundance has been lost. Non-native species were virtually absent from saturated ecosystems along northern shorelines (ecosystems 1 and 7) (Appendix F4 and G4) due to high tree canopy coverage and the lack of a large seed pool due to low amounts of nearby urban and agricultural land cover. Along the southern Lake Huron shoreline, despite a large seed pool for non-native species along the southern Lake Huron shoreline, non-native species also were practically absent from ecosystem 3 due largely to the combined effects of soil inundation and relatively high tree canopy coverage. However, non-native species were locally abundant in ecosystems 6 and 8 along the eastern Lake Michigan shorelines, where tree canopy coverage was markedly lower than that of ecosystem 3 (Appendix J4). Non-native species such as Japanese barberry (*Berberis thunbergii* DC.), forget-me-not (*Myosotis scorpioides* L.), and bittersweet nightshade (*Solanum dulcamara* L.) were locally common in ecosystems 6 and 8. In addition, the coverage of highly aggressive native species, such as reed canary grass, has increases considerably in occurrences of ecosystem 6 (especially along the Muskegon River), as a result of disturbances such as grazing.

Additional factors to consider in assigning restoration priorities are site size and landscape context. Restoration of a large coastal wetland complex, composed of numerous forested and non-forested wetland types will have higher conservation benefit than restoration of an individual swamp that is not part of an intact coastal wetland complex. In addition, restoration of swamps that are located adjacent to in tact upland forests is a higher priority than restoration of sites where the adjacent uplands have been degraded. Furthermore, conservation benefits generally increase with increasing size of the site restored. However, size of the entire coastal wetland complex is more important than size of the individual swamp that is the target of restoration.

Successional stages of coastal swamps also must be taken into account when assigning restoration priorities (Sprugel 1991). Because the ecosystem classification and descriptions emphasize physiography, hydrologic regime, and soil properties, ecosystem identification is possible regardless of the present vegetation (Allen and Wilson 1991). For example, swamps dominated by paper birch, trembling aspen, and balsam poplar may be an early successional stage of ecosystem 1 along northern Lake Michigan and Lake Huron. Thus, restoration of a paper birch-trembling aspen-balsam poplar swamp would be a high priority if it was located in a swale or depression within a former embayment along the northern Lake Michigan or Lake Huron shoreline, the substrate was saturated sapric muck over sand, and ground-cover species characteristic of ecosystem 1 were present. Efforts to restore such a site would include promoting regeneration of northern white-cedar, possibly by constructing exclosures so that excessive browsing by deer would not elminate recruitment of northern white-cedar. At sites where the hydrologic regime, soil properties, and vegetation have been altered to the extent that it is no longer possible to determine the ecosystem type, the cost of restoration may be prohibitively high.

SUMMARY AND CONCLUSIONS

Introduction

Great Lakes coastal wetland research and efforts to restore coastal wetlands have focused primarily on herbaceous meadows and marshes. However, considerably less research and restoration effort has focused on swamp forests that occur immediately inland of the herbaceous coastal wetlands. Although swamp forests are generally considered restricted to land higher than the maximum lake level, their hydrologic regime is largely influenced by the Great Lakes through the effect of lake-level fluctuation on local groundwater hydrology. In addition, due to the characteristic location of coastal swamp forests, at the interface between upland ecosystems and herbaceous wetlands that extend into the lakes, they provide refuge for numerous plant and animal species, and they may buffer the effects of upland land use on the lakes. Thus, for the purposes of restoration and management, swamp forests along the Great Lakes shorelines should be considered an integral part of the coastal wetland complex.

Over the last 200 years, substantial portions of herbaceous wetlands along the Great Lakes shorelines have been lost. Substantial losses of swamp forest also have occurred, due largely to logging and drainage for agricultural land use. However, despite the widespread distribution of coastal swamp forests and their spatial and functional connections between terrestrial and aquatic ecosystems, a systematic characterization of them is lacking. A detailed understanding of swamp forests along the Great Lakes shorelines, including their hydrologic regime, soil properties, vegetation composition and structure, and the geographic distribution of different swamp types would contribute substantially to the success of coastal wetland restoration. Thus, we applied a landscape ecosystem approach to classify and describe swamp forests along the Lake Michigan and Lake Huron shorelines.

Study Area and Methods

Field sampling was conducted in summer 2002 and 2003. A total of 447 plots were sampled in 42 swamp forests along Lake Michigan and Lake Huron. At each plot, physiography, hydrology, and soil data were recorded, and the overstory, understory, and ground-cover vegetation was sampled. Field data were integrated with aerial photo interpretation and GIS analyses to classify coastal swamp forests. Multivariate analyses (detrended correspondence analysis and canonical correspondence analysis) were conducted to confirm the distinctness of the ecosystem types and determine interrelationships among physical site factors, stand structure, and ground-cover species composition. Historical and present land cover was analyzed to assist in prioritizing restoration efforts among ecosystem types based on their historical abundance and the proportion of each type that has been lost.

Results

A three-level, hierarchical classification was developed for swamp forests along the Lake Michigan and Lake Huron shorelines. Classification proceeded in a top-down manner by dividing the shoreline into Major and Minor Shoreline Segments that were progressively more homogeneous in physiography and climate. Each minor shoreline segment contained a mosaic of Ecosystem Types, where the number of ecosystem types and their spatial pattern reflected fine-scale patterns of physiography, hydrology, soil, and vegetation. A total of two Major Shoreline Segments, four Minor Shoreline Segments, and nine Ecosystem Types were classified as follows:

I. Lake Huron and northern Lake Michigan
(former embayments)

- A. Northern Lake Huron and northern Lake Michigan
  1. Saturated swales and groundwater seepages
  2. Semipermanently inundated swales
- B. Southern Lake Huron
  3. Seasonally inundated swales and depressions
  4. Saturated swales and groundwater seepages
  5. Intermittently inundated islands

II. Eastern Lake Michigan (drowned river mouths)

C. Northwestern Lower Michigan

6. Seasonally inundated flat valley floor
7. Saturated groundwater seepages along valley margins

D. Southwestern Lower Michigan

8. Seasonally inundated flat valley floor
9. Saturated groundwater seepages along valley margins

Major shoreline segments (I and II) were distinguished on the basis of gross physiographic characteristics resulting in the occurrence of swamp forests in a different generic type of landform along each segment–former embayments along Lake Huron and northern Lake Michigan, and drowned river mouths along eastern Lake Michigan (Table 2, Figures 3–6). Each major shoreline segment was divided into a northern and southern Minor Shoreline Segment (A–D) on the basis of climatic and physiographic characteristics that have a strong influence on hydrologic regime, soil properties, and species distribution (Table 2, Figure 7). Two or three ecosystem types were nested within each minor shoreline segment.

Ecosystem types of each minor shoreline segment were distinguished by their position in relation to the shoreline, and the corresponding physiography, hydrology, soil, and vegetation (Figures 8–11). Along each minor shoreline segment, ecosystems located at a low elevation and close to shore (ecosystems 2, 3, 5, 6, and 8) were characterized by periodic inundation of the soil surface, a substrate of mineral soil (or shallow sapric muck over mineral soil in ecosystem 2), and the forest canopy was dominated by hardwoods, primarily red ash and silver maple. The ecosystem type of each minor shoreline segment located further from shore and at a higher elevation (ecosystems 1, 4, 7, and 9) was characterized by saturated, organic soil, and the forest canopy was dominated by northern white-cedar. Numerous conifers such as balsam fir, white spruce, black spruce, eastern hemlock, and tamarack were often present along with several hardwoods, such as black ash, paper birch, red maple, and yellow birch (Tables 2 and 3).

The ecological classification was supported by detrended correspondense analysis (DCA) and canonical correspondence analysis (CCA). Ecosystem types were well distinguished in the ordination space of the first two DCA axes (Figure 12). In the ordination, ecosystem types were distinguished primarily along a hydrologic gradient, where ecosystems characterized by inundation of the soil surface (ecosystems 2, 3, 6, and 8) were clearly separated from those characterized by saturated soil (ecosystems 1 and 7). CCA revealed interrelationships among environmental and stand structure variables and ground-cover species composition that further corroborated the classification. Hydrologic and soil variables were more important in explaining variation among sites than stand structure variables (Table 4). Range of soil surface pH and height of the high-water mark had the strongest influence on the analysis.

Comparison of historical and present land cover along the shorelines was used to develop restoration priorities among ecosystem types. Historically, the northern Lake Michigan and Lake Huron shoreline was dominated almost exclusively by conifer-dominated swamp. In contrast, the historical abundance of hardwood-dominated swamp was considerably greater than that of conifer-dominated swamp along southern Lake Huron. Whereas substantial areas of conifer-dominated swamp remain along the northern shorelines, conifer-dominated swamp has been virtually eliminated along southern Lake Huron. Thus, restoration of saturated, conifer-dominated swamp (ecosystem 4) is a high priority along southern Lake Huron.

Along the eastern Lake Michigan shoreline, drowned river-mouth valleys of northwestern Lower Michigan historically contained approximately equal amounts of hardwood- and conifer-dominated swamp. However, in southwestern Lower Michigan, the historical abundance of hardwood-dominated swamp was markedly greater than that of conifer-dominated swamp. Similar to the southern Lake Huron shoreline, conifer-dominated swamp has been practically eliminated from drowned river-mouth valleys of southwestern Lower Michigan. Therefore, restoration of saturated, conifer-dominated swamp (ecosystem 9) in groundwater seepages along the margin of drowned river-mouth valleys of southwestern Lower Michigan is a high priority. Otherwise, restoration effort should focus on sites with the best landscape context and those that can be restored at the lowest cost.

Conclusions

1. A landscape ecosystem approach, involving the simultaneous integration of climate, physiography, hydrology, soil, and vegetation, was applied to classify and describe swamp forests along the Lake Michigan and Lake Huron shorelines. By subdividing the shorelines geographically into major and minor shoreline segments that were progressively more homogeneous in physiography and climate, the classification provides a sound basis to interpret regional patterns of coastal swamp types.

2. Within each minor shoreline segment, swamp ecosystem types can be distinguished by their position in relation to the shoreline and their corresponding physiography, hydrology, soil, and vegetation. Along each minor shoreline segment, ecosystem types located closest to shore are characterized by inundation of the soil surface, a substrate of mineral soil, and the forest canopy is dominated by hardwoods, primarily red ash and silver maple. Ecosystem types located further from shore are characterized by saturated, organic soil, and the forest canopy is dominated by conifers, primarily northern white-cedar.

3. The Great Lakes have a strong influence on the hydrologic regime of swamp forests along their shorelines. Forty of the 42 study sites were located above the maximum lake level. The influence of the Great Lakes on the hydrologic regime of these swamps is indirect through the effect of lake-level fluctuation on local groundwater hydrology. In inundated ecosystems near the shore, surface water may persist through mid-summer, corresponding to seasonal high lake levels. Late in the growing season, the water table may fall well below the surface. In the two ecosystems located below the maximum lake level, the soil surface may remain inundated throughout the growing season when lake levels are high. These ecosystems were characterized by widely scattered red ash trees, low overstory basal area and tree canopy coverage, and a graminoid-dominated ground cover, composed of many species characteristic of open meadows.

4. Topographic relief in combination with hydrologic regime has a strong influence on species composition of the coastal swamps. In inundated ecosystem types, the depth and duration of inundation is reduced on microsites elevated above the general ground level, thereby providing sites for the establishment and recruitment of tree species that could not otherwise persist under the prolonged inundation. In saturated ecosystems, microtopographic heterogeneity promotes a wide range of soil surface pH. Although ground water rich in base cations and bicarbonate maintains a high soil pH, the soil surface of mounds and hummocks above the influence of ground water is very strongly acid. Therefore, numerous acidifiles occurred adjacent to calcifiles in saturated ecosystems due to local acid and circumneutral conditions on hummocks and hollows, respectively.

5. Swamp forests along the Great Lakes shoreline play a considerable role in maintaining regional biodiversity. A total of 23 trees, 41 shrubs, and 239 herbaceous species were recorded in sample plots in the coastal swamps. In addition to supporting a large number of plant species, coastal swamp forests are of marked importance in maintaining animal populations. Due to the characteristic location of coastal swamps, at the interface between upland ecosystems and herbaceous wetlands that extend into the Great Lakes, these swamps undoubtedly provide refuge for bald eagle, red-shouldered hawk, blandings turtle, spotted turtle, crayfish, snails, beaver, and many other animals.

6. Because coastal swamp forests along the Great Lakes shorelines are an integral part of the coastal wetland complex, a detailed understanding of the types of swamp forest occurring along a given stretch of the shoreline and their pattern in relation to elevation, hydrologic regime, and soil properties provides a substantial contribution to coastal wetland restoration. Due to the virtual elimination of conifer-dominated swamp along southern shorelines over the last 200 years, restoration effort should be directed toward saturated, conifer-dominated ecosystem types along the southern shorelines. Along northern shorelines, because the present abundance of hardwood- and conifer-dominated ecosystem types is roughly proportional to their historical abundance, restoration effort should focus on sites with the best landscape context and those that can be restored at the lowest cost.

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LITERATURE CITED

Albert, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. USDA For. Serv. Gen. Tech. Rep. NC-178. 250 pp. + map.

Albert, D.A., S.R. Denton, and B.V. Barnes. 1986. Regional landscape ecosystems of Michigan. School of Natural Resources, University of Michigan. Ann Arbor, Mich. 32 pp.

Albert, D.A., G.A. Reese, S.R. Crispin, M.R. Penskar, L.A. Wilsmann, and S.J. Ouwinga. 1988. A survey of Great Lakes marshes in the southern half of Michigan’s Lower Peninsula. Report to MDNR, Land and Water Management Division. Michigan Natural Features Inventory report number 1988-07. 116 pp.

Albert, D.A., G.A. Reese, M.R. Penskar, L.A. Wilsmann, and S.J. Ouwinga. 1989. A survey of Great Lakes marshes in the northern half of Michigan’s Lower Peninsula and throughout Michigan’s Upper Peninsula. Report to MDNR, Land and Water Management Division. Michigan Natural Features Inventory report number 1989-01. 124 pp.

Allen, R.B., and J.B. Wilson. 1991. A method for determining indigenous vegetation from simple environmental-factors, and its use for vegetation restoration. *Biol. Conserv.* 56:265-280.

Anderson, J.R., E.E. Hardy, J.T. Roach, and R.E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. US Geol. Surv. Prof. Paper 964 28 pp.

Baker, M.E. and B.V. Barnes. 1998. Landscape ecosystem diversity of river floodplains in northwestern Lower Michigan, U.S.A. *Can. J. For. Res*. 28:1405-1418.

Barnes, B.V. 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. *Can. J. Bot.* 54:19-24.

Barnes, B.V. 1996. Silviculture, landscape ecosystems, and the iron law of the site. *Forstarchiv* 67:226-235.

Barnes, B.V., K.S. Pregitzer, T.A. Spies, and V.H. Spooner. 1982. Ecological forest site classification. *J. For*. 80:493-498.

Barnes, B.V., D.R. Zak, S.R. Denton, and S.H. Spurr. 1998. Forest Ecology. 4th ed. John Wiley and Sons. New York. 774 pp.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406-1419.

Bedford, K.W. 1992. The physical effects of the Great Lakes on tributaries and wetlands. *J. Great Lakes Res.* 18:571-589.

Bell, D.T. 1974. Tree stratum composition and distribution in the streamside forest. *Am. Midl. Nat.* 92:35-46.

Bishop, C.T. 1990. Historical variation of water levels in Lakes Erie and Michigan-Huron. *J. Great Lakes Res.* 16:406-425.

Boelter, D.H., and E.S. Verry. 1977. Peatland and water in the northern Lake States. USDA For. Serv. Gen. Tech. Rep. NC-31. 22 pp.

Brunk, I.W. 1961. Changes in the levels of Lakes Michigan and Huron. *J. Geophysical Res.* 6:3329-3335.

Cherkauer, D.S., and P.F. McKereghan. 1991. Ground-water discharge to lakes: focusing in embayments. *Ground Water* 29:72-80.

Chow-Fraser, P. 1998. A conceptual model to aid restoration of Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. *Wetlands Ecol. and Manage.* 6:5-17.

Chow-Fraser, P., and D.A. Albert. 1998. Biodiversity Investment Areas: Coastal Wetland Ecosystems. State of the Lake Ecosystem Conference background paper. US Environmental Protection Agency and Environment Canada, Buffalo, N.Y.

Comer, P.J., and D.A. Albert. 1993. A survey of wooded dune and swale complexes in Michigan. Report to Michigan Dept. Nat. Res., Land and Water Management Division (CZM Project 13C-4.0) Michigan Natural Features Inventory. Lansing, MI. 45 pp + appendices.

Comer, P.J., D.A. Albert, H.A. Wells, B.L. Hart, J.B. Raab, D.L. Price, D.M. Kashian, R.A. Corner, and D.W. Schuen. 1995a. Michigan's presettlement vegetation, as interpreted from the General Land Office Surveys 1816-1856. Michigan Natural Features Inventory. Lansing, MI. Geographic data layer in raster GRID format.

Comer, P.J., D.A. Albert, H.A. Wells, B.L. Hart, J.B. Raab, D.L. Price, D.M. Kashian, R.A. Corner, and D.W. Schuen. 1995b. Michigan's native landscape, as interpreted from the General Land Office Surveys 1816–1856. Report to the US Envrionmental Protection Agency, Water Division, and Michigan Dept. Nat. Res., Wildlife Division. Michigan Natural Features Inventory. Lansing, MI. 76 pp.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRue. 1979. Classification of wetlands and deepwater habitats of the United States. USFWS Div. Biol. Serv. FWS/OBS-79/31.

Deeter, E.B., and A.E. Matthews. 1926. Soil survey of Tuscola County, Michigan. Washington, D.C. USDA Bur. Chem. and Soils, Series 1926, No. 27. 28 pp. + 1 map.

Denton, S.R. and B.V. Barnes. 1987. Tree species distributions related to climatic patterns in Michigan. *Can. J. For. Res.* 17:613-629.

Derecki, J.A. 1985. Effect of channel changes in the St. Clair River during the present century. *J. Great Lakes Res.* 11:201-207.

Dixon, M.D., M.G. Turner, and C. Jin. 2002. Riparian tree seedling distribution on Wisconsin River sandbars: controls at different spatial scales. *Ecol. Monogr.* 72:465-485.

Dorr, J.A.Jr, and D.F. Eschman. 1970. Geology of Michigan. 3rd ed. University of Michigan Press. Ann Arbor, MI. 476 pp.

Duncan, D.P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (*Larix laricina*) in Minnesota. *Ecology* 35:498-521.

Edsall, T.A., B.A. Manny, and C.N. Raphael. 1988. The St. Clair River and Lake St. Clair, Michigan: an ecological profile. US Fish and Wildlife Service. Biol. Rep. 87(7.10).

Eschman, D.F., and P.F. Karrow. 1985. Huron Basin glacial lakes: a review. *In* Karrow, P.F., and P.E. Calkin (eds.). Quaternary Evolution of the Great Lakes. Geol. Assoc. Canada. Special Paper 30.

ESRI (Environmental Systems Research Institute). 2000. ArcView v. 3.2. Geographic Information Systems Software. Redlands, California, USA.

Gauch, H.G. Jr. 1982. Multivariate Analysis in Community Ecology. Cambridge Univ. Press. Cambridge, MA. 297 pp.

Goforth, R.R., D. Stagliano, J. Cohen, M. Penskar, Y.M. Lee, and J. Cooper. 2001. Biodiversity analysis of selected riparian ecosystems within a fragmented landscape. Report for Michigan Great Lakes Protection Fund and Michigan Dept. of Environmental Quality, Office of the Great Lakes. Michigan Natural Features Inventory report number 2001-06. 148pp.

Gomes, A.R.S., and T.T. Kozlowski. 1980. Growth responses and adaptations of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiol.* 66:267-271.

Hansel, A.K., D.M. Mickelson, A.F. Schneider, and C.E. Larsen. 1985. Late Wisconsinan and Holocene history of the Lake Michigan Basin. *In* Karrow, P.F., and P.E. Calkin (eds.). Quaternary Evolution of the Great Lakes. Geol. Assoc. Canada. Special Paper 30.

Heath, R.T. 1992. Nutrient dynamics in Great Lakes coastal wetlands: future directions. *J. Great Lakes Res.* 18:590-602

Herdendorf, C.E. 1990. Great Lakes estuaries. *Estuaries* 13:493-503.

Herdendorf, C.E. 1992. Lake Erie coastal wetlands: an overview. *J. Great Lakes Res.* 18:533-551.

Hiebert, R.D., D.A. Wilcox, and N.B. Pavlovic. 1986. Vegetation patterns in and among pannes (calcareous intradunal ponds) at the Indiana Dunes National Lakeshore, Indiana. *Am. Midl. Nat.* 116:276-281.

Hill, M.O. 1979. TWINSPAN-a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics. Cornell University. Ithaca, NY.

Hill, M.O., and H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.

Hook, D.D. 1984. Waterlogging tolerance of lowland tree species of the south. *S. J. Applied For.* 8:136-149.

Hosner, J.F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. *For. Sci.* 6:246-251.

Host, G.E., K.S. Pregitzer, C.W. Ramm, D.P. Lusch, and D.T. Cleland. 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern Lower Michigan. *Can. J. For. Res.* 18:659-668

Hough, J.L. 1963. The prehistoric Great Lakes of North America. *American Scientist* 51:84-109.

Huenneke, L.F. 1982. Wetlands of Tompkins County, New York. *Bull. Torrey Bot. Club* 109:51-63.

Huenneke, L.F., and R.R. Sharitz. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *Am. Midl. Nat.* 115:328-335.

Hupp, C.R., and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* 66:670-681.

Jones, R.H., B.G. Lockaby, and G.L. Somers. 1996. Effects of microtopography and disturbance on fine-root dynamics in wetland forests of low order stream floodplains. *Am. Midl. Nat.* 136:57-71.

Kaplowitz, M.D., and J. Kerr. 2003. Michigan residents' perceptions of wetlands and mitigation. *Wetlands* 23:267-277.

Kashian, D.M., and B.V. Barnes. 2000. Landscape influence on the spatial and temporal distribution of the Kirtland's warbler at the Bald Hill burn, northern Lower Michigan, U.S.A. *Can. J. For. Res.* 31:1895-1904.

Kashian, D.M, B.V. Barnes, and W.S. Walker. 2001. Landscape ecosystems of northern Lower Michigan and the occurrence and management of the Kirtland's warbler. *For. Sci.* 49:140-158.

Keddy, P.A., and A.A. Reznicek. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *J. Great Lakes Res.* 12:25-36.

Keough, J.R, T.A. Thompson, G.R. Gunthenspergen, and D.A. Wilcox. 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. *Wetlands* 19:821-834.

Kowalski, K.P., and D.A. Wilcox. 1999. Use of historical and geospatial data to guide the restoration of a Lake Erie coastal marsh. *Wetlands* 19:858-868.

Lapin, M., and B.V. Barnes. 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. *Conserv. Biol.* 9:1148-1158.

Larsen, C.E. 1985. Lake level, uplift, and outlet incision, the Nippising and Algoma Great Lakes. *In* Karrow, P.F., and P.E. Calkin (eds.). Quaternary Evolution of the Great Lakes. Geol. Assoc. Canada. Special Paper 30.

Larsen, C.E. 1994. Beach ridges as monitors of isostatic uplift in the upper Great Lakes. *J. Great Lakes Res.* 20:108-134.

Larson, G., and R. Schaetzl. 2001. Origin and evolution of the Great Lakes. *J. Great Lakes Res.* 27:518-546.

Lawhead, H.F. 1961. Discussion of paper by Ivan W. Brunk, 'Changes in the levels of Lakes Michigan and Huron.' *J. Geophysical Res.* 66:4324-4329.

McCune, B., and M.J. Mefford. 1999. PC-ORD for windows: multivariate analysis of ecological data, version 4.01. MjM Software. Gleneden Beach, Oregon.

McDermott, R.E. 1954. Effects of saturated soil on seedling growth of some bottomland hardwood species. *Ecology* 35:36-41.

MDNR. 2001. IFMAP (Integrated Forest Monitoring and Assessment Prescription)/GAP (Gap Analysis Program) 2000 Michigan Land Cover. Geographic data layer in raster GRID format. Available on-line from MDIT-CGI (Michigan Department of Information Technology-Center for Geographic Information) at <www.michigan.gov/cgi>.

Minc, L.D. 1997. Great Lakes coastal wetlands: an overview of controlling abiotic factors, regional distribution, and species composition. Michigan Natural Features Inventory report number 1997-01. 307pp.

Minc, L.D., and D.A. Albert. 1998. Great Lakes coastal wetlands: Abiotic and Floristic Characterization. Michigan Natural Features Inventory report number 1998-05. 13 pp. + appendices.

Mitsch, W.J., and V. Bouchard. 1998. Enhancing the roles of coastal wetlands of the North American Great Lakes. *Wetlands Ecol. and Manage.* 6:1-3.

Moon, J.W., J.O. Veatch, R.E. Pasco, E.H. Hubbard, and R.L. Donahue. 1938. Soil survey of Saginaw County, Michigan. Washingon D.C. USDA Bur. Chem. and Soils, Series 1933, No. 19. 53 pp. + map.

National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series, No. 24. Sustainable Development Branch, Environment Canada, and Polyscience Publications Inc. Montreal, Quebec. 452 pp.

Olson, J.S. 1958. Lake Michigan dune development. 3. Lake-level, beach, and dune oscillations. *J. Geol.* 66:473-483.

Palik, B.J., P.C. Goebel, L.K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. *Ecol. App.* 10:189-202.

Paratley, R.D., and T.J. Fahey. 1986. Vegetation-environment relations in a conifer swamp in central New York. *Bull. Torrey Bot. Club* 113:357-371.

Pearsall, D.R. 1995. Landscape ecosystems of the University of Michigan Biological Station: ecosystem diversity and ground-cover diversity. Ph.D. Thesis. University of Michigan. Ann Arbor, Mich. 396 pp.

Pregitzer, K.S., and B.V. Barnes. 1984. Classification and composition of the upland hardwood and conifer ecosystems of the Cyrus H. McCormick Experimental Forest, Upper Peninsula, Michigan. *Can. J. For. Res*. 14:362-375.

Quinn. F.H. 2002. Secular changes in Great Lakes water level seasonal cycles. *J. Great Lakes Res.* 28:451-165.

Quinn, F.H., and C.E. Sellinger. 1990. Lake Michigan record levels of 1838, a present perspective. *J. Great Lakes Res.* 16:133-138.

Rowe, J.S. 1961. The level of integration concept and ecology. *Ecology* 42:420-427.

Schwintzer, C.R., and T.J. Tomberlin. 1982. Chemical and physical characteristics of shallow ground waters in northern Michigan bogs, swamps, and fens. *Am. J. Bot.* 69:1231-1239.

Siegel, D.I., and P.H. Glaser. 1987. Groundwater flow in a bog-fen complex, Lost River peatland, northern Minnesota. *J. Ecol.* 75:743-754.

Spies, T.A., and B.V. Barnes. 1985. A multi-factor ecological classification of the northern hardwood and conifer ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan. *Can J. For. Res*. 15:961-972.

Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability–what is natural vegetation in a changing environment. *Biol. Conserv.* 58:1-18.

Stephenson, D.E., and D.B. Hodgson. 1996. Root zone moisture gradients adjacent to a cedar swamp in southern Ontario. *In*: Mulamoottil, G., B.G. Warner, and E.A. McBean (eds.). Wetlands: environmental gradients, boundaries, and buffers. CRC Press, Inc. 298 pp.

Swanson, D.K., and D.F. Grigal. 1989. Vegetation indicators of organic soil properties in Minnesota. *Soil Sci. Soc. Am. J.* 53:491-495.

Tepley, A.J., J.G. Cohen, and D.A. Albert. 2003. Swamp forests of the Lake Huron shoreline. Report for the Michigan Dept. of Environmental Quality, MI Coastal Mgmt. Program (EPA project number 02-309-01b). Michigan Natural Features Inventory report number 2003-06. 65 pp.

ter Braak, C.F.J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.

ter Braak C.F.J., and P. Šmilauer. 1998. CANOCO–software for canonical community ordination, version 4.02. Centre for Biometry Wageningen, CRPO-DLO, Wageningen, The Netherlands.

Thien, S.J. 1979. A flow diagram for teaching texture-by-feel analysis. *J. Agronomic Education* 8:54-55.

Thompson, T.A. 1992. Beach-ridge development and lake-level variation in southern Lake Michigan. *Sedimentary Geol.* 80:305-318.

Thompson, T.A. and S.J. Beadke. 1995. Beach-ridge development in Lake Michigan: shoreline behavior in response to quasi-periodic lake-level events. *Marine Geol.* 129:163-174.

Thompson, T.A., and S.J. Beadke. 1997. Strand-plain evidence for late Holocene lake-level variations in Lake Michigan. *Geol. Soc. Amer. Bull.* 109:666-682.

Titus, J.H. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. *Bull. Torrey Bot. Club* 117:429-437.

USDA. 1999. Soil Taxonomy: a basic system of soil classification for making and interpreting soil surveys. 2nd ed. USDA Nat. Res. Cons. Service. Agriculture Handbook 436. 871 pp.

USFWS. 1994. The impact of Federal programs on wetlands. Vol. II. The Everglades, Coastal Louisiana, Galveston Bay, Puerto Rico, California's Central Valley, Western Riparian Areas, Southeastern and Western Alaska, the Delmarva Peninsula, North Carolina, Northeastern New Jersey, Michigan, and Nebraska. US Department of Interior, Fish and Wildlife Service, Washington, DC, USA.

USGS. 1984–1992. United States Geological Survey (USGS) Topographic Series. Digital Elevation Model (DEM). Derived from USGS standard 1:24,000 topographic series map resources. Geographic data layer if raster GRID format. Resolution, 90 m. Available on-line at <edc.usgs.gov/products/elevation/dem.html>.

Visocky, A.P. 1977. Hydrologic study of Illonois Beach State Park. Illinois State Water Survey Circular 128. 48 pp.

Vitt, D.H., H. Crum, and J.A. Snider. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in Northern Michigan. *Mich. Bot.* 14:190-200.

Walker, W.S., B.V. Barnes, and D.M. Kashian. 2001. Landscape ecosystems of the Mack Lake Burn, northern Lower Michigan, and the occurrence of the Kirtland's warbler. *For. Sci.* 49:119-139.

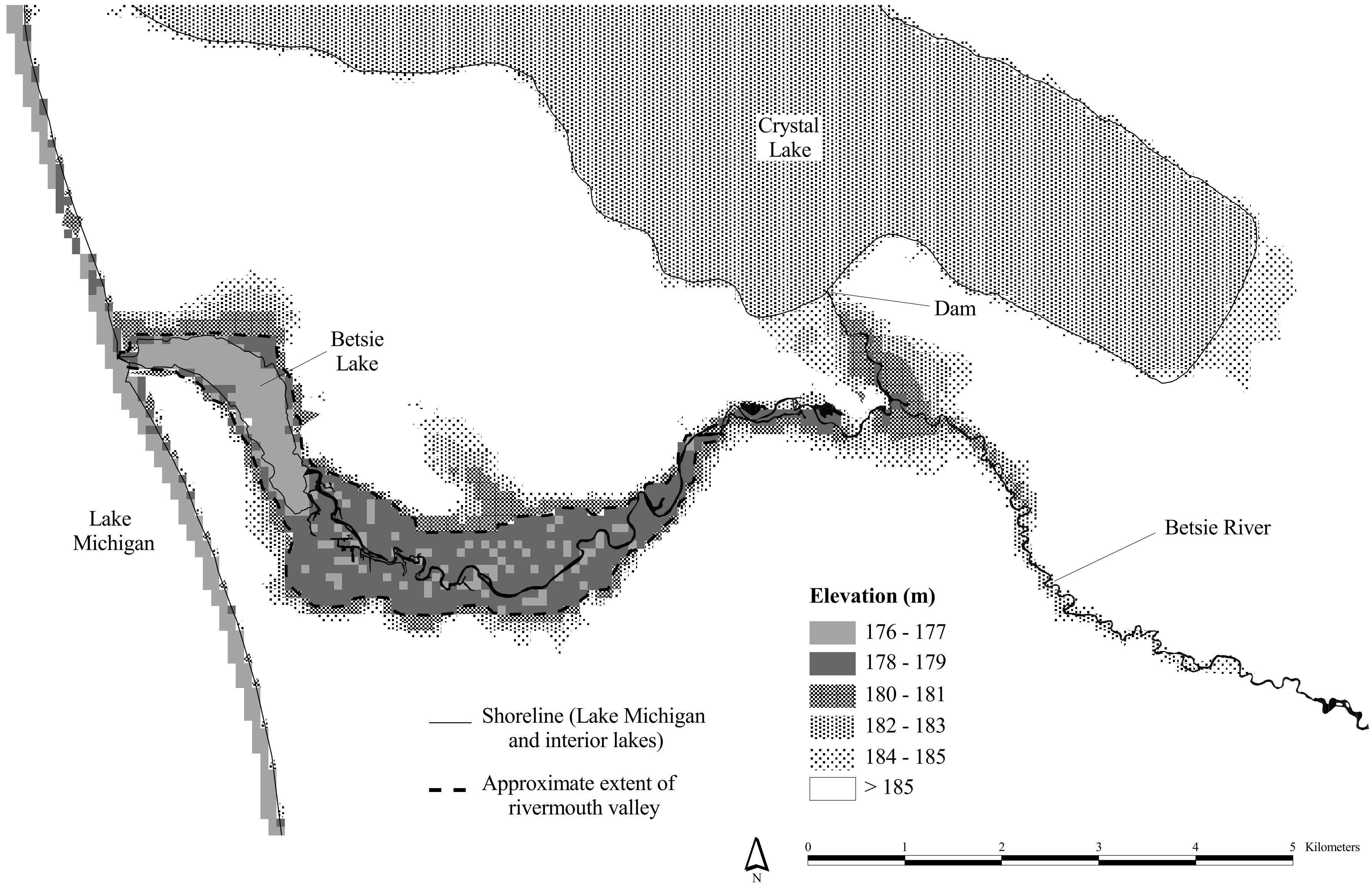
Wilcox, D.A., and H.A. Simonin. 1987. A chronosequence of aquatic macrophyte communities in dune ponds. *Aquatic Biol.* 28:227-242.

Wilcox, D.A., and T.H. Whillans. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. *Wetlands* 19:835-587.

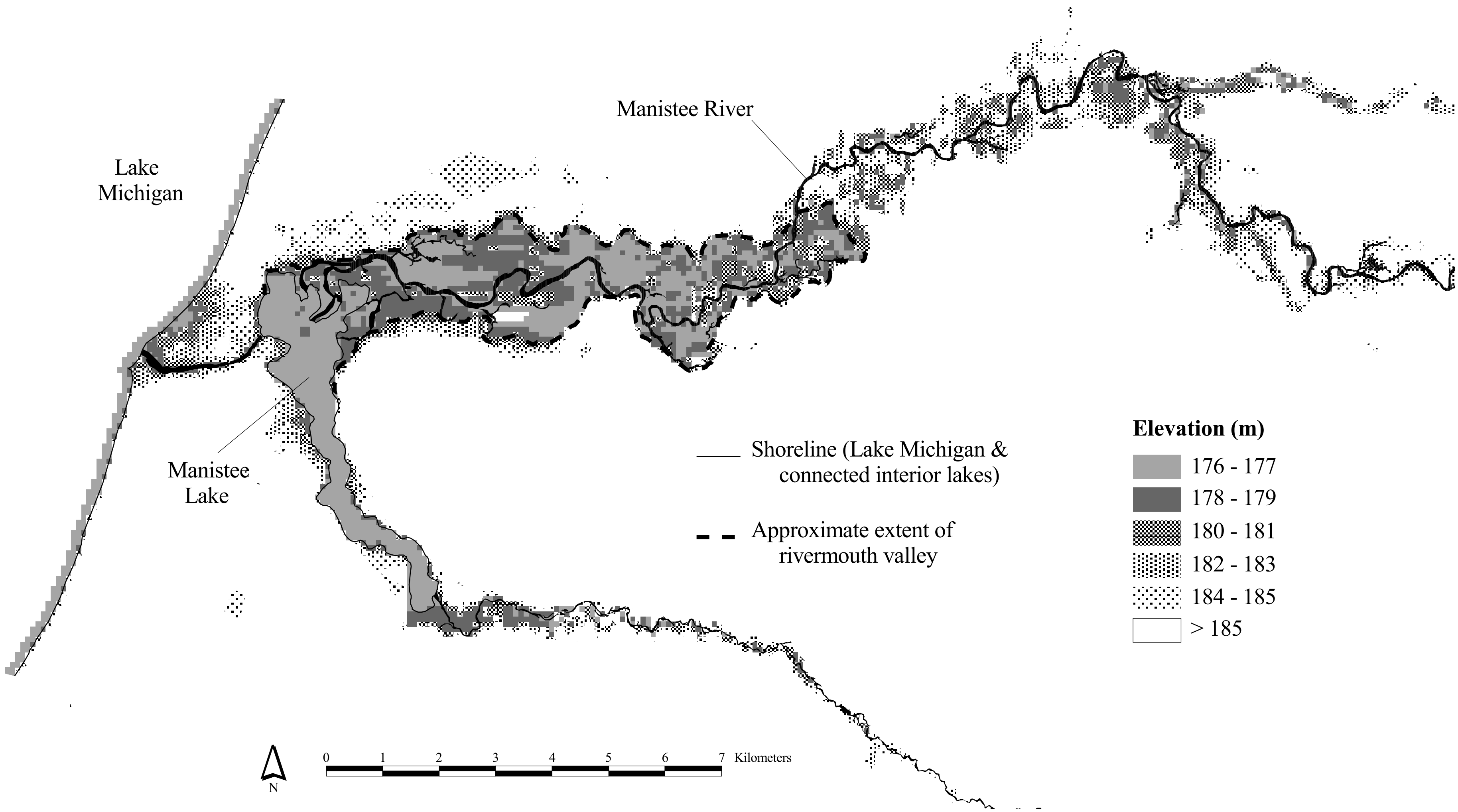
Williams, C.E., W.J. Moriarity, G.L. Walters, and L. Hill. 1999. Influence of inundation potential and forest overstory on the ground-layer vegetation of Allegheny Plateau riparian forests. *Am. Midl. Nat.* 141:323-338.

Zak, D.R., G.E. Host, and K.S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Can. J. For. Res.* 19:1521-1526.

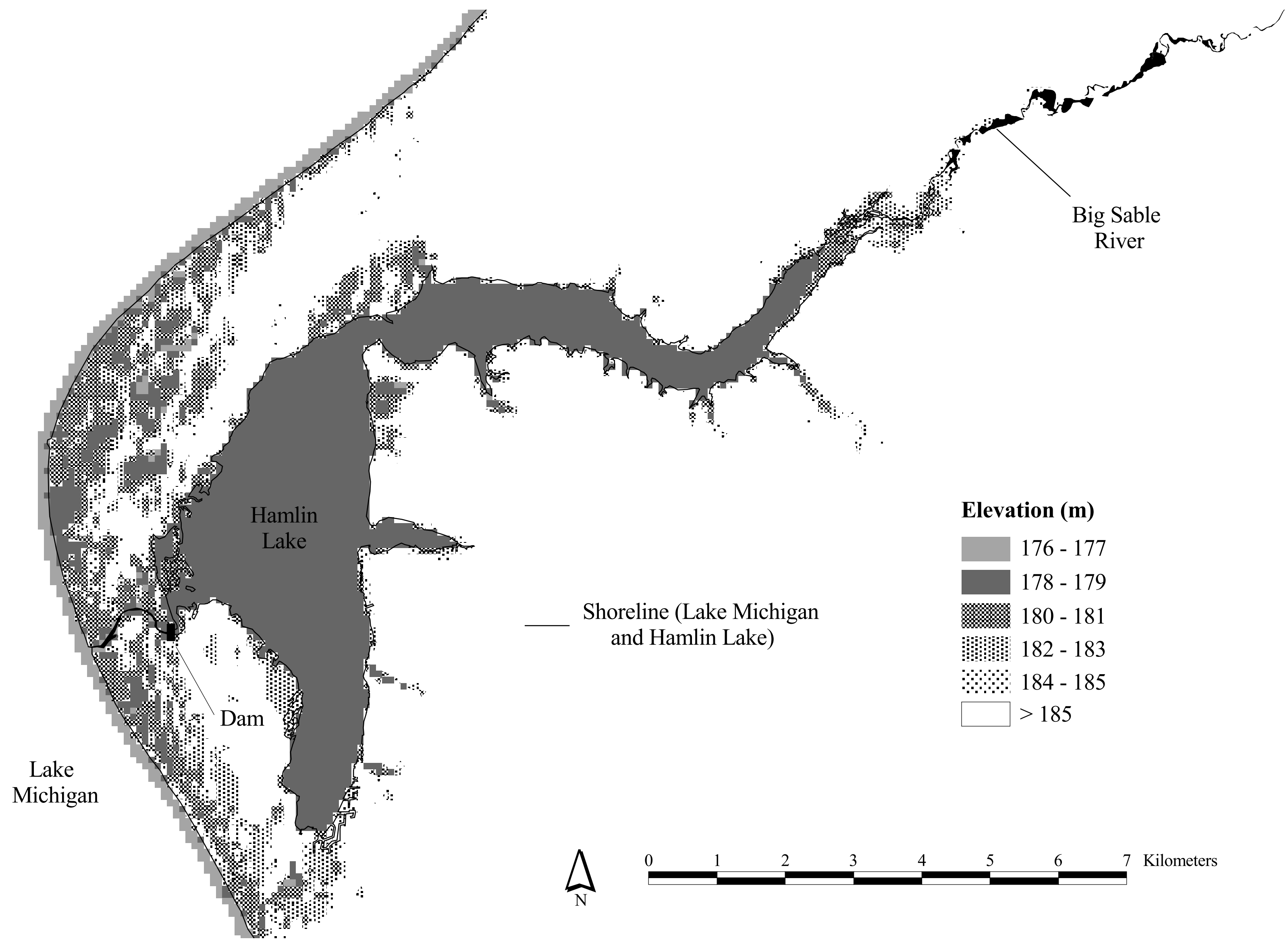
APPENDICES



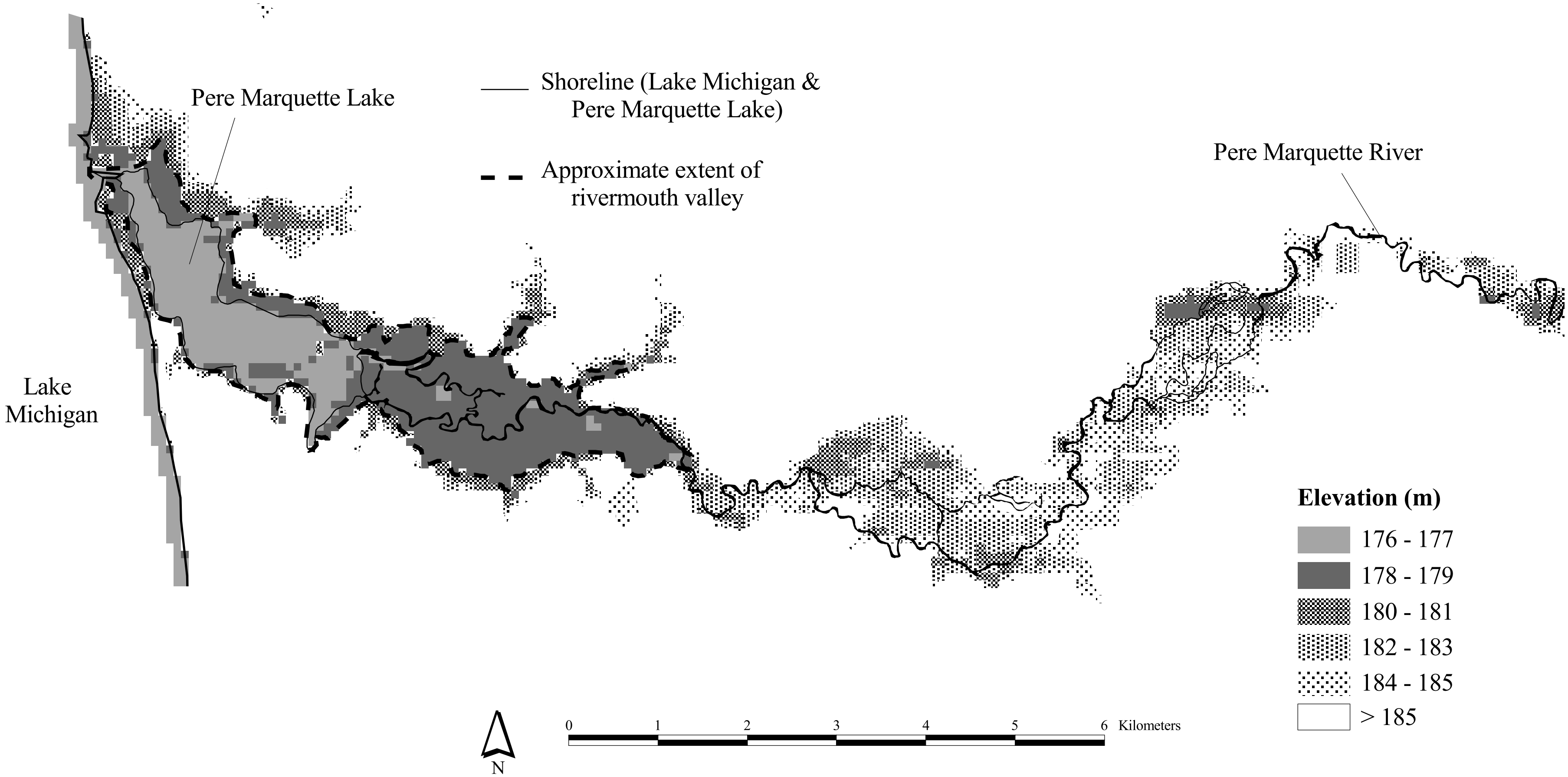
Appendix A1. Comparison of the broad, flat drowned river-mouth valley of the Betsie River, northwestern Lower Michigan, to the narrow, steeper valley upstream.



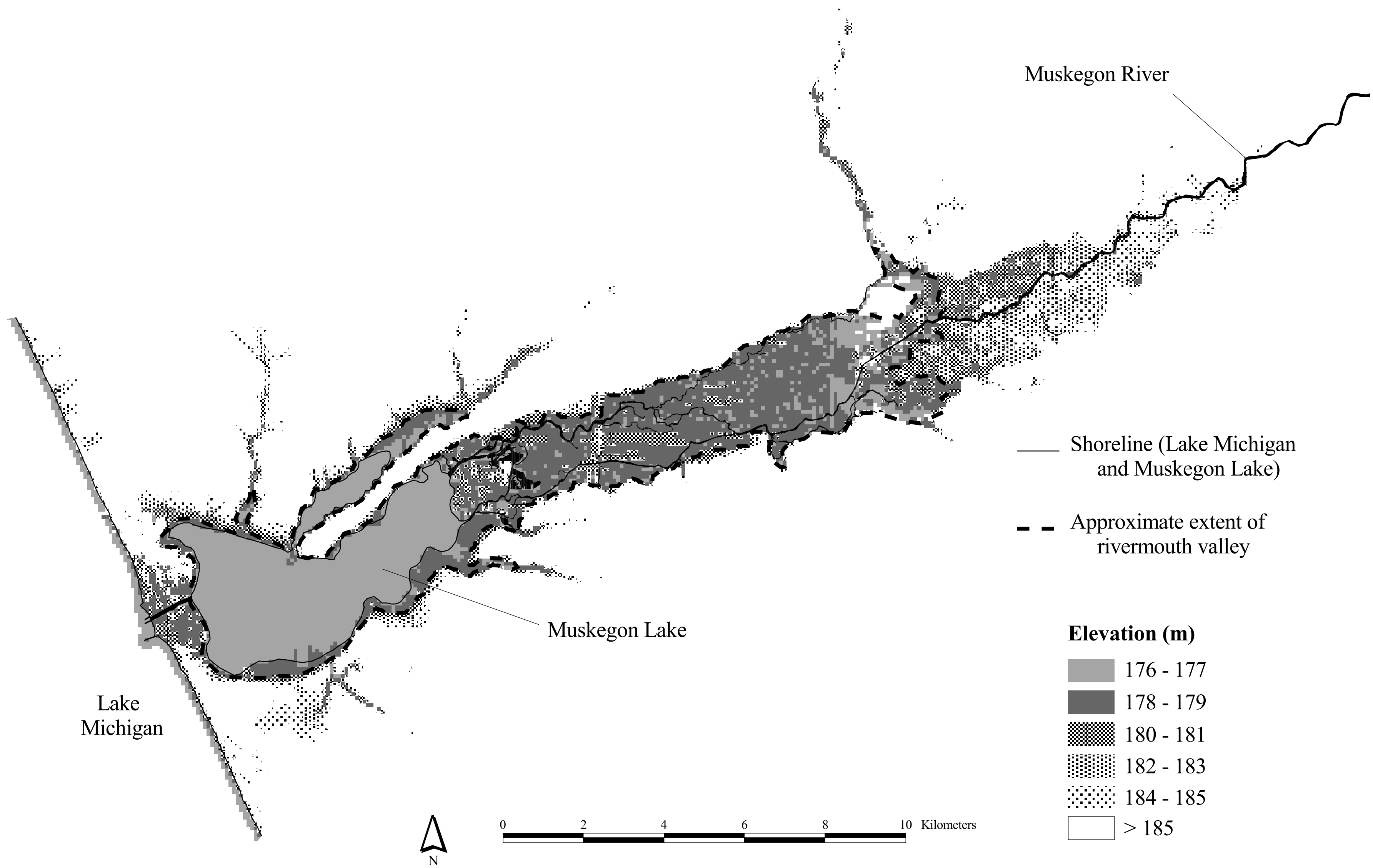
Appendix A2. Comparison of the broad, flat drowned river-mouth valley of the Manistee River, northwestern Lower Michigan, to the narrow, steeper valley upstream.



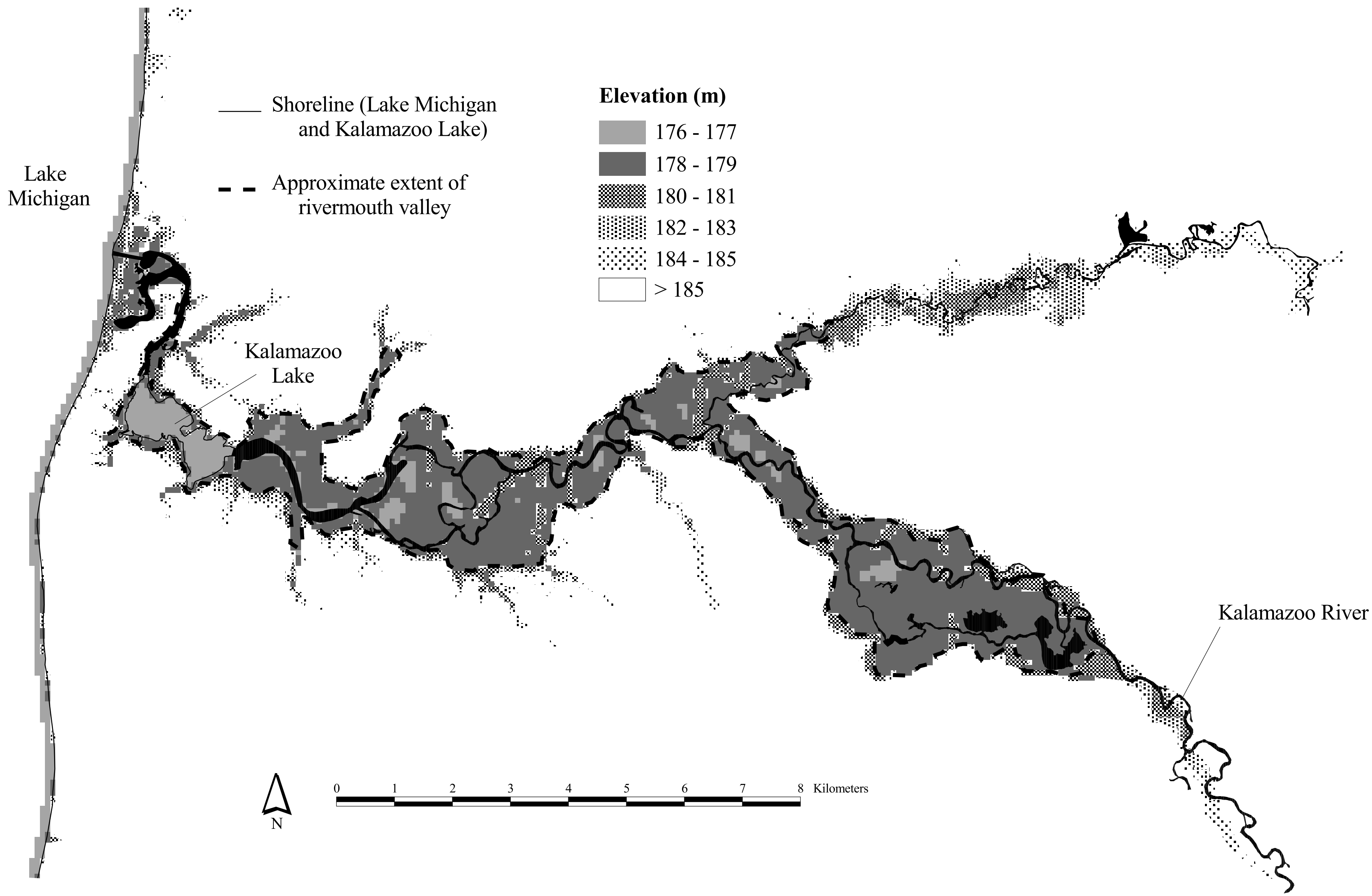
Appendix A3. Map of the drowned river mouth of the Big Sable River, where a dam at the outlet of Hamlin Lake has caused water of Hamlin Lake to submerge most of the natural drowned rivermouth valley.



Appendix A4. Comparison of the broad, flat drowned river-mouth valley of the Pere Marquette River, northwestern Lower Michigan, to the narrow, steeper valley upstream.



Appendix A5. Comparison of the broad, flat drowned river-mouth valley of the Muskegon River, southwestern Lower Michigan, to the narrow, steeper valley upstream.



Appendix A6. Comparison of the broad, flat drowned river-mouth valley of the Kalamazoo River, southwestern Lower Michigan, to the narrow, steeper valley upstream.

Appendix B. Ecological classification of swamp forests along the Lake Michigan and Lake Huron shorelines.[1]

I. Lake Huron and the northern Lake Michigan (former embayments)

A. Norhtern Lake Huron and northern Lake Michigan (Subsections VIII.1 and VII.6)

1. Saturated swales and gently sloping groundwater seepages; sapric muck over fine sand (average depth to sand 27 cm, clay or limestone bedrock occasionally present within 200 cm of the soil surface); northern white-cedar/*Mitella nuda, Coptis trifolia* (15 sites, 165 plots)
2. Semipermanently inundated swales; sapric muck over fine sand (depth to sand < 20 cm, cobble layer or bedrock present within 100 cm of the soil surface); Red ash/*Carex stricta* (1 site, 20 plots)

B. Southern Lake Huron (Subsections VI.6 and VI.5)

3. Seasonally inundated swales and depressions; fine sand over clay; silver maple–red ash–(American elm)[2]/*Glyceria striata, Boehmeria cylindrica* (16 sites, 132 plots)
4. Somewhat poorly drained to poorly drained shallow swales and gently sloping groundwater seepages; fine sand or sapric muck over fine sand (water table within 60 cm of the soil surface); northern white-cedar–tamarack/*Solidago gigantea, Smilacina stellata* (1 site, 1 plot)
5. Intermittently inundated flat terrain on Heisterman and Maisou Islands; fine sand over limestone bedrock (bedrock within 100 cm of the soil surface, clay layer < 20 cm thick present above the bedrock); Red ash/*Carex stricta, Calamagrostis canadensis* (1 site, 12 plots)

II. Eastern Lake Michigan (drowned river mouths)

C. Northwestern Lower Michigan (Subsection VII.4)

6. Seasonally inundated flat drowned rivermouth valley floor; shallow alluvial deposits (20–50 cm deep) over fine sand; red ash–silver maple–(American elm)[2]/*Carex lacustris* (3 sites, 65 plots)
7. Saturated gently sloping groundwater seepages along margins of drowned rivermouth valleys; sapric and hemic muck over marl (combined depth of sapric and hemic muck > 150 cm); northern white-cedar–eastern hemlock–yellow birch–black ash–red maple/*Osmunda cinnamomea* (3 sites, 12 plots)

D. Southwestern Lower Michigan (Subsection VI.3)

8. Seasonally inundated flat drowned rivermouth valley floor; shallow alluvial deposits (20–50 cm deep) over fine sand; silver maple–red ash–(American elm)[2]/*Saururus cernuus, Peltandra virginica* (2 sites, 40 plots)
9. Saturated gently-sloping groundwater seepages along margins of drowned rivermouth valleys; sapric and hemic muck over marl (depth to marl > 100 cm); northern white-cedar–tamarack–eastern hemlock–yellow birch–black ash–red maple/*Osmunda cinnamomea* (not quantitatively sampled)

[1] Ecosystem types are named for their hydrologic regime (regime modifiers follow Cowardin et al. 1979), landform, substrate type, canopy dominants, and one or two of the most characteristic ground-cover species

[2] Parentheses indicate canopy dominant prior to introduction of Dutch elm disease

Appendix C

Descriptions of landscape ecosystem types along
the Lake Michigan and Lake Huron shorelines

Ecosystem Type 1. Saturated swales and gently sloping groundwater seepages; sapric muck over fine sand (average depth to sand 27 cm, clay or limestone bedrock occasionally present within 200 cm of the soil surface); northern white-cedar/*Mitella nuda, Coptis trifolia*

SYNOPSIS: Located in former embayments along the northern Lake Michigan and Lake Huron shorelines (subsections VIII.1 and VII.6). Narrow, linear swales situated between low beach ridges, and gently sloping groundwater seepages along the outer margin of the embayment. Saturated sapric muck over fine sand; neutral at the soil surface, very strongly acid on hummocks. Northern white-cedar overstory; northern white-cedar–balsam fir understory; continuous, diverse ground-cover layer. Fifteen sites, 165 plots.

Physiography

Swales and depressions situated between low beach ridges within former embayments along the northern Lake Michigan and Lake Huron shorelines. Also in gently sloping groundwater seepages along the margin of the embayment and at the footslope of high beach ridges. Former embayments contain a series of beach ridges (typically less than 5 m high and 10–30 m wide) and intervening swales (often less than 30 m wide) oriented parallel to the shoreline. The ridge and swale topography developed as sand was reworked by wave action and built up and resorted by wind during the progressive recession of lake levels following glacial retreat and post-glacial uplift.

Hydrology

Groundwater-fed (saturated); water table is close to the surface in the early part of the growing season and capillary water saturates the sapric muck; later in the growing season the water table falls below the surface, but water is retained in small pores of the sapric muck and it remains saturated; surface water not present during the growing season except in small, local depressions.

Due to curvature of the shoreline, groundwater flow converges in embayments, and water levels within inter-ridge swales may be higher than lake levels; water-level fluctuation in the swales often parallels lake-level fluctuation.

Soil

SUBSTRATE: Sapric muck 27 (7–80) cm deep, over fine sand; clay occasionally present within 200 cm of the soil surface; limestone bedrock present within 200 cm of the soil surface on the Garden and Stonington Peninsulas, and in Alpena County.

pH: Neutral, 7.1 (5.8–7.8), at the soil surface; mildly alkaline, 7.7 (7.2–8.0), at 50 cm; moderately alkaline, 7.9 (7.8–8.0), at 100 cm; moderately alkaline, 7.9 (7.8–8.0), below 100 cm. Very strongly acid, 4.4 (4.0–5.3), on hummocks.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): northern white-cedar (81/81). Additional species: paper birch, black ash, balsam fir, white spruce, black spruce, balsam poplar, red maple, tamarack, trembling aspen. Mean basal area: 56.8 m^2/ha. Mean stem density: 2,145/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): northern white-cedar (52), balsam fir (34). Other common species: black ash, speckled alder, paper birch, red maple, black spruce, white spruce, tamarack, mountain maple. Mean large understory density: 1,187/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): balsam fir (45), alder-leaved buckthorn (13), speckled alder (12). Other common species: red maple, Canada fly honeysuckle, balsam poplar, black ash, northern white-cedar, trembling aspen, black spruce, white spruce, paper birch, Labrador tea, wild black currant. Mean small understory density: 1,067/ha.

GROUND COVER: Abundant forb species: *Rubus pubescens*, *Mitella nuda*, *Trientalis borealis*, *Coptis trifolia*, *Linnaea borealis*, *Maianthemum canadense*, *Cornus canadensis*, *Polygala paucifolia*, *Pyrola asarifolia*. Abundant graminoids: *Carex pedunculata*, *Carex trisperma*, *Carex eburnea*, *Carex arctata*, *Carex leptalea*. Abundant ferns: *Equisetum arvense*, *Dryopteris cristata*, *Gymnocarpium dryopteris*, *Botrichyium virginianum*. Abundant shrubs: *Alnus rugosa*, *Gaultheria hispidula*, *Lonicera canadensis*, *Rhamnus alnifolia*, *Ribes americanum*, *Spiraea alba*. Abundant tree species: balsam fir, red maple, black ash, northern white-cedar, paper birch.

Comments

All sites were characterized by pit-and-mound topography that developed as result of windthrow, or from the buildup of organic matter at the base of trees. Due to the combined influence of strong winds coming off the lakes, shallow rooting, and dense, evergreen foliage, windthrow is a common disturbance. Multiple treefall gaps are common, and the resulting high light levels on the forest floor account, in part, for the persistence of moderately tolerant and intolerant tree species (e.g., paper birch, black ash, red maple, balsam poplar, and trembling aspen).

Because rooting is restricted to the organic soil, variability among sites in overstory tree size and density is largely related to organic soil depth. In general, tree density decreased and tree size increased with increasing organic soil depth. For example, dominant overstory species were of similar age at Nahma and Epoufette Bay, but organic soil depth at Nahma (7–22 cm) was lowest of all sites, and organic soil at Epoufette Bay was considerably deeper (35–50 cm). Although Nahma was characterized by the highest tree density (2,970/ha) and smallest tree size (average dbh of northern white-cedar, 13.3 cm) of all sites, tree density at Epoufette Bay (1,820/ha) was among the lowest and tree size (average dbh of northern white-cedar, 19.5 cm) was among the highest of all sites.

Excessive browsing by deer has greatly reduced recruitment of northern white-cedar seedlings. Few seedlings taller than the depth of the winter snowpack were observed.

Similar Ecosystems

Distinguished from ecosystems 7 and 9 by shallower organic soil, lack of hemic organic matter or marl, greater density and basal area of northern white-cedar, lower density and abundance of deciduous species in the forest canopy, and lower coverage of cinnamon fern in the ground cover. In addition, although low numbers of balsam fir, white spruce, and black spruce trees were present at most sites in ecosystem 1, these species were absent from ecosystems 7 and 9.

Distinguished from ecosystem 2 by higher elevation and greater distance from the shore, lack of surface water during the growing season, higher tree density and basal area, and dominance by northern white-cedar rather than red ash.

Research Basis

NUMBER OF SITES: 15

TOTAL NUMBER OF PLOTS: 165

Brulee Point	Sec. 30, T42N, R1W Mackinac Co.	10 plots
Chippewa Point	Sec. 25, T39N, R21W Delta Co.	5 plots
Duck Bay	Sec. 12, T41N, R1W Mackinac Co.	10 plots
El Cajon Bay	Sec. 15, T31N, R9E Alpena Co.	10 plots

Research Basis (continued)

Epoufette Bay	Sec. 4&5, T42N, R7W Mackinac Co.	10 plots
Hog Island Point	Sec. 35, T43N, R8W Mackinac Co.	5 plots
Misery Bay	Sec. 22, T31N, R9E, Alpena Co.	20 plots
Nahma	Sec. 19, T40N, R19W Delta Co.	5 plots
Ogontz North	Sec. 15, T40N, R20W Delta Co.	5 plots
Ogontz West	Sec. 21, T40N, R20W Delta Co.	5 plots
Paquin Lake	Sec. 35, T42N, R2W Mackinac Co.	20 plots
Portage Bay	Sec. 28, T39N, R18W Delta Co.	5 plots
Seiner's Point	Sec. 5, T41N, R12W Mackinac Co.	5 plots
St. Martin Bay	Sec. 22, T42N, R2W Mackinac Co.	20 plots
Voight Bay	Sec. 14, T41N, R1W Mackinac Co.	10 plots

Ecosystem Type 2. Semipermanently inundated swales; sapric muck over fine sand (depth to sand < 20 cm, cobble layer or bedrock present within 100 cm of the soil surface); Red ash/*Carex stricta*

SYNOPSIS: Located in former embayments along the northern Lake Michigan and Lake Huron shorelines (subsections VIII.1 and VII.6). Narrow, linear swales situated between low beach ridges (typically one of the first swales from shore). Semipermanently inundated sapric muck over fine sand (depth to mineral soil < 20 cm); neutral at the soil surface, mildly to moderately alkaline below the surface. Red ash overstory; red ash–balsam fir understory; sedge-dominated ground-cover layer with relatively low species diversity due to prolonged inundation during the growing season. One site, 20 plots.

Physiography

Narrow, linear swales situated between low beach ridges within former embayments along the northern Lake Michigan and Lake Huron shorelines. Former embayments contain a series of beach ridges (typically less than 5 m high and 10–30 m wide) and intervening swales (often less than 30 m wide) oriented parallel to the shoreline. The ridge and swale topography developed as sand was reworked by wave action and built up and resorted by wind during the progressive recession of lake levels following glacial retreat and post-glacial uplift. Located in one of the first swales from the shoreline. Elevation of the bottom of the swale may be lower than the maximum lake level

Hydrology

Groundwater-fed (semipermenently inundated); water table is above the soil surface early in the growing season, and surface water may persist throughout the growing season when lake levels are high; when surface water is not present the water table remains close to the soil surface. Water depth, 8 (1–23) cm in early July 2002; high water mark, 36 (14–50) cm above the soil surface.

Directly influenced by Great Lakes water levels because elevation of the bottom of the swale may be slightly lower than the maximum lake level.

Soil

SUBSTRATE: Sapric muck 13 (8–18) cm deep, over fine sand. Cobble layer or limestone bedrock present within 100 cm of the soil surface.

pH: Neutral, 7.3 (7.2–7.4), at the soil surface; mildly alkaline, 7.8, at 50 cm; mildly alkaline, 7.8, at 100 cm. Hummocks are generally circumneutral, but hummocks higher than the high water level may have acid soil.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): red ash (81/79). Additional species: red maple, paper birch, tamarack, black ash, northern white-cedar, balsam fir. Mean basal area: 21.3 m^2/ha. Mean stem density: 913/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): red ash (47), balsam fir (43). Other common species: black spruce, red maple, black ash, silver maple, tamarack, northern white-cedar, paper birch. Mean large understory density: 683/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): meadowsweet (45), speckled alder (44). Other common species: bog birch, red ash, balsam fir, red raspberry, silky dogwood, shrubby cinquefoil, swamp rose. Mean small understory density: 11,510/ha.

GROUND COVER: Abundant forb species: *Lycopus uniflorus, Lysimachia thyrsiflora, Iris versicolor,* *Mentha arvensis, Campanula aparinoides, Polygonum amphibium, Rubus pubescens, Poetntilla palustris.* Abundant graminoids: *Carex stricta, Calamagrostis canadensis, Carex lacustris, Carex intumescens.* Abundant ferns: *Thelypteris palustris, Onoclea sensibilis*. Abundant shrubs: *Spiraea alba, Betula pumila, Rubus strigosus, Alnus rugosa, Cornus amomum*. Abundant tree species: red ash, red maple, silver maple, paper birch.

Comments

Typically located in one of the first swales from the shore. Elevation of the bottom of the swale may be lower than the maximum lake level. Directly influenced by Great Lakes water levels and receives groundwater that is channeled into the embayment from higher terrain further inland.

The distribution of tree species is largely determined by hydrology and microtopography. Red ash was common in low parts of the swale, and high water marks up to 50 cm above the soil surface were recorded on boles of red ash trees. However, species including balsam fir, red maple, and paper birch were restricted to higher ground along the outer margin of the swale. Trees may be absent from the lowest part of the swale, which often contains wet meadow vegetation. Periodic low lake levels permit tree seedling establishment in the lowest part of the swale, but subsequent high lake levels kill the seedlings.

Tree density and tree canopy coverage are low due to prolonged inundation of the soil surface during the growing season. Shrubs including speckled alder, meadowsweet, and bog birch, and graminoids, such as tussock sedge, may be abundant due to relatively low tree canopy coverage.

Similar Ecosystems

Distinguished from ecosystem 1 by closer proximity to shore and lower elevation. Also distinguished from ecosystem 1 by inundation of the soil surface during the growing season, shallower organic soil, and dominance by red ash rather than northern white-cedar.

Distinguished from ecosystem 3 by greater water depth, longer duration of inundation, and higher water table late in the growing season. Also distinguished from ecosystem 3 by the presence of a shallow layer of sapric muck, rather than mineral soil, at the soil surface. Prolonged growing season inundation and a high water table when surface water recedes result in markedly lower overstory basal area and tree canopy coverage than ecosystem 3. The low tree canopy coverage permits a greater abundance of shrubs and graminoids than in ecosystem 3.

Distinguished from ecosystem 5 by substantial groundwater inputs, resulting in annual inundation of the soil surface and maintaining a high water table late in the growing season. Both ecosystems may be located at elevations below the maximum lake level, and are directly influenced by Great Lakes water levels. However, ecosystem 2 receives substantial groundwater inputs due to seepage from higher terrain further inland, but such inputs are minimal in ecosystem 5 due to its location on small islands with little terrain at a higher elevation. Also distinguished from ecosystem 5 by the occurrence of species with a northerly range (e.g., *Alnus rugosa, Iris versicolor, Abies balsamea*).

Research Basis

NUMBER OF SITES: 1

NUMBER OF PLOTS: 20

Ossineke	Sec. 18, T29N, R9E Alpena Co.	20 plots

Ecosystem Type 3. Seasonally inundated swales and depressions; fine sand over clay; silver maple–red ash–(American elm)/*Glyceria striata, Boehmeria cylindrica*

SYNOPSIS: Located in former embayments along the southern Lake Huron shoreline (subsections VI.6 and VI.5). Linear swales and broad depressions situated between low beach ridges. Seasonally inundated fine sand over clay; neutral at the soil surface, mildly to moderately alkaline below the surface. Silver maple–red ash overstory (with American elm prior to Dutch elm disease); American elm–red ash–silver maple understory; sparse ground-cover layer and low ground-cover species diversity due to inundation of the soil surface during the growing season. Sixteen sites, 132 plots.

Physiography

Narrow, linear swales and broad, irregular depressions situated between low beach ridges within former embayments along the southern Lake Huron shoreline. Generally at a higher elevation than the maximum lake level. Former embayments contain a series of beach ridges (typically less than 5 m high and 10–30 m wide) and intervening swales (often less than 30 m wide) oriented parallel to the shoreline. The ridge and swale topography developed as sand was reworked by wave action and built up and resorted by wind during the progressive recession of lake levels following glacial retreat and post-glacial uplift. In parts of Saginaw Bay, swales may be wider than 30 m, and the regular patterning of ridges and swales in relation to the shoreline may be lacking due to the large size of the embayment and the small amount of sand available to be reworked as water levels receded.

Hydrology

Groundwater-fed (seasonally inundated); water table is above the soil surface early in the growing season (low rises 10–30 cm above the water level occur at some sites); surface water is absent late in the growing season and the water table may fall more than 100 cm below the soil surface. Water depth 12 (0–28) cm in late June and early July 2002–2003; high water mark 26 (8–46) cm above the soil surface.

Due to curvature of the shoreline, groundwater flow converges in embayments; water levels within swales may be higher than lake levels due to large groundwater inputs and shallow depth to impervious clay and bedrock; water-level fluctuation in the swales generally parallels that of the Great Lakes.

Soil

SUBSTRATE: Fine sand over clay; depth to clay usually less than 200 cm.

pH: Neutral, 7.2 (5.8–8.0), at the soil surface; mildly alkaline, 7.6 (7.2–7.8), at 50 cm; mildly alkaline, 7.7 (7.5–8.0), at 100 cm; moderately alkaline, 7.9 (7.8–8.0) below 100 cm.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): red ash (41/46), silver maple (35/37), eastern cottonwood (14/5). Additional species: American elm, swamp white oak. Mean basal area: 37.2 m^2/ha. Mean stem density: 812/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh)*: Most abundant species (% of large understory density): American elm (45), red ash (41), silver maple (12). Other common species: swamp white oak, black ash, bur oak, choke cherry, buttonbush. Mean large understory density: 1,223/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): red ash (61), silky dogwood (11). Other common species: American elm, red-osier dogwood, Michigan holly, riverbank grape, silver maple. Mean small understory density: 1,476/ha.

GROUND COVER: Abundant forbs: *Boehmeria cylindrica, Impatiens capensis, Cicuta maculata, Lycopus uniflorus, Scutellaria lateriflora, Lysimachia thyrsiflora, Aster lateriflorus, Pilea pumila, Viola* spp., *Cicuta bulbifera, Sium suave*. Abundant graminoids: *Glyceria striata, Carex lacustris, Elymus virginicus, Carex stricta, Carex stipata, Carex oligosperma, Carex muskingumensis, Carex gracillima, Carex amphibola, Carex intumescens*. Abundant ferns: *Onoclea sensibilis, Athyrium filix-femina, Thelypteris palustris.* Abundant woody vines: *Vitis riparia, Parthenocissus quinquefolia, Toxicodendron radicans*. Abundant shrubs: *Cornus amomum, Ribes americanum, Rubus strigosus, Rosa palustris, Ilex verticillata, Viburnum trilobum*. Abundant tree species: red ash, silver maple, American elm, swamp white oak.

Comments

Tree species distribution is largely determined by water depth and microtopography. Red ash and silver maple are common throughout the ecosystem. However, eastern cottonwood and swamp white oak are restricted to low rises, and these species were absent from sites that lacked such microtopography. Prior to the introduction of Dutch elm disease, American elm probably also reached canopy size on low rises, but most American elm trees now die before attaining canopy size.

The draw down of the water table late in the growing season permits relatively deep rooting, and windthrow is less common than in other coastal swamp types. Deep rooting also enables development of relatively high tree canopy coverage. The combination of inundation of the soil surface during the growing season and relatively high tree canopy coverage result in a sparse, patchy distribution of ground-cover vegetation and low coverage of shrubs.

Although ecosystem 3 is typically located at a higher elevation than the maximum lake level, the hydrologic regime is indirectly regulated by the Great Lakes. Near the shore, groundwater head gradients are forced to adjust to lake-level fluctuation in order to maintain continuous flow. Such adjustments affect local groundwater elevation. The effects of such adjustments may extend far inland in Saginaw Bay due to the flat topography and shallow depth to impervious clay and bedrock.

Swales at Kirk Road and Gotham Road were located closer to the shore and at a lower elevation than the other sites. As a result, water depth and the duration of inundation was greater than that of the other sites, and the water table remained closer to the surface after surface water recedes. Because soil aeration was poor relative to that of the other sites, swales at Kirk Road and Gotham Road contained a shallow layer of sapric muck (< 15 cm deep).

Similar Ecosystems

Distinguished from ecosystem 2 by shallower water depth, shorter duration of inundation, greater depth to the water table late in the growing season, and mineral rather than organic soil (other than exceptions noted above). Also distinguished from ecosystem 2 by the lack of northern white-cedar, balsam fir, and red maple in the canopy.

Distinguished from ecosystem 8 by shallower water depth and longer duration of inundation. Also distinguished from ecosystem 8 by sparse, patchy distribution of ground-cover vegetation rather than continuous coverage.

Research Basis

NUMBER OF SITES: 16

NUMBER OF PLOTS: 132

Research Basis (continued)

Bay Port Swale	Sec. 2, T16N, R9E Huron Co.	7 plots
Bay City Campground	Sec. 32, T15N, R5E Bay Co.	4 plots
Bradleyville	Sec. 15, T14N, R7E Tuscola Co.	4 plots
Gotham Road	Sec. 29, T15N, R8E Tuscola Co.	3 plots
King Road	Sec. 11, T14N, R7E Tuscola Co.	15 plots
Kirk Road	Sec. 29, T15N, R8E Tuscola Co.	4 plots
Lakeport	Sec. 20, T8N, R17E St. Clair Co.	4 plots
Pigeon North	Sec. 2, T16N, R9E Huron Co.	4 plots
Pigeon South	Sec. 11, T16N, R9E Huron Co.	15 plots
Pinconning	Sec. 30, T17N, R5E Bay Co.	15 plots
Tobico Swamp	Sec. 24, T15N, R4E Bay Co.	20 plots
Vanderbilt Park	Sec. 21, T14N, R7E Tuscola Co.	2 plots
Weale Road	Sec. 14, T16N, R9E Huron Co.	5 plots
Weale Train Tracks	Sec. 14, T 16N, R9E Huron Co.	2 plots
Wigwam Bay	Sec. 15, T18N, R5E Arenac Co.	20 plots
Wildfowl Swale	Sec. 29, T17N, R9E Huron Co.	8 plots

Ecosystem Type 4. Somewhat poorly drained to poorly drained shallow swales and gently sloping groundwater seepages; fine sand or sapric muck over fine sand (water table within 60 cm of the soil surface); northern white-cedar–tamarack/*Solidago gigantea*, *Smilacina stellata*

SYNOPSIS: Located in former embayments along the southern Lake Huron shoreline (subsections VI.6 and VI.5). Shallow swales situated between low beach ridges, and gently sloping groundwater seepages at the footslope of larger ridges. Somewhat poorly drained to poorly drained fine sand or saturated sapric muck over fine sand; neutral at the soil surface, strongly acid on hummocks. Northern white-cedar–tamarack overstory; white ash–spicebush–prickly-ash–choke cherry understory; continuous, diverse ground-cover layer. Historical occurrence of conifer-dominated swamp along Saginaw Bay is documented in GLO survey records, but it was virtually eliminated due primarily to conversion to agriculture. One plot, one site.

Physiography

Shallow swales and depressions situated between low beach ridges within former embayments along the southern Lake Huron shoreline. Also in gently sloping groundwater seepages at the footslope of larger ridges and along outer margins of embayments. Former embayments contain a series of beach ridges (typically less than 5 m high and 10–30 m wide) and intervening swales (often less than 30 m wide) oriented parallel to the shoreline. The ridge and swale topography developed as sand was reworked by wave action and built up and resorted by wind during the progressive recession of lake levels following glacial retreat and post-glacial uplift. Although swales close to shore are characterized by a wide range of water-level fluctuation, the water table may be maintained close to the surface throughout the growing season in swales further from the shore. Also, local topographic and soil characteristics may maintain water table close to the surface.

Hydrology

Groundwater-fed (saturated); surface water not present except in small local depressions; local topography and soil characteristics maintain the water table close to the soil surface throughout the growing season. Depth to water table, 30 cm in late June 2003.

Due to curvature of the shoreline, groundwater flow converges in embayments, and water levels within swales may be higher than lake levels.

Soil

SUBSTRATE: Fine sand or shallow sapric muck (less than 30 cm deep) over fine sand.

pH: Neutral, 7.0, at the soil surface; mildly alkaline, 7.4, at 50 cm; moderately alkaline, 7.8, at 100 cm.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): northern white-cedar (94/92). Additional species: tamarack, paper birch, white ash. Mean basal area: 64.6 m^2/ha. Mean stem density: 1,800/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): prickly-ash (50), choke cherry (50). Mean large understory density: 400/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): prickly-ash (26), choke cherry (21), white ash (18), Japanese barberry (18). Other common species: spicebush, Canada fly honeysuckle, serviceberry, riverbank grape, swamp white oak. Mean small understory density: 3,900/ha.

GROUND COVER: Abundnat forbs: *Solidago gigantea, Fragaria virginiana, Rubus pubescens, Smilacina stellata, Maianthemum canadense, Aralia nudicaulis, Clematis virginiana, Galium asprellum, Galium triflorum*. Abundant graminoids: *Carex leptalea, Carex pedunculata*, *Glyceria striata*. Abundnat woody vines: *Toxicodendron radicans, Parthenocissus quinquefolia, Vitis riparia*. Abundant shrubs: *Lonicera dioica, Prunus virginiana, Euonymus obovata, Amelanchier* spp., *Cornus alternifolia, Cornus amomum, Zanthoxylum americanum, Berberis thunbergii*. Abundant tree species: white ash, swamp white oak, silver maple.

Comments

General Land Office (GLO) survey records indicate the historical occurrence of conifer-dominated swamps along Saginaw Bay. The conifer-dominated swamps were much less abundant than hardwood-dominated swamps, and they were generally located further inland and at a higher elevation. However, nearly all conifer-dominated swamps have been eliminated, due primarily to conversion to agriculture.

One plot was sampled at Bay Port. The Bay Port site is a beach ridge and swale complex where the majority of the swales were inundated (ecosystem 3), but several small occurrences of ecosystem 4 were located inland of the inundated swales. Coniferous trees (northern white-cedar and tamarack) were restricted to low rises near the outer swale margins. The sample plot was located on such a low rise, approximately 50 cm above the bottom of the adjacent swale. The substrate was fine sand and the depth to the water table was 30 cm. The plot was dominated by northern white-cedar trees 86 years old, with low numbers of tamarack trees. Numerous cut stumps of northern white-cedar indicate previous dominance by northern white-cedar. The entire ground surface of the adjacent swale was inundated by water up to 20 cm deep (late June 2003). Silver maple and red ash were the dominant species of the inundated swale, and there were no cut stumps of northern white-cedar. More extensive occurrences of ecosystem 4 probably occurred on shallow sapric muck, but these sites were most likely drained and converted for agricultural use.

Similar Ecosystems

Distinguished from ecosystem 3 by the absence of standing water during the growing season, other than in small, local depressions, and dominance by conifers rather than hardwoods. However, hardwood species including black ash, red maple, yellow birch, and American elm may historically have been common canopy species of ecosystem 4. Also distinguished from ecosystem 3 by greater coverage of shrubs in the understory, and greater species richness and total coverage of the ground-cover layer.

Distinguished from ecosystem 1 by greater abundance of tamarack, and the absence of balsam fir, black spruce, white spruce, and balsam poplar. Also distinguished from ecosystem 1 by the abundance of spicebush and lack of mountain ash and mountain maple in the understory. In addition, numerous ground-cover species of ecosystem 1, including *Gaultheria hispidula, Linnaea borealis*, and *Pyrola asarifolia* are absent from ecosystem 4.

Research Basis

NUMBER OF SITES: 1

NUMBER OF PLOTS: 1

Bay Port Saturated	Sec. 2, T16N, R9E Huron Co.	1 Plot

Ecosystem Type 5. Intermittently inundated flat terrain on Heisterman and Maisou Islands; fine sand over limestone bedrock (bedrock within 100 cm of the soil surface, clay layer < 20 cm thick present above the bedrock); Red ash/*Carex stricta*, *Calamagrostis canadensis*

SYNOPSIS: Flat terrain on Heisterman and Maisou Islands along the southern Lake Huron shoreline (subsections VI.6 and VI.5). Intermittently flooded fine sand over limestone bedrock (bedrock within 100 cm of the soil surface); neutral at the soil surface, mildly to moderately alkaline below the surface. Low tree density and low canopy coverage. Red ash overstory; red ash understory; graminoid-dominated ground cover. One site, 12 plots.

Physiography

Broad, flat terrain on the eastern side of Heisterman and Maisou Islands along the southern Lake Huron shoreline. Located at an elevation below the maximum water level of Lake Huron. Prevailing westerly winds and wave action led to the formation of low beach ridges and intervening swales along the western shore of the islands, but the east side is characterized by a long, gradual slope above the shore. Limestone bedrock is within 100 cm of the soil surface.

Hydrology

Directly influenced by the Great Lakes (intermittently inundated); water table is usually below the soil surface, but inundation of the soil surface occurs during periodic high lake levels. Water table within 60 cm of the soil surface in late June 2002.

Due to location at an elevation below the maximum lake level, the hydrololgic regime is directly influenced by lake levels; little influence of groundwater seepage from higher terrain due to the small size of the islands and small amount of terrain at a higher elevation;

Soil

SUBSTRATE: fine sand, < 100 cm deep, over limestone bedrock; layer of clay < 20 cm thick present immediately above the bedrock.

pH: Neutral, 7.2, at the soil surface; neutral, 7.2, at 50 cm; mildly alkaline, 7.8, at 100 cm.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): red ash (90/92). Additional species: silver maple, American elm, bur oak. Mean basal area: 22.3 m^2/ha. Mean stem density: 808/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): red ash (99). Other common species: silver maple. Mean large understory density: 521/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): red ash (39), silky dogwood (45). Other common species: black raspberry, red raspberry, American elm. Mean small understory density: 275/ha.

GROUND COVER: Abundant forb species: *Scutellaria galericulata, Lathyrus palustris, Lysimachia thyrsiflora, Galium triflorum, Impatiens capensis, Boehmeria cylindrica, Polygonum amphibium, Lycopus uniflorus*. Abundand graminoids: *Calamagrostis canadensis, Carex stricta, Carex lacustris, Glyceria striata*. Abundant ferns: *Onoclea sensibilis, Thelypteris palustris*. Abundant woody vines: *Parthenocissus quinquefolia, Vitis riparia*. Abundant shrubs: *Cornus amomum, Rubus strigosus, Rubus occidentalis*. Abundant tree species: red ash, silver maple.

Comments

Hydrologic regime is dominated by Great Lakes water levels. Because small portions of Heisterman and Maisou Islands are at a higher elevation than ecosystem 5, groundwater seepage from higher terrain has little influence on the hydrology, and the soil surface is inundated only during years when lake levels are high.

Characterized by widely scattered, small trees and a continuous, graminoid-dominated ground-cover layer. The soil surface may be inundated throughout the growing season when lake levels are high. Prolonged inundation may kill overstory trees, thereby promoting growth of herbaceous species characteristic of open meadows (e.g., *Carex stricta*, *Calamagrostis canadensis*, *Scutellaria galericulata*, *Lathyrus palustris*, *Polygonum amphibium*, and *Thelypteris palustris*). Recruitment of tree seedlings into the sapling layer may be restricted to several consecutive years of low lake level.

Because rooting is limited to the shallow layer of mineral soil above the limestone bedrock, tree mortality may also be high when lake levels are low due to low soil-water availability.

Similar Ecosystems

Distinguished from ecosystem 3 by broad, flat topography, occurrence of limestone bedrock within 100 cm of the soil surface, and lack of standing water during the growing season, except when lake levels are high. Also distinguished from ecosystem 3 by lower tree density, lack of silver maple in the canopy, greater abundance of graminoids, and greater total coverage of the ground-cover layer.

Distinguished from ecosystem 2 by broad, flat topography and the lack of surface water during the growing season, except when lake levels are high. Also distinguished from ecosystem 2 by mineral soil rather than shallow sapric muck, greater depth to the water table late in the growing season, except when lake levels are high, and the absence of coniferous trees in the forest canopy.

Ecosystem type 5 may resemble alvars due to the flat topography, shallow soil over limestone bedrock, and relatively open, glade-like vegetation structure. However, the soil is generally deeper than that of alvars, and characteristic alvar species (e.g., *Schizachyrium scoparium*, *Sporobolus heterolepis*, *Carex scirpoidea Eleocharis compressa*, *Muhlenbergia richardsonis*, and *Geum triflorum*) were absent from Heisterman and Maisou Islands.

Research Basis

NUMBER OF SITES: 1 (due to the low number of plots on Maisou Island and its close proximity to Heisterman Island, the islands were treated as one site).

NUMBER OF PLOTS: 12

Heisterman Island	Sec. 32, T17N, R9E Huron Co.	10 Plots
Maisou Island	Sec. 5, T16N, R9E Huron Co.	2 Plots

Ecosystem Type 6. Seasonally inundated flat drowned rivermouth valley floor; shallow alluvial deposits (20–50 cm deep) over fine sand; red ash–silver maple–(American elm)/*Carex lacustris*

SYNOPSIS: Located in drowned river-mouth valleys along the eastern Lake Michigan shoreline in northwestern Lower Michigan (subsection VII.4). Flat valley floor. Seasonally flooded loam to silty clay loam over fine sand (depth to sand < 50 cm); neutral at the soil surface, mildly alkaline below the surface. Red ash–silver maple overstory; red ash–speckled alder–buttonbush understory; continuous, sedge-dominated ground cover. Three sites, 65 plots.

Physiography

Flat drowned river-mouth valley floor along the eastern Lake Michigan shoreline. Drowned river-mouth valleys are generally broader and flatter than the river floodplain further upstream. Within the river-mouth valleys forests are generally restricted to terrain at a higher elevation than the maximum lake level.

Hydrology

Groundwater-dominated, with stream inputs (seasonally inundated); soil surface is inundated early in the growing season, but when lake levels are low, the water table may fall well below the soil surface later in the growing season; when lake levels are high, surface water may persist throughout much of the growing season. High water mark, 82 (42–100) cm above the soil surface; water table 30–100 cm below the soil surface in mid summer.

Strong influence by stagnant groundwater rather than flowing water from over-the-bank flooding is indicated by the shallow depth of alluvial deposits (< 50 cm), and the small size or absence of a natural levee along the stream channel.

Soil

SUBSTRATE: Shallow alluvial deposits (loam to silty clay loam) 40 (20–50) cm deep, over fine sand.

pH: Neutral, 7.3 (7.0–7.8), at the soil surface; mildly alkaline, 7.6 (7.4–7.8), at 50 cm; mildly alkaline, 7.8 (7.6–8.0), at 100 cm; mildly alkaline, 7.8 (7.8–8.0), below 100 cm.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): red ash (62/66), silver maple (33/25). Additional species: American elm, black ash. Mean basal area: 26.2 m^2/ha. Mean stem density: 699/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): red ash (33), speckled alder (28), buttonbush (11). Other common species: silver maple, black ash, Michigan holly, nannyberry, silky dogwood, riverbank grape, red-osier dogwood. Mean large understory density: 1,617/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): speckled alder (38), silky dogwood (20), red ash (18). Other common species: Michigan holly, Japanese barberry, red-osier dogwood, nannyberry, swamp rose. Mean small understory density: 969/ha.

GROUND COVER: Abundant forb species: *Symplocarpus foetidus, Boehmeria cylindrica, Myosotis scorpioides*, *Iris virginica*, *Lysimachia nummularia*, *Anemone canadensis, Galium triflorum, Lysimachia ciliata*. Abundant graminoid species: *Carex lacustris, Carex stricta, Calamagrostis canadensis, Elymus virginicus, Leersia oryzoides*, *Phalaris arundinacea*, *Carex bebbii*, *Carex vulpinoidea*. Abundant fern species: *Onoclea sensibilis, Matteuccia struthiopteris*, *Athyrium filix-femina*. Abundant woody vines:

Parthenocissus quinquefolia, Vitis riparia, Toxicodendron radicans. Abundant shrubs: *Cornus amomum, Alnus rugosa, Sambucus canadensis, Ilex verticillata, Cornus stolonifera, Rosa palustris, Ribes americanum*. Abundnat tree species: red ash, silver maple, American elm.

Comments

The horizontal and vertical position of the mouths of Lake Michigan tributaries has changed following water-level fluctuation after glacial retreat and post-glacial uplift. During Chippewa low water levels, river mouths were located within the present Lake Michigan basin. The rise in water level following isostatic uplift forced river mouths inland of the modern shoreline. Later, as water levels receded, the river mouths were partially closed by growth of sand spits and baymouth bars, which were later covered by higher dunes. As a result, the mouths of most Lake Michigan tributaries contain a shallow inland lake, at the same elevation as Lake Michigan, and connected to it by a short, narrow channel. Herbaceous vegetation dominates the lowest part of the valley, immediately adjacent to the inland lake. Swamp forest occurs inland of the open meadows, and at slightly higher elevations.

Tree density is low due to inundation of the soil surface throughout most, or all, of the growing season when lake levels are high. Large numbers of standing dead trees and dead branches on live trees indicate the stress on trees due to prolonged inundation of the soil surface. Low tree canopy coverage favors sedges in the ground cover. Several consecutive years of high lake levels may kill overstory trees, enabling expansion of herbaceous species from adjacent meadows. Recruitment of tree seedlings into the sapling layer may depend upon several consecutive years of low lake level.

Similar Ecosystems

Distinguished from ecosystem 8 by greater abundance of red ash, lower abundance of silver maple, and the occurrence of speckled alder in the understory. Also distinguished from ecosystem 8 by lower species richness of the ground-cover layer, greater abundance of *Carex lacustris*, and lack of *Saururus cernuus*.

Distinguished from ecosystem 3 by greater water depth, and shorter duration of inundation, except when lake levels are high. Also distinguished from ecosystem 3 by lower tree density and basal area, lower tree canopy coverage, and the occurrence of speckled alder in the understory. In addition, the ground cover of ecosystem 6 is continuous and dominated by graminoids, rather than sparse, patchy, and dominated by forbs, as in ecosystem 3.

In general, the drowned river-mouth valley is broader and flatter than floodplains further upstream. The flat valley floor of the rivermouth is characterized by smaller tree size, lower tree density, lower tree canopy coverage, and a higher coverage of sedges in the ground cover than the first bottom of the floodplain further upstream.

Research Basis

NUMBER OF SITES: 3

NUMBER OF PLOTS: 65

Betsie River	Sec. 36, T26N, R16W Benzie Co.	20 plots
Manistee River	Sec. 2&5, T21N, R16W and Sec. 33&36, T22N, R16W Manistee Co	30 Plots
Pere Marquette River	Sec. 30, T18N, R17W Mason Co.	15 plots

Ecosystem Type 7. Saturated gently sloping groundwater seepages along margins of drowned rivermouth valleys; sapric and hemic muck over marl (combined depth of sapric and hemic muck > 150 cm); northern white-cedar–eastern hemlock–yellow birch–black ash–red maple/*Osmunda cinnamomea*

SYNOPSIS: Located in drowned river-mouth valleys along the eastern Lake Michigan shoreline in northwestern Lower Michigan (subsection VII.4). Gently sloping groundwater seepages along valley margins. Saturated sapric and hemic muck over marl (combined depth of sapric and hemic muck > 150 cm); neutral at the soil surface, very strongly acid on hummocks. Northern white-cedar–eastern hemlock–yellow birch–black ash–red maple overstory; northern white-cedar–speckled alder–black ash–red ash understory; diverse, continuous ground-cover layer. Three sites, 12 plots.

Physiography

Gently sloping groundwater seepages at the base of steep slopes along margins of drowned river-mouth valleys along the eastern Lake Michigan shoreline.

Hydrology

Groundwater-fed (saturated); water table at or slightly below the soil surface throughout the growing season; surface water not present except in small, local depressions.

Soil

SUBSTRATE: Greater than 150 cm combined thickness of sapric and hemic muck over marl; surface soil is sarpic muck (> 30 cm deep), layers of sapric and hemic muck extend from 30 to > 150 cm.

pH: Mildly alkaline, 7.5 (7.2–7.8), at the soil surface; mildly alkaline, 7.7 (7.6–7.8), at 50 cm; mildly alkaline, 7.8 (7.7–8.0), at 100 cm; moderately alkaline, 7.9 (7.8–8.0), below 100 cm. Very strongly acid, 4.2 (4.0–4.5), on hummocks.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): northern white-cedar (58/61), eastern hemlock (14/9), black ash (8/12), red maple (9/7). Additional species: yellow birch, red ash, tamarack, paper birch. Mean basal area: 43.3 m^2/ha. Mean stem density: 1,321/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh):* Most abundant species (% of large understory density): northern white-cedar (29), black ash (24), speckled alder (20), red ash (19). Other common species: eastern hemlock, yellow birch, mountain maple, American elm, basswood. Mean large understory density: 1,225/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): speckled alder (24), red ash (23), black ash (20), tamarack (9), northern white-cedar (7). Other common species: Japanese barberry, red raspberry, spicebush, Michigan holly, wild black currant. Mean small understory density: 2,008/ha.

GROUND COVER: Abundant forb species: *Rubus pubescens, Coptis trifolia, Mitella nuda, Impatiens capensis, Lysimachia ciliata, Lycopus uniflorus, Maianthemum canadense, Mitella diphylla, Clematis virginiana, Galium triflorum, Solidago patula, Fragaria virginiana, Aster lateriflorus*. Abundant graminoid species: *Glyceria striata, Carex trisperma, Carex leptalea, Carex gracillima, Carex eburnea, Leersia oryzoides, Carex arctata, Carex lacustris, Carex pedunculata*. Abundant fern species: *Osmunda cinnamomea, Onoclea sensibilis, Equisetum arvense, Dryopteris cristata, Athyrium filix-femina, Thelypteris palustris, Gymnocarpium dryopteris, Osmunda regalis*. Abundant woody vines: *Parthenocissus* *quinquefolia*. Abundant shrubs: *Cornus stolonifera, Acer spicatum, Lindera benzoin, Alnus rugosa, Viburnum trilobum, Barbarea vulgaris, Lonicera canadensis, Ribes americanum*. Abundant tree species: black ash, northern white-cedar, red maple, red ash, paper birch, northern red oak, eastern hemlock, yellow birch, tamarack, eastern white pine.

Comments

Groundwater seepages account for a small portion of the drowned river-mouth valley along large rivers, such as the Manistee and Pere Marquette, but they may account for the majority of the valley in smaller rivers, such as the Betsie and Big Sable.

All sites were characterized by pit-and-mound topography that developed as result of windthrow, or from the buildup of organic matter at the base of trees. Due to the combined influence of shallow rooting and dense, evergreen foliage, windthrow is a common disturbance. Multiple treefall gaps are common, and the resulting high light levels on the forest floor account in part for the persistence of moderately tolerant tree species (e.g., red maple, black ash, and yellow birch).

Similar Ecosystems

Distinguished from ecosystem 1 by deeper organic soil, lower overstory stem density, lower basal area, lower canopy coverage, and greater abundance of deciduous species in the canopy. Also distinguished from ecosystem 1 by greater abundance of cinnamon fern in the ground cover.

Additional research is necessary to compare groundwater seepages along the outer margin of drowned river-mouth valleys to groundwater seepages along the outer floodplain margin further upstream. Field observations suggest that they are similar in overstory and understory species composition and structure, but the dominant ground-cover species upstream is royal fern rather than cinnamon fern.

Research Basis

NUMBER OF SITES: 3

NUMBER OF PLOTS: 12

Betsie River	Sec. 36, T26N, R16W Benzie Co.	4 plots
Manistee River	Sec. 33, T22N, R33W Manistee Co.	4 plots
Big Sable River	Sec. 28&33, T20N, R17W Mason Co.	4 plots

Ecosystem Type 8. Seasonally inundated flat drowned rivermouth valley floor; shallow alluvial deposits (20–50 cm deep) over fine sand; silver maple–red ash–(American elm)/*Saururus cernuus, Peltandra virginica*

SYNOPSIS: Located in drowned river-mouth valleys along the eastern Lake Michigan shoreline in southwestern Lower Michigan (subsection VI.3). Flat valley floor. Seasonally inundated alluvial soil (loam to silty clay loam) over fine sand; neutral at the soil surface, mildly to moderately alkaline below the surface. Silver maple–red ash overstory; silver maple–red ash–American elm–buttonbush understory; forb- and graminoid-dominated ground cover. Two sites, 40 plots.

Physiography

Flat drowned river-mouth valley floors along the eastern Lake Michigan shoreline in southwestern Lower Michigan. Drowned river-mouth valleys are generally broader and flatter than the river floodplain further upstream. Within the river-mouth valleys forests are generally restricted to terrain at a higher elevation than the maximum lake level.

Hydrology

Groundwater dominated, with stream inputs (seasonally inundated); soil surface is inundated early in the growing season, when lake levels are low, the water table may fall 100 cm below the soil surface later in the growing; when lake levels are high, surface water may persist throughout much of the growing season when lake levels are high. High water mark, 82 (42–100) cm above the soil surface; water table 30–100 cm below the soil surface in mid summer.

Strong influence by stagnant groundwater rather than flowing water from over-the-bank flooding is indicated by the shallow depth of alluvial deposits (< 50 cm), and the small size or absence of a natural levee along the stream channel.

Soil

SUBSTRATE: Shallow alluvial deposits (loam to silty clay loam) 40 (20–50) cm deep, over fine sand.

pH: Neutral, 7.2 (6.8–7.5), at the soil surface; mildly alkaline, 7.7 (7.4–7.8), at 50 cm; moderately alkaline, 7.9 (7.8–8.0), at 100 cm; moderately alkaline, 8.0 (7.8–8.0), below 100 cm.

Vegetation

OVERSTORY: Dominants (% of basal area / % of stem density): silver maple (76/64), red ash (20/29). Additional species: American elm. Mean basal area: 45.1 m^2/ha. Mean stem density: 530/ha.

UNDERSTORY: *Large understory (1.5–9.0 cm dbh)*: Most abundant species (% of large understory density): silver maple (29), red ash (17), buttonbush (10). Other common species: American elm, riverbank grape, poison ivy. Mean large understory density: 260/ha.

Small understory (taller than 50 cm and < 1.5 cm dbh): Most abundant species (% of small understory density): buttonbush (66), red ash (24). Other common species: silver maple, poison ivy, American elm. Mean small understory density: 308/ha.

GROUND COVER: Abundant forb species: *Boehmeria cylindrica*, *Saururus cernuus*, *Peltandra virginica, Laportea canadensis, Lysimachia ciliata, Scutellaria lateriflora, Aster lateriflorus, Physostegia virginiana, Pilea pumila, Lysimacchia nummularia*, *Myosotis scorpioides*. Abundant graminoid species: *Phalaris arundinacea, Leersia oryzoides, Cinna arundinacea, Carex grayi, Carex lacustris, Elymus virginicus,* *Calamagrostis canadensis*. Abundant woody vines: *Toxicodendron radicans, Vitis riparia, Parthenocissus quinquefolia*. Abundant shrubs: *Cephalanthus occidentalis, Salix* spp., *Sambucus canadensis, Lindera benzoin*. Abundant tree species: silver maple, American elm, red ash.

Comments

The horizontal and vertical position of the mouths of Lake Michigan tributaries has changed following water-level fluctuation after glacial retreat and post-glacial uplift. During Chippewa low water levels, river mouths were located within the present Lake Michigan basin. The rise in water level following isostatic uplift forced river mouths inland of the modern shoreline. Later, as water levels receded, the river mouths were partially closed by growth of sand spits and baymouth bars, which were later covered by higher dunes. As a result, the mouths of most Lake Michigan tributaries contain a shallow inland lake, at the same elevation as Lake Michigan, and connected to it by a short, narrow channel. Herbaceous vegetation dominates the lowest part of the valley, immediately adjacent to the inland lake. Swamp forest occurs inland of the open meadows, and at slightly higher elevations.

The forest of the flat valley floor adjacent to the river mouth is characterized by widely spaced trees, low tree canopy coverage, and continuous coverage of graminoids and forbs in the ground cover. Shrubs are generally not abundant, but dense clumps of buttonbush or willow occur locally in microsites that remain inundated too long for trees to become established.

Similar Ecosystems

Distinguished from ecosystem 6 by considerably greater total overstory basal area, greater density and basal area of silver maple in the overstory, and the absence of speckled alder in the understory. Also distinguished from ecosystem 6 by lower coverage of graminoids and greater coverage of *Saururus cernuus* and *Peltandra virginica* in the ground cover.

Distinguished from ecosystem 3 by greater water depth, and shorter duration of inundation when lake levels are low. Also distinguished from ecosystem 3 by continuous rather than sparse, patchy ground-cover vegetation.

Research Basis

NUMBER OF SITES: 2

NUMBER OF PLOTS: 40

Muskegon River	Sec. 10&11, T10N, R16W Muskegon Co.	20 plots
Kalamazoo River	Sec. 8,17,&22, T3N, R15W Allegan Co.	20 plots

Ecosystem Type 9. Saturated gently-sloping groundwater seepages along margins of drowned rivermouth valleys; sapric and hemic muck over marl (depth to marl > 100 cm); northern white-cedar– tamarack–eastern hemlock–yellow birch–black ash–red maple/*Osmunda cinnamomea*

SYNOPSIS: Located in drowned river-mouth valleys along the eastern Lake Michigan shoreline in southwestern Lower Michigan (subsection VI.3). Gently sloping groundwater seepages along valley margins. Saturated sapric and hemic muck over marl (combined depth of sapric and hemic muck > 100 cm); neutral at the soil surface, very strongly acid on hummocks. Northern white-cedar–tamarack–eastern hemlock–yellow birch–black ash–red maple overstory; northern white-cedar–black ash–red ash–American elm understory; diverse, continuous ground-cover layer. Not quantitatively sampled.

Physiography

Gently sloping groundwater seepages at the base of steep slopes along the outer margin of drowned river-mouth valleys along the eastern Lake Michigan shoreline in southwestern Lower Michigan.

Hydrology

Groundwater-fed (saturated); water table at or slightly below the soil surface throughout the growing season; surface water not present during the growing season except in small, local depressions.

Soil

SUBSTRATE: Greater than 100 cm combined thickness of sapric and hemic muck over marl; surface soil is sarpic muck up to 50 cm deep; layers of sapric and hemic muck extend to at least 100 cm.

pH: Mildly alkaline, 7.2, at the soil surface; mildly alkaline, 7.5, at 50 cm; moderately alkaline, 8.0, at 100 cm; moderately alkaline, 8.0, below 100 cm. Very strongly acid, 4.5, on hummocks.

Vegetation

OVERSTORY: Dominants: northern white-cedar, eastern white pine, eastern hemlock, tamarack, red maple, black ash, and yellow birch. Additional species: red ash, American elm,

UNDERSTORY: Common species: northern white-cedar, black ash, red ash, American elm. Additional species: spicebush, Michigan holly, poison sumac, black ash, red maple.

GROUND COVER: Abundant forb species: *Solidago patula, Saururus cernuus, Thalictrum dasycarpum, Solidago rugosa, Sium suave, Lysimachia ciliata, Aster lateriflorus, Anemone canadensis, Maianthemum canadense*. Abundant graminoids: *Carex eburnea, Carex intumescens, Elymus virginicus.* Abundant shrubs: *Euonymus obovata, Lindera benzoin*. Abundant ferns: *Onoclea sensibilis, Osmunda cinnamomea, Osmunda regalis, Thelypteris palustris*. Abundant tree seedlings: eastern white pine, red maple, black ash.

Comments

Not quantitatively sampled. However, based on aerial photo interpretation, similar conifer-dominated groundwater seepages occur along the outer margin of drowned rivermouth valleys of several rivers in southwestern Lower Michigan.

Groundwater seepages along the outer margin of drowned rivermouth valleys are less extensive in southwestern than northwestern Lower Michigan. The lesser abundance of groundwater seepages in southwestern Lower Michigan may be related to the warmer climate and longer growing season, which result in greater rates of organic matter decomposition and less accumulation of organic matter along the outer margin of the valley. Also, the lesser abundance of groundwater seepages in southwestern than northwestern Lower Michigan may reflect differences in the historical development of the river-mouth valleys due to greater rates of isostatic uplift in the north.

Similar Ecosystems

Distinguished from ecosystem 7 by lower basal area of northern white-cedar, and greater abundance of deciduous tree species in the canopy (e.g., black ash, red maple, and yellow birch). Also distinguished from ecosystem 7 by lower abundance of speckled alder and greater abundance of spicebush in the understory.

Research Basis

NUMBER OF SITES: Not quantitatively sampled.

NUMBER OF PLOTS: Physiography, hydrology, soil, and vegetation data presented above are based on field reconnaissance and one plot sampled in a groundwater seepage along the outer margin of the Kalamazoo River floodplain upstream of the river mouth.

Appendix D1. Comparison of large understory[1] composition among eight swamp ecosystems along the Lake Huron and Lake Michigan shorelines.[2]

	Lake Huron and northern Lake Michigan Shorelines					Eastern Lake Michigan Shoreline		
	Northern Shoreline		Southern Shoreline			Northern Shoreline		Southern Shoreline
Species	1	2	3	4	5	6	7	8
Tree Species								
Thuja occidentalis	615 (52)	5 (1)	1 (0)	--	--	3 (0)	350 (29)	--
Abies balsamea	403 (34)	295 (43)	--	--	--	--	--	--
Fraxinus nigra	72 (6)	5 (1)	3 (0)	--	--	60 (4)	292 (24)	--
Fraxinus pennsylvanica	0 (0)	320 (47)	500 (41)	--	517 (99)	538 (33)	233 (19)	45 (17)
Ulmus americana	--	--	549 (45)	--	--	6 (0)	--	18 (7)
Acer saccharinum	1 (0)	3 (0)	147 (12)	--	4 (1)	67 (4)	--	75 (29)
Other Tree Species	28 (2)	55 (8)	15 (1)	--	--	7 (0)	67 (5)	--
Shrub Species								
Alnus rugosa	67 (6)	--	--	--	--	459 (28)	242 (20)	--
Prunus virginiana	--	--	4 (0)	200 (50)	--	--	--	--
Zanthoxylum americanum	--	--	--	200 (50)	--	--	--	--
Cephalanthus occidentalis	--	--	2 (0)	--	--	174 (11)	--	25 (10)
Ilex verticillata	--	--	--	--	--	118 (7)	--	--
Viburnum lentago	--	--	--	--	--	75 (5)	--	--
Vitis riparia	--	--	2 (0)	--	--	19 (1)	42 (3)	88 (34)
Other Shrub Species	--	--	--	--	--	92 (6)	--	10 (4)
TOTAL	1,187 (100)	683 (100)	1,223 (100)	400 (100)	521 (100)	1,617 (100)	1,225 (100)	260 (100)

[1] 1.5–9.0 cm dbh

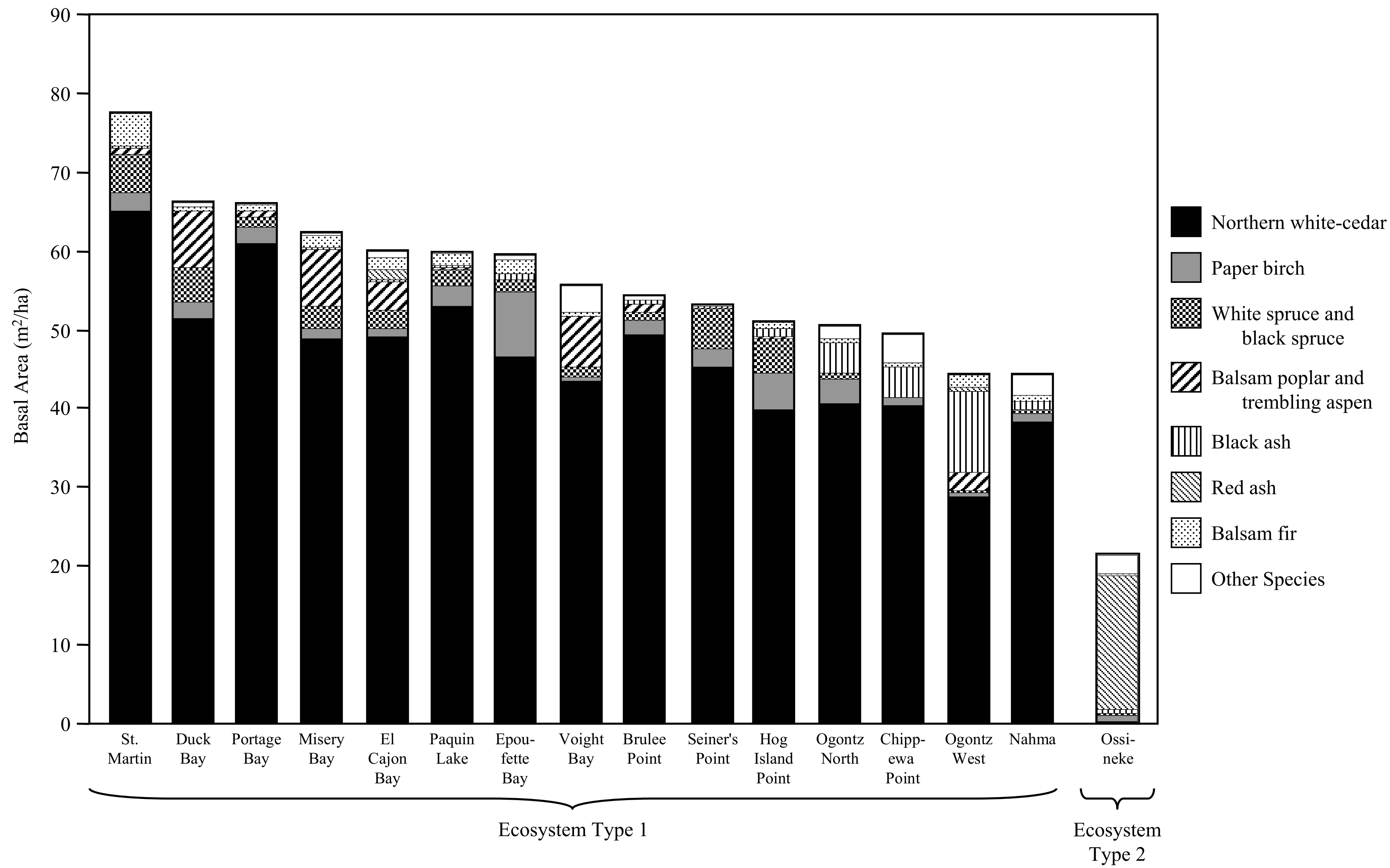
[2] Values are stems/ha, average percentage of total sapling density is in parentheses

Appendix D2. Comparison of small understory[1] composition among eight swamp ecosystems along the Lake Huron and Lake Michigan shorelines.[2]

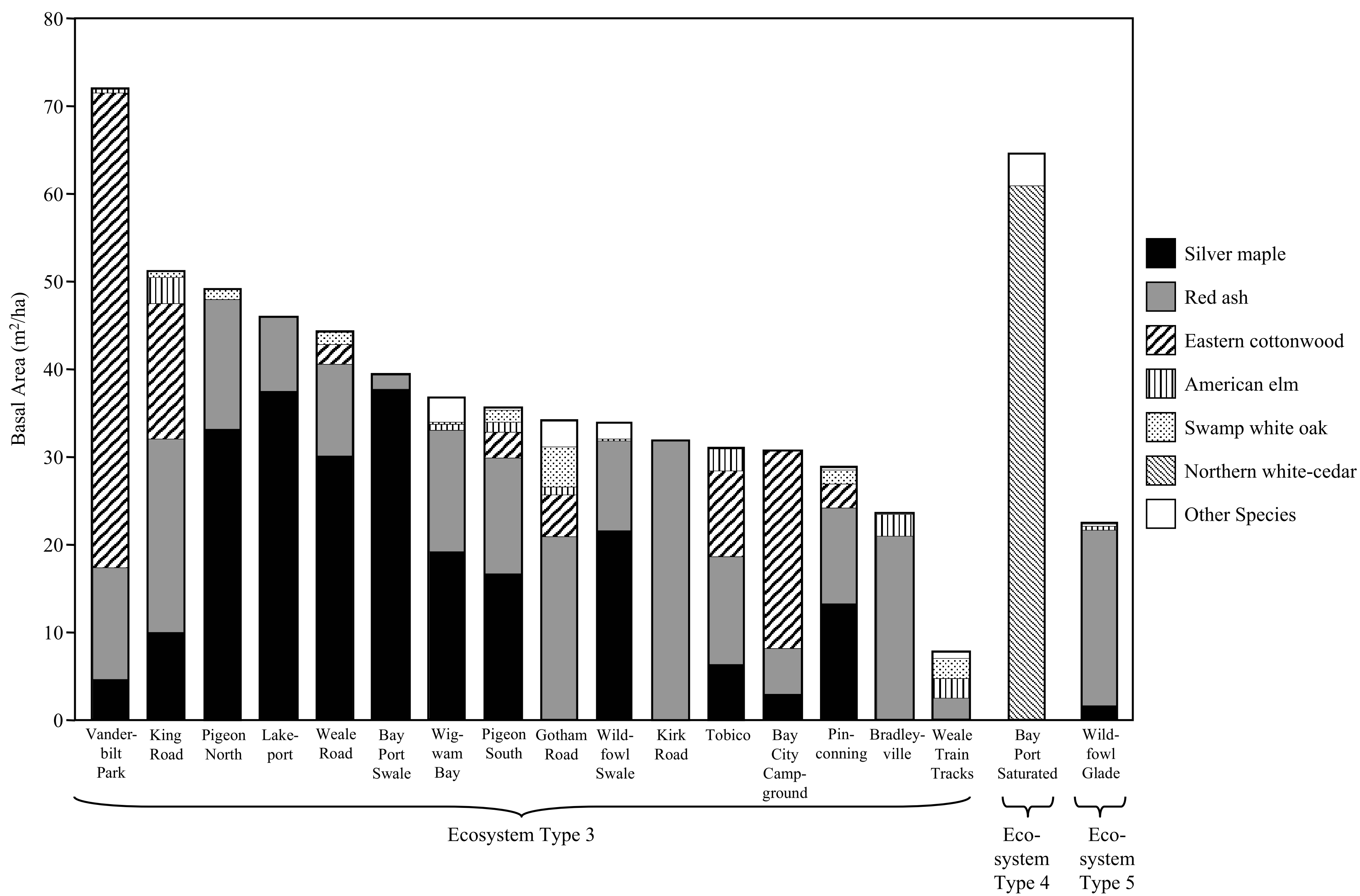
	Lake Huron and northern Lake Michigan Shorelines					Eastern Lake Michigan Shoreline		
	Northern Shoreline		Southern Shoreline			Northern Shoreline		Southern Shoreline
Species	1	2	3	4	5	6	7	8
Tree Species								
Abies balsamea	482 (45)	140 (1)	--	--	--	--	--	--
Thuja occidentalis	19 (2)	5 (0)	--	--	--	--	150 (7)	--
Larix laricina	0 (0)	15 (0)	--	--	--	--	183 (9)	--
Populus balsamifera	39 (4)	--	--	--	--	--	--	--
Acer rubrum	61 (6)	--	--	--	--	--	8 (0)	--
Fraxinus nigra	21 (2)	--	4 (0)	--	--	--	392 (20)	--
Fraxinus pennsylvanica	0 (0)	115 (1)	867 (61)	--	108 (39)	171 (18)	467 (23)	75 (24)
Ulmus americana	--	--	108 (8)	--	8 (3)	2 (0)	--	3 (1)
Acer saccharinum	--	--	12 (1)	--	--	2 (0)	--	8 (2)
Fraxinus americana	--	--	--	700 (18)	--	--	--	--
Other Tree Species	63 (6)	30 (0)	4 (0)	100 (3)	--	--	92 (5)	--
Shrub Species								
Alnus rugosa	133 (12)	5,045 (44)	--	--	--	368 (38)	475 (24)	--
Rhamnus alnifolia	141 (13)	--	--	--	--	--	--	--
Spiraea alba	1 (0)	5,165 (45)	1 (0)	--	--	--	--	--
Betula pumila	--	630 (5)	--	--	--	--	--	--
Lonicera canadensis	51 (5)	--	--	100 (3)	--	--	--	--
Prunus virginiana	--	--	1 (0)	800 (21)	--	--	8 (0)	--
Zanthoxylum americanum	--	--	7 (0)	1,000 (26)	--	--	--	--
Rubus strigosus	3 (0)	80 (1)	5 (0)	--	8 (3)	--	33 (2)	--
Ilex verticillata	1 (0)	5 (0)	66 (5)	--	--	57 (6)	17 (1)	--
Cornus amomum	--	20 (0)	154 (11)	--	125 (45)	193 (20)	--	--
Cephalanthus occidentalis	--	--	28 (2)	--	--	12 (1)	--	203 (66)
Berberis thunbergii	--	--	--	700 (18)	--	49 (5)	108 (5)	--
Cornus stolonifera	--	--	92 (6)	--	--	22 (2)	17 (1)	--
Rubus occidentalis	--	--	2 (0)	--	25 (9)	--	--	--
Vitis riparia	--	--	16 (1)	200 (5)	--	13 (1)	8 (0)	--
Other Shrub Species	53 (5)	260 (2)	59 (4)	300 (8)	--	81 (8)	50 (2)	20 (7)
TOTAL	1,067 (100)	11,510 (100)	1,426 (100)	3,900 (100)	275 (100)	969 (100)	2,008 (100)	308 (100)

[1] taller than 50 cm and < 1.5 cm dbh

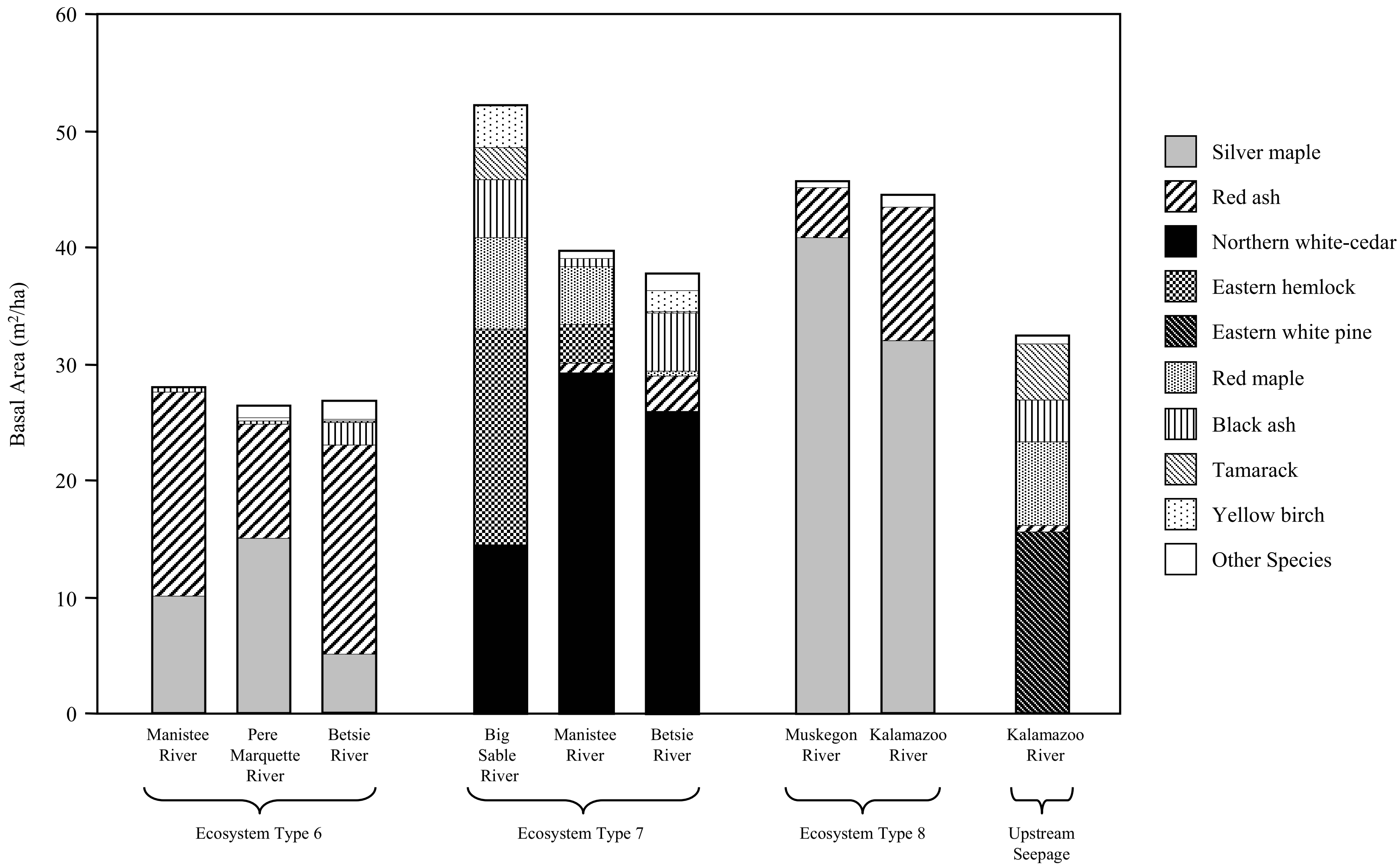
[2] Values are seedplings/ha, average percentage of total seedling density is in parentheses



Appendix E1. Comparison of overstory species composition among 15 swamp forests of ecosystem type 1 and 1 swamp of ecosystem 2 along the northern Lake Michigan and Lake Huron shorelines.



Appendix E2. Comparison of overstory species composition among 16 swamp forests of ecosytem type 3, 1 swamp of ecosystem 4, and 1 swamp of ecosystem 5 along the southern Lake Huron shoreline.



Appendix E3. Comparison of overstory species composition among three swamp forests of ecosystem type 6 and two swamps of ecosystem 7 along the eastern Lake Michigan shoreline in northwestern Lower Michigan, and two swamps of ecosystem 8 and a groundwater seepage along the the outer margin of the floodplain of the Kalamazoo River upstream of the rivermouth in southwestern Lower Michigan.

Appendix F1. Comparison of overstory species composition among eight swamp forests sampled along the northern Lake Michigan shoreline in 2003 (percentages of total stem density and basal area are in parentheses).

	Portage Bay (n = 5)	Epoufette Bay (n = 10)	Seiner's Point (n = 5)	Hog Island Point (n = 5)	Ogontz North (n = 5)	Chippewa Point (n = 5)	Ogontz West (n = 5)	Nahma (n = 5)
Thuja occidentalis								
Stems/ha	2,090 (90)	1,410 (78)	1,560 (83)	1,610 (79)	1,840 (81)	1,730 (82)	1,080 (51)	2,570 (87)
BA (m^2/ha)	60.9 (92)	46.7 (77)	45.2 (85)	39.8 (78)	40.7 (80)	40.4 (83)	28.8 (62)	38.2 (88)
Avg dbh (cm)	18.3	19.5	18.1	16.6	16.0	16.4	17.5	13.3
Betula papyrifera								
Stems/ha	130 (6)	175 (10)	130 (7)	210 (9)	70 (3)	40 (2)	20 (1)	50 (2)
BA (m^2/ha)	2.1 (3)	8.0 (15)	2.4 (4)	4.6 (9)	2.8 (6)	0.9 (2)	0.5 (1)	1.2 (2)
Avg dbh (cm)	14.0	22.8	14.5	16.2	21.8	17.0	16.8	16.6
Fraxinus nigra								
Stems/ha	--	60 (3)	--	60 (3)	240 (12)	150 (6)	720 (40)	110 (3)
BA (m^2/ha)	--	0.7 (1)	--	0.8 (2)	3.8 (8)	3.9 (6)	10.5 (25)	1.1 (2)
Avg dbh (cm)	--	11.9	--	13.1	13.8	17.3	13.1	11.0
Picea glauca								
Stems/ha	--	65 (3)	130 (6)	70 (3)	--	--	--	--
BA (m^2/ha)	--	1.7 (4)	4.0 (7)	2.9 (6)	--	--	--	--
Avg dbh (cm)	--	17.4	19.0	22.3	--	--	--	--
Abies balsamea								
Stems/ha	50 (2)	100 (6)	20 (1)	50 (3)	20 (1)	40 (3)	90 (5)	90 (3)
BA (m^2/ha)	0.7 (1)	2.0 (3)	0.3 (1)	0.8 (2)	0.5 (1)	0.4 (1)	1.6 (4)	0.8 (2)
Avg dbh (cm)	13.5	14.9	13.8	13.9	17.0	11.6	14.9	10.8
Picea mariana								
Stems/ha	40 (2)	--	50 (2)	70 (3)	10 (0)	10 (0)	10 (0)	20 (1)
BA (m^2/ha)	1.3 (2)	--	1.1 (2)	1.4 (3)	0.9 (2)	0.1 (0)	0.4 (1)	0.4 (1)
Avg dbh (cm)	19.0	--	16.3	15.5	34.4	10.5	21.1	16.1
Acer rubrum								
Stems/ha	--	10 (1)	10 (1)	--	40 (2)	--	--	120 (4)
BA (m^2/ha)	--	0.4 (1)	0.1 (0)	--	1.4 (3)	--	--	2.4 (5)
Avg dbh (cm)	--	21.2	10.8	--	20.4	--	--	15.6

Appendix F1. (continued)

	Portage Bay (n = 5)	Epoufette Bay (n = 10)	Seiner's Point (n = 5)	Hog Island Point (n = 5)	Ogontz North (n = 5)	Chippewa Point (n = 5)	Ogontz West (n = 5)	Nahma (n = 5)
Larix laricina								
Stems/ha	--	--	--	--	--	190 (7)	--	10 (0)
BA (m^2/ha)	--	--	--	--	--	2.9 (6)	--	0.1 (0)
Avg dbh (cm)	--	--	--	--	--	13.5	--	9.2
Populus balsamifera								
Stems/ha	10 (0)	--	--	10 (0)	--	--	20 (1)	--
BA (m^2/ha)	0.8 (1)	--	--	0.4 (1)	--	--	1.3 (3)	--
Avg dbh (cm)	30.9	--	--	22.5	--	--	28.5	--
Populus tremuloides								
Stems/ha	--	--	--	--	--	--	10 (1)	--
BA (m^2/ha)	--	--	--	--	--	--	0.9 (3)	--
Avg dbh (cm)	--	--	--	--	--	--	33.5	--
Betula alleghaniensis								
Stems/ha	--	--	--	--	--	20 (1)	--	--
BA (m^2/ha)	--	--	--	--	--	0.7 (1)	--	--
Avg dbh (cm)	--	--	--	--	--	20.8	--	--
Fraxinus pennsylvanica								
Stems/ha	--	--	--	--	--	--	10 (1)	--
BA (m^2/ha)	--	--	--	--	--	--	0.4 (1)	--
Avg dbh (cm)	--	--	--	--	--	--	21.7	--
Tsuga canadensis								
Stems/ha	--	--	--	--	20 (1)	--	--	--
BA (m^2/ha)	--	--	--	--	0.3 (1)	--	--	--
Avg dbh (cm)	--	--	--	--	13.2	--	--	--

Appendix F2. Comparison of large understory (1.6–9.0 cm dbh) species composition among eight swamp forests sampled along the northern Lake Michigan shoreline in 2003 (values are stems/ha, percentage of total stem density is in parentheses).

Species	Portage Bay (n = 5)	Epoufette Bay (n = 10)	Seiner's Point (n = 5)	Hog island Point (n = 5)	Ogontz North (n = 5)	Chippewa Point (n = 5)	Ogontz West (n = 5)	Nahma (n = 5)
Thuja occidentalis	320 (64)	340 (20)	380 (43)	600 (62)	480 (69)	680 (49)	120 (17)	2,180 (68)
Abies balsamea	260 (27)	1,290 (75)	1,320 (50)	320 (34)	220 (16)	1,000 (44)	40 (4)	460 (11)
Alnus rugosa	60 (5)	30 (2)	--	--	40 (4)	140 (5)	680 (45)	60 (1)
Fraxinus nigra	--	30 (2)	--	--	40 (3)	--	280 (34)	400 (16)
Betula papyrifera	20 (3)	20 (1)	40 (6)	40 (3)	--	--	--	20 (1)
Picea mariana	--	--	--	--	60 (4)	--	--	20 (1)
Acer rubrum	--	--	--	--	20 (3)	--	--	20 (0)
Larix laricina	--	--	--	--	--	40 (2)	--	--
Picea glauca	--	--	20 (1)	--	--	--	--	--
Acer spicatum	--	10 (1)	--	--	--	--	--	--
TOTAL	660 (100)	1,720 (100)	1,760 (100)	960 (100)	860 (100)	1,860 (100)	1,120 (100)	3,160 (100)

Appendix F3. Comparison of small understory (taller than 50 cm and < 1.5 cm dbh) species composition among eight swamp forests sampled along the northern Lake Michigan shoreline in 2003 (values are stems/ha, percentage of total stem density is in parentheses).

Species	Portage Bay (n = 5)	Epoufette Bay (n = 10)	Seiner's Point (n = 5)	Hog island Point (n = 5)	Ogontz North (n = 5)	Chippewa Point (n = 5)	Ogontz West (n = 5)	Nahma (n = 5)
TREES								
Abies balsamea	440 (91)	910 (63)	2,220 (75)	1,020 (25)	740 (41)	240 (61)	80 (2)	220 (46)
Acer rubrum	--	10 (1)	120 (4)	700 (10)	40 (2)	--	--	40 (8)
Fraxinus nigra	--	90 (6)	--	140 (3)	60 (16)	--	20 (0)	--
Populus balsamifera	20 (7)	--	--	160 (21)	--	--	100 (13)	--
Thuja occidentalis	--	130 (9)	20 (1)	--	--	20 (4)	--	40 (8)
Betula papyrifera	--	--	--	80 (1)	120 (5)	--	--	--
Picea mariana	--	--	--	--	160 (22)	--	20 (1)	--
Picea glauca	--	--	--	20 (0)	40 (2)	--	80 (2)	--
Acer spicatum	--	20 (1)	--	60 (2)	--	--	40 (1)	--
Populus tremuloides	--	--	--	--	--	--	60 (1)	--
Sorbus americana	--	--	40 (1)	--	--	--	--	--
SHRUBS								
Rhamnus alnifolia	--	--	--	140 (4)	--	--	1,960 (35)	--
Alnus rugosa	20 (2)	90 (6)	--	140 (4)	220 (7)	60 (15)	920 (47)	60 (13)
Lonicera canadensis	--	140 (10)	180 (6)	440 (28)	--	--	--	--
Ledum groenlandicum	--	50 (3)	340 (11)	--	--	--	--	100 (21)
Ribes americana	--	--	--	60 (1)	40 (1)	20 (20)	--	--
Amelanchier spp.	--	--	40 (1)	--	--	--	--	--
Rubus strigosus	--	--	--	20 (1)	20 (5)	--	--	--
Ilex verticillata	--	--	--	--	--	--	--	20 (4)
Ribes cynosbati	--	--	--	20 (1)	--	--	--	--
TOTAL	480 (100)	1,440 (100)	2,960 (100)	3,000 (100)	1,440 (100)	340 (100)	3,280 (100)	480 (100)

Appendix F4. Comparison of ground-cover species composition among eight swamp forests sampled along the norhtern Lake Michigan shoreline in 2003 (values are frequency (%), average percent coverage is in parentheses).

Species[1]	Portage Bay (n = 25)	Epou-fette Bay (n = 50)	Hog Island Point (n = 25)	Seiner's Point (n = 25)	Ogontz North (n = 25)	Chipp-ewa Point (n = 25)	Ogontz West (n = 25)	Nahma (n = 25)
TREES								
Abies balsamea	88 (1.6)	46 (2.7)	40 (3.5)	68 (4.7)	64 (1.0)	24 (0.3)	28 (0.3)	36 (0.6)
Acer rubrum	96 (1.1)	30 (0.5)	36 (1.1)	24 (0.3)	68 (1.4)	24 (0.2)	4 (0.0)	76 (1.0)
Betula papyrifera	12 (0.1)	20 (0.2)	20 (0.2)	4 (0.0)	20 (0.2)	16 (0.2)	12 (0.1)	40 (0.4)
Fagus grandifolia	--	--	--	--	--	--	--	4 (0.0)
Fraxinus americana	--	--	--	--	--	--	--	4 (0.0)
Fraxinus nigra	8 (0.1)	36 (0.6)	40 (0.4)	--	40 (0.5)	44 (0.5)	32 (0.3)	4 (0.0)
Picea glauca	--	2 (0.0)	4 (0.0)	16 (0.2)	--	--	--	--
Picea mariana	16 (0.2)	--	--	--	--	--	--	--
Populus balsamifera	4 (0.0)	2 (0.0)	4 (0.0)	--	--	--	4 (0.0)	--
Prunus serotina	--	2 (0.0)	--	--	--	--	--	--
Thuja occidentalis	48 (0.5)	22 (0.5)	40 (0.5)	28 (0.4)	16 (0.2)	8 (0.1)	8 (0.1)	44 (0.6)
TALL SHRUBS								
Acer spicatum	12 (0.2)	28 (0.4)	16 (0.2)	--	--	4 (0.0)	--	--
Alnus rugosa	--	--	4 (0.1)	4 (0.0)	4 (0.1)	--	8 (0.2)	12 (0.2)
Amelanchier spp.	4 (0.0)	--	--	4 (0.0)	12 (0.1)	--	12 (0.2)	--
Cornus amomum	4 (0.0)	--	4 (0.0)	--	--	--	--	--
Cornus stolonifera	--	--	--	--	--	4 (0.0)	12 (0.2)	--
Ilex verticillata	--	2 (0.0)	--	--	--	--	12 (0.1)	36 (0.4)
Prunus virginiana	--	--	--	--	--	--	4 (0.1)	--
Salix spp.	4 (0.0)	--	--	--	--	--	--	4 (0.0)
Sorbus americana	20 (0.2)	8 (0.1)	12 (0.1)	--	--	--	--	--
SHORT SHRUBS								
Epigea repens	--	--	--	8 (0.4)	--	--	--	--
Ledum groenlandicum	4 (0.1)	--	--	8 (0.3)	--	--	--	--
Lonicera canadensis	--	22 (0.6)	8 (0.6)	16 (0.7)	--	--	--	--
Rhamnus alnifolia	--	--	--	--	--	4 (0.0)	8 (0.4)	--
Ribes americanum	4 (0.0)	--	4 (0.2)	4 (0.0)	--	4 (0.0)	4 (0.0)	--
Rosa palustris	--	--	--	--	--	--	--	8 (0.1)
Rubus strigosus	--	--	--	--	4 (0.2)	--	--	--
Taxus canadensis	--	2 (0.0)	4 (0.0)	--	--	--	--	--
Vaccinium myrtilloides	24 (0.3)	--	--	--	--	--	--	4 (0.0)
Vaccinium oxycoccos	--	--	--	--	--	--	--	4 (0.0)
FORBS								
Anemone canadensis	--	--	--	--	4 (0.0)	--	12 (0.3)	--
Aralia nudicaulis	16 (0.3)	4 (0.1)	4 (0.0)	--	--	4 (0.1)	4 (0.1)	--
Aster ciliolatus	--	--	8 (0.1)	--	12 (0.2)	4 (0.1)	28 (0.6)	28 (1.8)
Aster lateriflorus	--	--	--	--	8 (0.1)	28 (0.4)	20 (0.3)	24 (0.5)
Aster macrophyllus	--	2 (0.1)	--	--	--	--	--	--
Aster spp.	--	--	--	--	4 (0.0)	--	--	--
Bidens connatus	--	--	--	--	--	--	4 (0.0)	--
Bidens frondosus	--	--	--	--	12 (0.1)	--	--	--

[1] non-native species are in italics

Appendix F4. (continued)

Species[1]	Portage Bay (n = 25)	Epou-fette Bay (n = 50)	Hog Island Point (n = 25)	Seiner's Point (n = 25)	Ogontz North (n = 25)	Chipp-ewa Point (n = 25)	Ogontz West (n = 25)	Nahma (n = 25)
FORBS (continued)								
Circaea alpina	--	6 (0.1)	--	--	--	--	20 (0.2)	--
Cirsium arvense	4 (0.1)	6 (0.2)	--	4 (0.0)	4 (0.1)	4 (0.0)	20 (0.5)	12 (0.2)
Clintonia borealis	--	10 (0.2)	4 (0.5)	--	--	--	--	16 (0.2)
Coptis trifolia	76 (1.0)	74 (3.5)	44 (0.5)	16 (0.2)	68 (1.5)	68 (1.5)	4 (0.1)	88 (4.0)
Corallorhiza maculata	4 (0.0)	--	--	--	--	--	--	--
Cornus canadensis	12 (0.2)	38 (1.3)	32 (0.8)	28 (0.6)	4 (0.1)	32 (0.6)	32 (0.6)	28 (0.4)
Cypripedium acaule	--	--	--	4 (0.0)	--	--	--	--
Drossera rotundifolia	--	--	--	--	--	--	--	12 (0.1)
Epilobium sp.	8 (0.1)	--	--	--	8 (0.1)	--	--	--
Eupatorium maculatum	--	--	--	--	4 (0.0)	--	--	4 (0.0)
Fragaria virginiana	--	--	--	--	--	8 (0.1)	12 (0.1)	8 (0.1)
Galium triflorum	8 (0.1)	30 (0.6)	--	--	44 (0.6)	68 (0.8)	16 (0.2)	44 (0.6)
Gaultheria hispidula	16 (0.3)	10 (0.4)	8 (0.2)	44 (2.1)	20 (0.3)	4 (0.0)	4 (0.0)	48 (0.8)
Geum canadense	--	--	--	4 (0.0)	--	--	28 (0.6)	--
Goodyera sp.	--	--	--	--	--	--	--	4 (0.0)
Habenaria obtusata	--	--	4 (0.0)	--	--	4 (0.0)	--	--
Hieraceum spp.	4 (0.0)	2 (0.0)	--	--	4 (0.1)	4 (0.1)	8 (0.1)	8 (0.1)
Hypericum boreale	--	--	--	--	--	4 (0.0)	--	--
Impatiens capensis	--	--	--	--	20 (0.4)	--	4 (0.0)	--
Iris versicolor	--	2 (0.0)	--	--	4 (0.1)	4 (0.1)	--	--
Linnaea borealis	40 (0.6)	52 (1.5)	28 (0.7)	28 (0.7)	4 (0.1)	20 (0.4)	--	24 (0.5)
Lycopus uniflorus	--	4 (0.2)	--	--	48 (1.5)	32 (0.4)	4 (0.0)	20 (0.2)
Lysimachia thyrsiflora	8 (0.1)	--	--	--	4 (0.0)	12 (0.1)	36 (0.6)	--
Maianthemum canadense	36 (0.4)	30 (0.3)	32 (0.4)	4 (0.1)	40 (0.4)	48 (0.5)	16 (0.2)	48 (0.5)
Mentha arvensis	--	--	--	--	--	8 (0.1)	--	--
Mimulus ringens	--	2 (0.0)	--	--	--	--	--	--
Mitella nuda	64 (2.3)	66 (2.3)	44 (0.5)	--	44 (0.7)	84 (1.8)	84 (1.1)	52 (1.0)
Oxalis acetosella	--	18 (1.0)	--	--	16 (0.2)	--	--	--
Polygala paucifolia	12 (0.2)	34 (0.8)	4 (0.0)	12 (0.2)	--	--	--	12 (0.2)
Polygonum hydropiperoid.	--	--	--	--	12 (0.1)	--	--	--
Polygonum sagittatum	--	--	--	--	16 (0.3)	--	--	--
Prunella vulgaris	--	--	--	--	4 (0.1)	8 (0.1)	4 (0.0)	8 (0.1)
Pyrola asarifolia	12 (0.2)	2 (0.0)	4 (0.0)	16 (0.3)	4 (0.0)	4 (0.0)	8 (0.1)	4 (0.0)
Ranunculus recurvatus	--	2 (0.0)	--	--	--	12 (0.2)	--	4 (0.0)
Rubus pubescens	4 (0.0)	52 (1.5)	68 (2.0)	44 (1.2)	60 (3.3)	64 (3.6)	100 (10.0)	44 (0.7)
Rumex orbiculata	--	--	--	--	--	--	4 (0.0)	--
Scutellaria galericulata	--	--	--	--	8 (0.1)	8 (0.1)	--	--
Scutellaria lateriflora	--	--	--	--	24 (0.4)	8 (0.1)	--	--
Smilacina trifolia	--	--	--	--	4 (0.0)	--	--	--
Solidago rugosa	--	2 (0.0)	--	--	4 (0.1)	8 (0.2)	4 (0.1)	--
Streptopus amplexifolius	--	2 (0.0)	--	--	--	--	--	--
Trientalis borealis	84 (1.5)	58 (1.1)	60 (1.8)	72 (1.6)	56 (1.1)	52 (0.6)	12 (0.1)	80 (1.3)
Viola spp.	--	12 (0.1)	--	--	16 (0.2)	16 (0.2)	--	40 (0.5)
GRAMINOIDS								
Bromus ciliatus	--	--	--	--	--	--	4 (0.0)	--

[1] non-native species are in italics

Appendix F4. (continued)

Species[1]	Portage Bay (n = 25)	Epou-fette Bay (n = 50)	Hog Island Point (n = 25)	Seiner's Point (n = 25)	Ogontz North (n = 25)	Chipp-ewa Point (n = 25)	Ogontz West (n = 25)	Nahma (n = 25)
GRAMINOIDS (continued)								
Calamagrostis canadensis	--	2 (0.1)	--	--	4 (0.0)	8 (0.1)	4 (0.0)	12 (0.1)
Carex arctata	--	--	--	4 (0.0)	--	8 (0.2)	40 (1.4)	16 (0.6)
Carex bebbii	--	2 (0.0)	--	--	--	--	--	--
Carex eburnea	16 (0.6)	8 (0.8)	8 (0.2)	8 (0.6)	16 (0.2)	12 (0.2)	8 (0.3)	32 (0.8)
Carex flava	--	4 (0.1)	--	--	--	--	--	--
Carex gracillima	--	--	--	--	--	--	8 (0.2)	--
Carex intumescens	--	--	--	--	20 (0.4)	8 (0.1)	32 (0.6)	48 (0.8)
Carex lacustris	--	--	--	--	4 (2.0)	--	32 (0.5)	--
Carex leptalea	8 (0.2)	--	--	--	12 (0.3)	32 (1.0)	40 (1.8)	12 (2.6)
Carex pedunculata	--	14 (0.4)	80 (12.0)	60 (2.2)	20 (0.7)	52 (1.6)	28 (0.9)	36 (1.3)
Carex stricta	--	--	--	--	16 (0.6)	24 (0.4)	--	--
Carex trisperma	84 (2.0)	56 (4.1)	32 (0.9)	80 (8.3)	64 (1.3)	20 (0.2)	12 (0.4)	72 (3.4)
Carex sp. #1	--	2 (0.1)	--	4 (0.2)	--	--	8 (0.5)	4 (0.1)
Carex sp. #2	--	--	--	4 (0.3)	--	--	--	--
Carex sp. #3	--	--	--	4 (0.2)	--	--	--	--
Glyceria canadensis	--	2 (0.1)	--	--	--	--	--	--
Glyceria striata	--	--	--	--	8 (0.2)	16 (0.2)	52 (8.4)	28 (0.3)
Leersia oryzoides	--	--	--	--	12 (0.2)	--	--	--
Panicum sp.	4 (0.0)	--	--	--	16 (0.2)	4 (0.0)	--	--
Scirpus atrovirens	--	--	--	--	4 (0.2)	--	--	--
Unknown grass	--	--	--	--	4 (0.1)	--	--	--
FERNS								
Athyrium filix-femina	--	--	--	--	--	4 (0.1)	--	8 (0.1)
Botrichyium virginianum	4 (0.0)	2 (0.0)	--	--	--	8 (0.1)	4 (0.0)	--
Dryopteris cristata	8 (0.1)	52 (1.8)	24 (0.8)	--	44 (1.0)	12 (0.2)	40 (1.0)	4 (0.1)
Equisetum arvense	32 (0.4)	2 (0.0)	--	--	20 (0.4)	76 (1.6)	92 (2.6)	16 (0.2)
Equisetum scirpoides	4 (0.1)	--	4 (0.1)	20 (0.2)	--	8 (0.1)	--	--
Gymnocarpium dryopteris	--	24 (1.2)	36 (0.6)	--	24 (0.8)	28 (0.6)	8 (0.1)	20 (1.0)
Huperzia lucidula	12 (0.1)	18 (0.3)	8 (0.1)	--	16 (0.2)	--	--	8 (0.1)
Lycopodium annotinum	--	--	--	--	12 (1.3)	--	--	--
Matteuccia struthiopteris	--	--	--	--	--	--	4 (0.2)	--
Onoclea sensibilis	--	--	--	--	16 (0.3)	--	12 (0.2)	4 (0.0)
Osmunda cinnamomea	--	--	--	--	4 (0.2)	--	4 (1.0)	--
Osmunda regalis	--	2 (0.2)	--	--	--	--	--	16 (0.3)
Thelypteris palustris	4 (0.0)	--	--	--	4 (0.1)	16 (0.3)	20 (0.4)	4 (0.0)
Woodsia ilvensis	--	--	--	--	--	--	24 (0.3)	4 (0.1)

[1] non-native species are in italics

Appendix G1. Comparison of overstory sepcies composition among eight swamp forests sampled along the northern Lake Huron shoreline in Northern Lower Michigan and eastern Upper Michigan in 2002 (percentages of total stem density and basal area are in parentheses).

	Ecosystem Type 1							Ecosystem Type 2
Species	St. Martin (n=20)	Duck Bay (n=10)	Misery Bay (n=20)	El Cajon Bay (n=20)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)	Ossi-nike (n=20)
Thuja occidentalis								
Stems/ha	1,863 (85)	1,335 (84)	1,520 (80)	1,405 (76)	2,155 (89)	2,015 (87)	2,485 (91)	8 (1)
BA (m^2/ha)	65.0 (83)	51.5 (77)	48.8 (78)	49.1 (78)	52.9 (89)	43.5 (78)	49.5 (91)	0.3 (2)
Avg dbh (cm)	19.0	21.6	20.8	21.1	16.6	16.3	15.5	19.1
Betula papyrifera								
Stems/ha	75 (4)	30 (2)	58 (3)	45 (3)	93 (4)	15 (1)	70 (3)	20 (3)
BA (m^2/ha)	2.3 (3)	2.0 (3)	1.4 (2)	1.1 (2)	2.6 (4)	0.5 (1)	1.6 (3)	0.7 (3)
Avg dbh (cm)	19.4	24.6	16.4	17.6	17.1	20.1	17.7	20.6
Abies balsamea								
Stems/ha	58 (3)	45 (3)	85 (6)	103 (8)	90 (4)	40 (2)	--	25 (4)
BA (m^2/ha)	4.0 (4)	0.6 (1)	1.4 (2)	1.6 (4)	1.7 (3)	0.5 (1)	--	0.3 (1)
Avg dbh (cm)	19.4	12.6	13.8	13.8	15.1	11.9	--	11.5
Picea glauca								
Stems/ha	95 (5)	55 (4)	--	5 (0)	45 (2)	15 (1)	--	--
BA (m^2/ha)	4.2 (7)	4.5 (6)	--	0.3 (0)	1.8 (3)	0.4 (1)	--	--
Avg dbh (cm)	23.5	29.8	--	27.9	22.6	19.6	--	--
Picea mariana								
Stems/ha	25 (1)	--	48 (3)	43 (2)	5 (0)	50 (2)	30 (1)	8 (1)
BA (m^2/ha)	0.9 (1)	--	2.9 (5)	1.9 (3)	0.2 (0)	0.9 (2)	1.1 (2)	0.1 (0)
Avg dbh (cm)	20.3	--	26.2	22.6	21.6	14.3	21.1	12.7
Populus balsamifera								
Stems/ha	15 (1)	90 (7)	5 (0)	23 (1)	5 (0)	120 (6)	40 (2)	--
BA (m^2/ha)	0.6 (1)	7.0 (12)	0.3 (1)	0.6 (1)	0.3 (1)	5.0 (9)	1.0 (2)	--
Avg dbh (cm)	22.1	35.3	29.9	21.2	25.6	22.4	17.9	--
Populus tremuloides								
Stems/ha	--	5 (0)	103 (6)	45 (3)	3 (0)	10 (1)	--	3 (0)
BA (m^2/ha)	--	0.1 (0)	6.9 (11)	3.0 (5)	0.2 (0)	1.4 (3)	--	0.0 (0)
Avg dbh (cm)	--	18.2	28.3	28.2	28.8	41.4	--	9.1

Appendix G1. (continued)

	Ecosystem Type 1							Ecosystem Type 2
Species	St. Martin (n=20)	Duck Bay (n=10)	Misery Bay (n=20)	El Cajon Bay (n=20)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)	Ossi-nike (n=20)
Populus tremuloides								
Stems/ha	--	5 (0)	103 (6)	45 (3)	3 (0)	10 (1)	--	3 (0)
BA (m^2/ha)	--	0.1 (0)	6.9 (11)	3.0 (5)	0.2 (0)	1.4 (3)	--	0.0 (0)
Avg dbh (cm)	--	18.2	28.3	28.2	28.8	41.4	--	9.1
Fraxinus nigra								
Stems/ha	25 (1)	--	--	13 (1)	3 (0)	--	50 (3)	20 (3)
BA (m^2/ha)	0.4 (1)	--	--	0.4 (2)	0.1 (0)	--	0.6 (1)	0.5 (2)
Avg dbh (cm)	12.2	--	--	19.5	13.3	--	11.3	16.6
Larix laricina								
Stems/ha	5 (0)	--	--	--	3 (0)	5 (0)	15 (1)	13 (2)
BA (m^2/ha)	0.1 (0)	--	--	--	0.0 (0)	0.1 (0)	0.4 (1)	0.4 (3)
Avg dbh (cm)	17.4	--	--	--	9.1	19.5	18.4	20.0
Pinus strobus								
Stems/ha	--	--	3 (0)	3 (0)	--	25 (1)	--	5 (1)
BA (m^2/ha)	--	--	0.2 (0)	0.3 (0)	--	3.1 (5)	--	0.0 (0)
Avg dbh (cm)	--	--	31.5	39.8	--	38.9	--	9.4
Fraxinus pensylvanica								
Stems/ha	--	--	10 (1)	43 (4)	--	--	--	760 (79)
BA (m^2/ha)	--	--	0.2 (0)	1.2 (2)	--	--	--	17.1 (81)
Avg dbh (cm)	--	--	13.9	18.1	--	--	--	18.4
Acer rubrum								
Stems/ha	--	--	10 (1)	8 (0)	--	--	--	48 (7)
BA (m^2/ha)	--	--	0.2 (0)	0.1 (0)	--	--	--	1.6 (7)
Avg dbh (cm)	--	--	16.6	11.7	--	--	--	20.4
Betula alleghaniensis								
Stems/ha	--	10 (1)	--	--	--	--	--	--
BA (m^2/ha)	--	0.4 (1)	--	--	--	--	--	--
Avg dbh (cm)	--	22.0	--	--	--	--	--	--

Appendix G1. (continued)

Species	Ecosystem Type 1							Ecosystem Type 2
	St. Martin (n=20)	Duck Bay (n=10)	Misery Bay (n=20)	El Cajon Bay (n=20)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)	Ossi-nike (n=20)
Acer saccharinum								
Stems/ha	--	--	--	--	--	--	--	3 (0)
BA (m^2/ha)	--	--	--	--	--	--	--	0.2 (0)
Avg dbh (cm)	--	--	--	--	--	--	--	28.7
Acer pensylvanicum								
Stems/ha	3 (0)	--	--	3 (0)	--	--	--	--
BA (m^2/ha)	0.1 (0)	--	--	0.0 (0)	--	--	--	--
Avg dbh (cm)	14.3	--	--	11.3	--	--	--	--
Sorbus americana								
Stems/ha	--	5 (0)	--	--	--	--	--	--
BA (m^2/ha)	--	0.1 (0)	--	--	--	--	--	--
Avg dbh (cm)	--	16.2	--	--	--	--	--	--
Fraxinus americana								
Stems/ha	--	--	--	3 (0)	--	--	--	--
BA (m^2/ha)	--	--	--	0.1 (1)	--	--	--	--
Avg dbh (cm)	--	--	--	23.5	--	--	--	--
Quercus rubra								
Stems/ha	--	--	--	--	--	--	--	3 (0)
BA (m^2/ha)	--	--	--	--	--	--	--	0.0 (0)
Avg dbh (cm)	--	--	--	--	--	--	--	10.7
Acer saccharum								
Stems/ha	--	--	--	10 (1)	--	--	--	--
BA (m^2/ha)	--	--	--	0.1 (0)	--	--	--	--
Avg dbh (cm)	--	--	--	12.9	--	--	--	--

Appendix G2. Comparison of large understory (1.6–9.0 cm dbh) species composition among eight swamp forests sampled along the northern Lake Huron shoreline in 2003 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 1							Ecosystem Type 2
Species	St. Martin (n=20)	Duck Bay (n=10)	Misery Bay (n=20)	El Cajon Bay (n=20)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)	Ossi-nike (n=20)
Thuja occidentalis	485 (90)	410 (67)	215 (72)	145 (20)	645 (84)	1,040 (81)	1,190 (80)	5 (1)
Abies balsamea	10 (2)	200 (33)	45 (15)	520 (72)	100 (13)	210 (16)	50 (3)	295 (43)
Fraxinus nigra	45 (8)	--	30 (10)	--	10 (1)	--	250 (17)	5 (1)
Fraxinus pennsylvanica	--	--	--	5 (1)	--	--	--	320 (47)
Picea mariana	--	--	--	--	--	20 (2)	--	25 (4)
Populus tremuloides	--	--	--	30 (4)	--	--	--	--
Betula papyrifera	--	--	5 (2)	--	--	10 (1)	--	5 (1)
Larix laricina	--	--	--	10 (1)	5 (1)	--	--	5 (1)
Acer rubrum	--	--	5 (2)	--	--	--	--	10 (1)
Acer saccharinum	--	--	--	8 (1)	--	--	--	3 (0)
Pinus strobus	--	--	--	--	--	--	--	10 (1)
Picea glauca	--	--	--	--	5 (1)	--	--	--
TOTAL	540 (100)	610 (100)	300 (100)	718 (100)	765 (100)	1,280 (100)	1,490 (100)	683 (100)

Appendix G3. Comparison of small understory (taller than 50 cm and < 1.5 cm dbh) species composition among eight swamp forests sampled along the northern Lake Huron shoreline in 2002 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 1							Ecosystem Type 2
Species	St. Martin (n=20)	Duck Bay (n=10)	Misery Bay (n=20)	El Cajon Bay (n=20)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)	Ossi-nike (n=20)
TREES								
Abies balsamea	5 (100)	80 (20)	75 (65)	785 (84)	--	410 (69)	--	140 (1)
Acer pensylvanicum	--	--	--	5 (1)	--	--	--	--
Acer spicatum	--	--	--	5 (1)	--	--	--	--
Fraxinus pennsylvanica	--	--	--	5 (1)	--	--	--	115 (1)
Larix laricina	--	--	--	5 (1)	--	--	--	15 (0)
Picea glauca	--	20 (5)	--	--	--	--	--	--
Picea mariana	--	--	--	10 (1)	--	--	--	10 (0)
Pinus strobus	--	--	--	--	--	--	--	20 (0)
Populus balsamifera	--	270 (66)	5 (4)	--	5 (33)	--	20 (4)	--
Populus tremuloides	--	40 (10)	35 (30)	95 (10)	--	--	--	--
Thuja occidentalis	--	--	--	10 (1)	--	60 (10)	--	5 (0)
SHRUBS								
Alnus rugosa	--	--	--	--	10 (67)	--	470 (92)	5,045 (44)
Amelanchier spp.	--	--	--	5 (1)	--	--	--	--
Betula pumila	--	--	--	--	--	--	--	630 (5)
Cornus amomum	--	--	--	--	--	--	--	20 (0)
Cornus rugosa	--	--	--	15 (2)	--	--	--	--
Ilex verticillata	--	--	--	--	--	--	--	5 (0)
Potentilla fruticosa	--	--	--	--	--	110 (19)	--	210 (2)
Rhamnus alnifolia	--	--	--	--	--	--	20 (4)	--
Rosa palustris	--	--	--	--	--	--	--	40 (0)
Rubus strigosus	--	--	--	--	--	--	--	80 (1)
Salix spp.	--	--	--	--	--	--	--	10 (0)
Spiraea alba	--	--	--	--	--	10 (2)	--	5,165 (45)
TOTAL	5 (100)	410 (100)	115 (100)	940 (100)	15 (100)	590 (100)	510 (100)	11,510 (100)

Appendix G4. Comparison of ground-cover species composition among eight swamp forests sampled along the northern Lake Huron shoreline in 2002 (values are frequency (%), average percent coverage is in parentheses).

	Ecosystem Type 1							Ecosystem Type 2
Species[1]	St. Martin (n = 20)	Duck Bay (n = 10)	Misery Bay (n = 20)	El Cajon Bay (n = 20)	Paquin Lake (n = 20)	Voight Bay (n = 10)	Brulee Point (n = 10)	Ossi-neke (n = 20)
TREES								
Abies balsamea	40 (0.4)	10 (0.1)	25 (0.7)	55 (3.0)	35 (0.4)	80 (1.8)	20 (0.2)	--
Acer rubrum	--	--	--	--	--	--	--	25 (0.3)
Acer saccharinum	--	--	--	--	--	--	--	20 (0.2)
Betula papyrifera	15 (0.2)	10 (0.1)	10 (0.1)	25 (0.3)	5 (0.5)	10 (0.1)	--	5 (0.5)
Fraxinus nigra	15 (0.2)	--	--	--	10 (0.2)	--	60 (0.9)	--
Fraxinus pennsylvanica	--	--	35 (0.6)	55 (1.0)	--	--	--	75 (1.2)
Larix laricina	--	--	--	--	--	--	10 (0.1)	--
Picea glauca	5 (0.5)	--	--	--	--	--	--	--
Picea mariana	--	--	--	5 (0.1)	--	--	10 (0.1)	--
Populus balsamifera	15 (0.3)	20 (0.3)	5 (0.5)	--	--	--	--	--
Populus tremuloides	--	--	20 (0.6)	20 (0.6)	--	--	--	--
Quercus rubra	--	--	--	5 (0.5)	--	--	--	--
Thuja occidentalis	20 (0.2)	--	5 (0.5)	--	30 (0.4)	10 (0.1)	--	--
TALL SHRUBS								
Acer pensylvanicum	--	10 (0.1)	--	--	10 (0.4)	--	--	--
Acer spicatum	20 (0.2)	20 (0.2)	--	5 (0.5)	--	--	--	--
Alnus rugosa	--	--	--	--	5 (0.5)	--	10 (2.5)	15 (0.7)
Amelanchier spp.	--	--	5 (0.5)	10 (0.2)	--	--	20 (0.2)	--
Cornus amomum	--	--	--	--	--	--	10 (0.2)	15 (0.2)
Ilex verticillata	--	--	--	--	--	--	10 (0.1)	5 (0.5)
Sambucus canadensis	5 (0.5)	--	--	--	--	--	20 (0.2)	--
Sorbus americana	5 (0.5)	--	--	--	10 (0.2)	--	--	--
Viburnum trilobum	--	--	--	--	--	--	10 (0.1)	--
SHORT SHRUBS								
Arctostaphylos uva-ursi	--	--	--	--	--	10 (0.5)	--	--
Betula pumila	--	--	--	--	--	--	--	15 (0.4)
Gaultheria hispidula	--	--	--	--	10 (0.1)	20 (0.6)	30 (1.1)	--

[1] non-native species are in italics

Appendix G4. (continued)

Species[1]	Ecosystem Type 1							Ecosystem Type 2
	St. Martin (n = 20)	Duck Bay (n = 10)	Misery Bay (n = 20)	El Cajon Bay (n = 20)	Paquin Lake (n = 20)	Voight Bay (n = 10)	Brulee Point (n = 10)	Ossi-neke (n = 20)
SHORT SHRUBS (continued)								
Ledum groenlandicum	--	--	--	--	5 (0.5)	--	--	--
Lonicera canadensis	--	--	5 (0.5)	5 (0.2)	--	30 (0.4)	--	--
Rhamnus alnifolia	--	--	--	10 (0.2)	5 (0.2)	--	10 (0.1)	--
Ribes americanum	--	--	--	5 (0.4)	--	--	10 (0.1)	--
Ribes cynosbati	--	--	--	--	--	10 (0.1)	10 (0.1)	--
Rosa palustris	--	--	--	--	--	20 (0.3)	--	--
Rubus parviflorus	--	--	--	5 (0.4)	--	--	--	--
Rubus strigosus	--	--	--	--	--	--	--	5 (0.9)
Spiraea alba	--	--	--	--	--	10 (0.7)	--	55 (3.5)
FORBS								
Actaea spp.	5 (0.2)	--	--	5 (0.2)	--	--	--	--
Allium spp.	--	--	--	--	--	20 (0.2)	--	--
Aralia nudicaulis	5 (0.4)	--	5 (0.8)	15 (1.5)	--	--	--	--
Aster ciliolatus	--	--	--	--	15 (0.4)	--	20 (0.2)	--
Aster lateriflorus	--	--	--	10 (0.1)	--	--	30 (0.5)	5 (0.5)
Aster macrophyllus	20 (0.2)	--	40 (0.4)	60 (2.0)	--	40 (0.4)	50 (1.0)	--
Aster puniceus	--	--	--	5 (0.5)	--	--	20 (0.2)	5 (0.1)
Aster spp.	--	--	10 (0.3)	5 (0.3)	--	--	--	--
Caltha palustris	5 (0.4)	--	--	5 (0.3)	--	--	--	--
Campanula aparinoides	--	--	--	--	--	--	20 (0.2)	50 (0.5)
Circaea alpina	5 (0.4)	10 (0.1)	--	--	--	--	--	--
Cirsium vulgare	--	--	5 (1.5)	--	--	--	--	--
Clematis virginiana	--	--	--	--	--	--	--	5 (0.5)
Clintonia borealis	15 (0.2)	10 (0.1)	--	--	--	--	--	--
Coptis trifolia	20 (0.3)	10 (0.1)	--	10 (0.1)	15 (0.2)	--	20 (0.6)	--
Cornus canadensis	10 (0.2)	--	--	10 (0.3)	--	--	40 (0.9)	--
Cypripedium spp.	5 (0.5)	--	--	--	--	10 (0.1)	--	--
Epipactis helleborine	--	10 (0.1)	--	25 (0.3)	--	--	--	--
Fragaria virginiana	10 (0.1)	--	--	--	--	10 (0.1)	20 (0.3)	5 (0.1)

[1] non-native species are in italics

Appendix G4. (continued)

	Ecosystem Type 1							Ecosystem Type 2
Species[1]	St. Martin (n = 20)	Duck Bay (n = 10)	Misery Bay (n = 20)	El Cajon Bay (n = 20)	Paquin Lake (n = 20)	Voight Bay (n = 10)	Brulee Point (n = 10)	Ossi-neke (n = 20)
FORBS (continued)								
Galium triflorum	20 (0.2)	30 (0.4)	--	15 (0.2)	--	10 (0.1)	40 (0.4)	25 (0.3)
Habenaria obtusata	--	--	--	--	5 (0.1)	--	--	--
Hieraceum aurantaiacum	--	--	--	--	5 (0.2)	--	--	--
Hieraceum spp.	--	10 (1.0)	--	--	--	10 (0.1)	--	--
Hypericum spp.	--	--	--	--	--	10 (0.1)	--	--
Impatiens capensis	--	--	--	--	--	--	--	10 (0.1)
Iris lacustris	--	--	--	5 (0.5)	--	10 (6.5)	--	--
Iris versicolor	5 (0.5)	--	--	--	--	--	--	25 (1.5)
Lathyrus palustris	--	--	--	--	--	--	--	10 (0.4)
Lilium michiganense	--	--	--	--	--	10 (0.1)	--	--
Linnaea borealis	20 (0.4)	--	--	15 (0.4)	5 (0.5)	40 (0.8)	40 (2.0)	--
Lycopus americanus	--	--	--	--	--	--	--	5 (0.5)
Lycopus uniflorus	--	--	--	5 (0.5)	--	--	30 (0.3)	60 (1.7)
Lysimachia thyrsiflora	--	--	--	--	--	--	--	85 (1.2)
Maianthemum canadense	75 (1.5)	50 (1.1)	25 (0.3)	55 (1.3)	20 (0.2)	30 (0.3)	50 (0.9)	--
Mentha arvensis	5 (0.5)	--	--	--	--	--	--	25 (1.0)
Mitella nuda	40 (1.1)	40 (2.9)	--	10 (0.6)	15 (0.9)	50 (0.7)	70 (1.9)	10 (0.5)
Oxalis stricta	5 (0.5)	--	--	--	--	--	--	--
Parnassia glauca	--	--	--	--	5 (0.1)	--	--	--
Petasites frigidus	5 (0.5)	--	15 (0.5)	30 (0.9)	--	--	10 (0.7)	--
Pinguicula vulgaris	--	--	--	--	--	10 (0.5)	--	--
Polygala paucifolia	45 (0.9)	10 (0.6)	--	10 (0.1)	--	60 (1.4)	--	--
Polygonum amphibium	--	--	--	--	--	--	--	25 (0.5)
Potentilla palustris	--	--	--	--	--	10 (0.1)	--	20 (0.5)
Potentilla simplex	--	--	--	--	--	10 (0.4)	--	--
Prenanthes altissima	--	10 (0.2)	--	--	--	--	--	--
Prunella vulgaris	10 (0.3)	--	--	--	5 (0.5)	20 (0.2)	20 (0.9)	--
Pyrola asarifolia	5 (0.5)	--	5 (0.2)	--	--	30 (1.9)	10 (0.2)	--
Ranunculus spp.	--	--	--	--	--	--	--	15 (0.6)

[1] non-native species are in italics

Appendix G4. (continued)

Species[1]	Ecosystem Type 1							Ecosystem Type 2
	St. Martin (n = 20)	Duck Bay (n = 10)	Misery Bay (n = 20)	El Cajon Bay (n = 20)	Paquin Lake (n = 20)	Voight Bay (n = 10)	Brulee Point (n = 10)	Ossi-neke (n = 20)
FORBS (continued)								
Rubus pubescens	15 (1.9)	10 (0.2)	--	10 (0.6)	15 (0.2)	--	60 (4.1)	45 (3.4)
Scutellaria galericulata	5 (0.5)	--	--	--	--	--	10 (0.1)	25 (0.3)
Senecio aureus	5 (0.3)	--	--	5 (0.2)	--	--	10 (0.1)	--
Smilacina stellata	--	--	--	5 (0.5)	--	--	--	--
Solidago rugosa	10 (0.1)	--	5 (0.1)	10 (0.4)	--	--	40 (1.1)	5 (0.5)
Solidago spp.	--	--	10 (0.1)	5 (0.1)	5 (0.5)	--	--	--
Streptopus amplexifolius	--	10 (0.1)	--	--	--	--	--	--
Taraxacum officionale	--	--	25 (0.5)	5 (0.1)	--	--	20 (0.3)	--
Trientalis borealis	65 (1.5)	40 (0.7)	10 (0.1)	15 (0.6)	70 (1.9)	--	50 (0.9)	--
Viola cucculata	--	--	20 (0.4)	--	--	--	--	--
Viola spp.	10 (0.1)	10 (0.2)	--	5 (0.1)	--	10 (0.1)	--	5 (0.5)
Unknown # 1	--	10 (0.1)	--	--	10 (0.2)	10 (0.1)	--	5 (0.5)
Unknown # 2	--	--	--	5 (0.5)	--	20 (0.2)	--	--
Unknown # 3	--	--	--	5 (0.5)	--	10 (0.4)	--	--
Unknown # 4	--	--	--	5 (0.5)	--	--	--	--
Unknown orchid	10 (0.1)	--	5 (0.5)	5 (0.5)	--	--	--	--
GRAMINOIDS								
Calamagrostis canadensis	--	--	--	--	--	--	10 (0.2)	85 (8.6)
Carex alpina	--	--	--	--	--	--	--	5 (0.4)
Carex amphibola	--	--	5 (0.5)	--	--	--	--	--
Carex arctata	--	10 (0.4)	--	--	--	--	--	--
Carex deweyana	--	--	20 (0.8)	30 (7.0)	--	--	--	--
Carex disperma	10 (1.2)	30 (0.6)	--	--	45 (2.6)	--	80 (1.5)	15 (1.2)
Carex eburnea	30 (0.4)	--	20 (0.3)	25 (1.2)	50 (0.8)	40 (1.6)	10 (1.2)	--
Carex gracillima	--	--	--	15 (0.3)	--	--	20 (2.7)	--
Carex hystericina	--	--	--	--	--	--	--	5 (0.1)
Carex intumescens	--	--	5 (0.3)	--	--	--	--	15 (2.3)
Carex lacustris	--	--	--	--	--	--	10 (0.5)	30 (2.6)
Carex pedunculata	70 (4.2)	10 (0.7)	--	--	5 (0.4)	--	--	--

[1] non-native species are in italics

Appendix G4. (continued)

	Ecosystem Type 1							Ecosystem Type 2
Species[1]	St. Martin (n = 20)	Duck Bay (n = 10)	Misery Bay (n = 20)	El Cajon Bay (n = 20)	Paquin Lake (n = 20)	Voight Bay (n = 10)	Brulee Point (n = 10)	Ossi-neke (n = 20)
GRAMINOIDS (continued)								
Carex richardsonii	--	--	--	5 (0.5)	--	--	--	--
Carex rosea	--	--	--	--	--	20 (0.2)	--	--
Carex spp. # 1	10 (0.2)	--	5 (0.1)	10 (0.5)	5 (0.1)	--	--	5 (0.8)
Carex spp. # 2	5 (0.2)	--	5 (1.3)	--	--	--	--	5 (0.5)
Carex spp. # 3	--	--	10 (0.4)	--	--	--	--	5 (0.2)
Carex stricta	--	--	--	5 (4.3)	--	--	20 (0.8)	75 (15.7)
Carex trisperma	--	--	--	--	10 (1.3)	--	--	--
Eleocharis spp.	--	--	--	--	--	10 (4.0)	--	--
Glyceria striata	10 (0.1)	--	--	--	5 (0.1)	--	10 (0.2)	--
Juncus spp.	--	--	--	--	--	10 (0.1)	--	--
Panicum spp.	--	--	--	--	10 (0.2)	--	--	--
Unknown grass #1	--	--	--	--	--	10 (0.1)	--	--
Unknown grass #2	--	--	--	5 (0.5)	--	--	--	--
FERNS								
Athyrium filix-femina	--	40 (4.7)	--	--	--	--	--	--
Botrichyium virginianum	25 (0.3)	--	25 (0.5)	10 (0.1)	--	30 (0.3)	50 (0.9)	--
Cystopteris bulbifera	--	--	--	15 (9.2)	--	--	--	--
Dryopteris cristata	5 (0.5)	20 (0.3)	--	--	--	--	10 (0.1)	--
Equisetum arvense	25 (1.4)	10 (0.1)	5 (1.5)	10 (0.3)	10 (0.4)	--	80 (11.6)	15 (0.6)
Equisetum palustre	10 (0.1)	--	--	--	5 (0.5)	--	--	--
Equisetum scirpoides	--	--	5 (0.1)	--	5 (0.5)	--	--	--
Gymnocarpium dryopteris	5 (0.5)	10 (0.2)	--	5 (0.2)	--	--	--	--
Onoclea sensibilis	--	--	--	--	--	--	--	20 (2.4)
Osmunda regalis	--	--	5 (0.5)	--	--	--	--	--
Pteridium aquilinum	--	--	--	5 (1.0)	--	--	--	--
Thelypteris palustris	--	--	--	--	--	--	--	45 (2.9)
Unknown fern	--	--	--	--	--	--	--	5 (0.1)

[1] non-native species are in italics

Appendix H1. Comparison of overstory species composition among 11 swamp forests sampled along the southern Lake Huron shoreline in 2003 (percentages of total stem density and basal area are in parentheses).

	Ecosystem Type 3										Ecosystem Type 4
Species	Vanderbilt Park (n = 2)	Pigeon North (n = 4)	Lakeport (n = 4)	Weale Road (n = 5)	Bay Port Swale (n = 7)	Gotham Road (n = 3)	Kirk Road (n = 4)	BCSP Campground (n = 4)	Bradley-ville (n = 4)	Weale Train Tracks (n = 2)	Bay Port Saturated (n = 1)
Acer saccharinum											
Stems/ha	100 (12)	400 (60)	388 (83)	730 (69)	714 (93)	--	--	75 (13)	--	--	--
BA (m^2/ha)	4.6 (8)	33.1 (56)	37.5 (83)	29.9 (68)	37.7 (95)	--	--	3.0 (14)	--	--	--
Avg dbh (cm)	22.6	29.4	29.8	20.9	23.6	--	--	21.8	--	--	--
Fraxinus pennsylvanica											
Stems/ha	625 (58)	213 (37)	63 (17)	280 (26)	71 (7)	733 (81)	1,175 (100)	363 (67)	800 (93)	150 (23)	--
BA (m^2/ha)	12.6 (18)	14.8 (41)	8.4 (17)	10.5 (24)	1.7 (5)	20.9 (57)	31.9 (100)	5.2 (20)	20.9 (92)	2.5 (27)	--
Avg dbh (cm)	15.0	28.8	40.2	20.8	16.4	16.7	16.9	13.0	17.0	14.6	--
Populus deltoides											
Stems/ha	300 (28)	--	--	20 (2)	--	50 (5)	--	113 (20)	--	--	--
BA (m^2/ha)	54.0 (74)	--	--	2.2 (4)	--	4.8 (12)	--	22.5 (66)	--	--	--
Avg dbh (cm)	47.2	--	--	36.1	--	34.1	--	49.5	--	--	--
Ulmus americana											
Stems/ha	25 (2)	--	--	10 (1)	--	17 (2)	--	--	75 (7)	200 (34)	--
BA (m^2/ha)	0.5 (1)	--	--	0.1 (0)	--	0.9 (3)	--	--	2.5 (8)	2.3 (31)	--
Avg dbh (cm)	16.4	--	--	10.2	--	26.6	--	--	18.6	11.7	--
Quercus bicolor											
Stems/ha	--	13 (2)	--	10 (1)	--	17 (2)	--	--	--	200 (36)	--
BA (m^2/ha)	--	1.1 (4)	--	1.3 (3)	--	4.7 (19)	--	--	--	2.2 (34)	--
Avg dbh (cm)	--	33.8	--	41.4	--	59.7	--	--	--	11.8	--
Quercus macrocarpa											
Stems/ha	--	--	--	--	--	83 (10)	--	--	--	50 (8)	--
BA (m^2/ha)	--	--	--	--	--	2.9 (9)	--	--	--	0.7 (7)	--
Avg dbh (cm)	--	--	--	--	--	19.8	--	--	--	13.1	--

Appendix H1. (continued)

Species	Ecosystem Type 3										Ecosystem Type 4
	Vanderbilt Park (n = 2)	Pigeon North (n = 4)	Lakeport (n = 4)	Weale Road (n = 5)	Bay Port Swale (n = 7)	Gotham Road (n = 3)	Kirk Road (n = 4)	BCSP Campground (n = 4)	Bradley-ville (n = 4)	Weale Train Tracks (n = 2)	Bay Port Saturated (n = 1)
Fraxinus nigra											
Stems/ha	--	--	--	10 (1)	--	--	--	--	--	--	--
BA (m^2/ha)	--	--	--	0.1 (0)	--	--	--	--	--	--	--
Avg dbh (cm)	--	--	--	10.6	--	--	--	--	--	--	--
Thuja occidentalis											
Stems/ha	--	--	--	--	--	--	--	--	--	--	1,650 (92)
BA (m^2/ha)	--	--	--	--	--	--	--	--	--	--	61.0 (94)
Avg dbh (cm)	--	--	--	--	--	--	--	--	--	--	20.8
Larix laricina											
Stems/ha	--	--	--	--	--	--	--	--	--	--	50 (3)
BA (m^2/ha)	--	--	--	--	--	--	--	--	--	--	1.7 (3)
Avg dbh (cm)	--	--	--	--	--	--	--	--	--	--	21.0
Fraxinus americana											
Stems/ha	--	--	--	--	--	--	--	--	--	--	100 (6)
BA (m^2/ha)	--	--	--	--	--	--	--	--	--	--	1.9 (3)
Avg dbh (cm)	--	--	--	--	--	--	--	--	--	--	15.6

Appendix H2. Comparison of understory sapling (1.6–9.0 cm dbh) composition among 11 coastal swamp forests sampled along the southern Lake Huron shoreline in 2002 (values are saplings/ha, percentages are in parentheses).

	Ecosystem Type 3										Ecosystem Type 4
Species	Vanderbilt Park (n = 2)	Pigeon North (n = 4)	Lakeport (n = 4)	Bay Port Swale (n = 7)	Weale Road (n = 5)	Gotham Road (n = 3)	Kirk Road (n = 4)	BCSP Campground (n = 4)	Bradley-ville (n = 4)	Weale Train Tracks (n = 2)	Bay Port Saturated (n = 1)
Ulmus americana	--	50 (13)	--	43 (10)	20 (4)	--	--	25 (2)	175 (25)	7,150 (80)	--
Fraxinus pennsylvanica	350 (100)	50 (8)	--	314 (47)	--	825 (95)	1,433 (97)	2,125 (97)	650 (68)	1,350 (17)	--
Acer saccharinum	--	725 (74)	150 (100)	343 (43)	420 (84)	--	--	25 (1)	50 (5)	--	--
Prunus virginiana	--	--	--	--	60 (12)	--	--	--	--	--	200 (50)
Zanthoxylum americanum	--	--	--	--	--	--	--	--	--	--	200 (50)
Quercus bicolor	--	25 (6)	--	--	--	--	--	--	--	100 (2)	--
Quercus macrocarpa	--	--	--	--	--	--	33 (3)	--	--	50 (1)	--
Cephalanthus occidentalis	--	--	--	--	--	25 (5)	--	--	--	--	--
Vitis riparia	--	--	--	--	--	--	--	--	25 (2)	--	--
TOTAL	350 (100)	850 (100)	150 (100)	700 (100)	500 (100)	850 (100)	1,467 (100)	2,175 (100)	900 (100)	8,650 (100)	400 (100)

Appendix H3. Comparison of small understory (taller than 50 cm and < 1.5 cm dbh) composition among 11 coastal swamps along the southern Lake

	Ecosystem Type 3										Ecosystem Type 4
Species	Vanderbilt Park (n = 2)	Pigeon North (n = 4)	Lakeport (n = 4)	Weale Road (n = 5)	Bay Port Swale (n = 7)	Gotham Road (n = 3)	Kirk Road (n = 4)	BCSP Campground (n = 4)	Bradley-ville (n = 4)	Weale Train Tracks (n = 2)	Bay Port Saturated (n = 1)
TREES											
Fraxinus pennsylvanica	650 (79)	275 (69)	--	100 (56)	457 (34)	1,000 (100)	533 (71)	4,000 (63)	1,225 (72)	4,750 (72)	--
Ulmus americana	--	50 (13)	--	20 (11)	--	--	--	--	175 (18)	1,400 (21)	--
Acer saccharinum	50 (4)	50 (13)	--	40 (22)	--	--	--	--	25 (1)	--	--
Quercus bicolor	--	--	--	--	--	--	--	--	--	--	100 (3)
Populus tremuloides	--	--	--	20 (11)	--	--	--	--	--	--	--
Fraxinus americana	--	--	--	--	--	--	--	--	--	--	700 (18)
Crataegus spp.	--	--	--	--	--	--	--	--	--	50 (1)	--
SHRUBS											
Cornus amomum	--	--	--	--	229 (17)	--	267 (27)	1,375 (17)	--	--	--
Cornus stolonifera	--	--	--	--	--	--	--	1,475 (17)	--	--	--
Zanthoxylum americana	--	--	--	--	--	--	--	--	50 (6)	--	1,000 (26)
Prunus virginiana	--	--	--	--	--	--	--	--	--	--	800 (21)
Berberis thunbergii	--	--	--	--	--	--	--	--	--	--	700 (18)
Ilex verticillata	--	--	--	--	543 (40)	--	--	--	--	--	--
Vitis riparia	--	--	--	--	--	--	--	25 (0)	75 (4)	150 (2)	200 (5)
Viburnum trilobum	--	--	--	--	--	--	--	250 (4)	--	--	--
Cornus foemina	--	25 (6)	--	--	--	--	--	--	--	200 (3)	--
Amelanchier spp.	--	--	--	--	--	--	--	--	--	--	200 (5)
Cephalanthus occidentalis	50 (17)	--	--	--	71 (5)	--	--	--	--	--	--
Lindera benzoin	--	--	--	--	--	--	--	--	--	--	100 (3)
Lonicera canadensis	--	--	--	--	--	--	--	--	--	--	100 (3)
Ribes americana	--	--	--	--	--	--	33 (2)	--	--	--	--
Rosa palustris	--	--	--	--	29 (2)	--	--	--	--	--	--
Rubus occidentalis	--	--	--	--	29 (2)	--	--	--	--	--	--
Rubus alleghaniensis	--	--	25 (100)	--	--	--	--	--	--	--	--
TOTAL	750 (100)	400 (100)	25 (100)	180 (100)	1,357 (100)	1,000 (100)	833 (100)	7,125 (100)	1,550 (100)	6,550 (100)	3,900 (100)

Appendix H4. Comparison of ground-cover species composition among 11 swamp forest along the southern Lake Huron shoreline in 2003 (values are frequency (%), average percent coverage is in parentheses).

	Ecosystem Type 3										Ecosystem Type 4
Species[1]	Vanderbilt Park (n = 10)	Pigeon North (n = 20)	Lakeport (n = 20)	Weale Road (n = 25)	Bay Port Swale (n = 35)	Gotham Road (n = 15)	Kirk Road (n = 20)	BCSP Campground (n = 20)	Bradley-ville (n = 20)	Weale Train Tracks (n = 10)	Bay Port Saturated (n = 5)
TREES											
Acer saccharinum	--	5 (0.0)	10 (0.0)	8 (0.1)	14 (0.1)	7 (0.0)	--	--	20 (0.1)	--	20 (0.1)
Fraxinus americana	--	--	--	--	--	--	--	--	--	--	20 (0.4)
Fraxinus pennsylvanica	50 (0.8)	15 (0.3)	--	4 (0.1)	31 (0.4)	13 (0.2)	15 (0.2)	35 (2.3)	65 (0.7)	70 (2.9)	--
Populus deltoides	--	--	--	4 (0.0)	--	--	--	--	--	--	--
Prunus serotina	30 (0.1)	--	--	--	--	--	--	--	25 (0.1)	--	--
Quercus bicolor	--	--	--	--	3 (0.0)	--	--	--	10 (0.1)	--	20 (0.4)
Ulmus americana	--	--	--	4 (0.0)	--	--	--	--	70 (0.5)	60 (1.0)	--
TALL SHRUBS											
Amelanchier spp.	--	--	--	--	--	--	--	--	10 (0.0)	--	40 (0.3)
Cephalanthus occidentalis	10 (0.1)	--	--	--	--	--	--	--	--	--	--
Cornus alternifolia	--	--	--	--	--	--	--	--	--	--	40 (0.3)
Cornus amomum	10 (0.0)	--	--	4 (0.0)	6 (0.1)	7 (0.1)	--	20 (2.2)	15 (0.0)	30 (0.2)	20 (0.2)
Cornus foemina	--	--	--	--	--	--	--	--	--	10 (0.2)	--
Cornus stolonifera	--	--	--	--	--	--	--	5 (0.1)	--	--	--
Ilex verticillata	--	--	--	--	9 (0.5)	--	--	--	--	--	--
Lindera benzoin	--	--	--	--	3 (0.0)	--	--	--	--	--	--
Prunus virginiana	--	--	--	--	--	--	--	--	5 (0.0)	--	40 (0.8)
Rhamnus cathartica	--	--	--	--	--	--	--	--	15 (0.0)	--	--
Viburnum trilobum	--	--	--	--	--	--	--	5 (1.8)	--	--	--
Zanthoxylum americanum	--	--	--	--	--	--	--	--	5 (0.1)	--	20 (0.2)
SHORT SHRUBS											
Berberis thunbergii	--	--	--	--	--	--	--	--	--	--	60 (0.2)
Euonymus obovatus	--	--	--	--	--	--	--	--	--	--	40 (0.6)
Lonicera dioica	--	--	--	--	--	--	--	--	--	--	60 (0.9)
Ribes cynosbati	--	--	--	4 (0.0)	--	--	--	--	--	--	--
Rosa palustris	--	--	--	--	--	--	--	--	5 (0.0)	--	--

[1] non-native species are in italics

Appendix H4. (continued)[1]

	Ecosystem Type 3										Ecosystem Type 4
Species[1]	Vanderbilt Park (n = 10)	Pigeon North (n = 20)	Lakeport (n = 20)	Weale Road (n = 25)	Bay Port Swale (n = 35)	Gotham Road (n = 15)	Kirk Road (n = 20)	BCSP Campground (n = 20)	Bradley-ville (n = 20)	Weale Train Tracks (n = 10)	Bay Port Saturated (n = 5)
WOODY VINES											
Parthenocissus quinquefolia	--	--	--	--	--	--	--	--	--	--	40 (0.3)
Toxicodendron radicans	--	--	--	--	--	--	--	--	5 (0.0)	--	80 (1.4)
Vitis riparia	40 (0.1)	--	5 (0.0)	--	--	--	--	--	25 (0.1)	--	20 (0.1)
FORBS											
Agrimonia gryopsepala	--	--	--	--	--	--	--	--	--	--	20 (0.1)
Aralia nudicaulis	--	--	--	--	--	--	--	--	--	--	60 (0.3)
Arisaema triphyllum	--	--	5 (0.1)	--	--	--	--	--	--	--	--
Aster puniceus	--	--	--	--	3 (0.0)	--	--	--	--	--	--
Boehmeria cylindrica	--	--	30 (0.3)	--	--	--	5 (0.0)	--	--	--	--
Cicuta bulbifera	--	--	--	--	9 (0.0)	13 (0.0)	--	--	--	--	--
Cicuta maculata	--	--	--	--	--	--	--	--	--	10 (0.2)	--
Circaea lutetiana	40 (0.3)	--	--	8 (0.0)	--	--	--	--	35 (0.2)	--	--
Clematis virginiana	--	--	--	--	--	--	--	--	--	--	20 (0.2)
Convolvulus arvensis	--	--	--	--	--	--	--	--	15 (0.1)	--	--
Erechtites hieraciifolia	10 (0.0)	--	--	--	--	--	--	--	40 (0.2)	--	--
Fragaria virginiana	--	--	--	--	--	--	--	--	--	--	60 (1.5)
Galium aparine	50 (0.2)	--	--	--	--	--	--	--	--	10 (0.0)	--
Galium asprellum	--	--	--	--	3 (0.0)	--	--	--	--	--	20 (0.2)
Galium triflorum	--	--	--	--	--	--	--	--	--	--	40 (0.2)
Geum canadense	30 (0.1)	--	5 (0.0)	4 (0.0)	--	--	--	--	15 (0.0)	--	--
Hackelia virginiana	10 (0.1)	--	--	--	--	--	--	--	--	--	--
Iris versicolor	--	--	--	--	6 (0.0)	7 (0.0)	--	--	--	--	--
Lemna trisulca	--	--	--	--	--	67 (13.0)	--	--	--	--	--
Lycopus americanus	--	--	--	--	--	7 (0.1)	10 (0.0)	--	--	--	--
Lycopus uniflorus	--	10 (0.2)	10 (0.1)	--	9 (0.1)	--	--	--	--	--	--
Lysimachia nummularia	40 (8.3)	--	--	--	--	--	--	--	--	--	--
Lysimachia thyrsiflora	--	--	--	4 (0.1)	14 (0.1)	--	35 (0.3)	5 (0.1)	--	--	--

[1] non-native species are in italics

Appendix H4. (continued)[1]

Species[1]	Ecosystem Type 3										Ecosystem Type 4
	Vanderbilt Park (n = 10)	Pigeon North (n = 20)	Lakeport (n = 20)	Weale Road (n = 25)	Bay Port Swale (n = 35)	Gotham Road (n = 15)	Kirk Road (n = 20)	BCSP Campground (n = 20)	Bradley-ville (n = 20)	Weale Train Tracks (n = 10)	Bay Port Saturated (n = 5)
FORBS (continued)											
Maianthemum canadense	--	--	--	--	--	--	--	--	--	--	60 (0.4)
Mentha arvensis	--	--	--	--	6 (0.0)	--	--	--	--	--	--
Osmorhiza claytonii	10 (0.1)	--	--	--	--	--	--	--	--	--	--
Pilea pumila	--	--	--	--	--	--	15 (0.0)	--	--	--	--
Potamogeton spp.	--	--	--	--	--	20 (0.1)	--	--	--	--	--
Prenanthes altissima	--	--	--	--	--	--	--	--	--	--	20 (0.1)
Ranunculus abortivus	--	--	--	4 (0.0)	--	--	--	--	--	--	--
Rorippa palustris	--	--	--	--	3 (0.0)	--	--	--	--	--	--
Rubus pubescens	--	--	--	--	--	--	--	--	--	--	40 (0.8)
Scutellaria lateriflora	--	5 (0.1)	--	--	--	--	5 (0.0)	--	--	10 (0.1)	--
Sium suave	--	--	--	--	3 (0.0)	--	--	--	--	--	--
Smilacina stellata	--	--	--	--	--	--	--	--	--	--	60 (0.6)
Solanum dulcamara	30 (0.2)	--	--	--	--	--	5 (0.0)	--	--	--	--
Solanum ptycanthum	--	--	--	--	--	--	--	--	10 (0.0)	--	--
Solidago gigantea	--	--	--	--	--	--	--	--	--	--	40 (2.4)
Solidago spp.	--	5 (0.9)	--	--	--	--	--	--	--	--	40 (0.2)
Taraxacum officionale	--	--	--	--	--	--	--	--	--	--	20 (0.1)
Viola spp.	--	--	--	4 (0.0)	--	--	--	--	--	--	--
GRAMINOIDS											
Calamagrostis canadensis	--	5 (0.0)	--	--	--	--	--	--	--	--	--
Carex lacustris	--	--	--	--	17 (0.2)	7 (0.0)	--	--	--	--	--
Carex leptalea	--	--	--	--	--	--	--	--	--	--	20 (6.0)
Carex muskingumensis	--	10 (0.1)	--	--	--	--	--	--	--	--	--
Carex pedunculata	--	--	--	--	--	--	--	--	--	--	60 (0.3)
Carex stipata	--	5 (0.1)	5 (0.0)	--	3 (0.0)	--	--	--	--	10 (0.1)	--
Carex stricta	--	--	--	--	46 (3.7)	--	--	--	--	--	--
Elymus virginicus	--	--	--	--	--	--	--	--	--	10 (0.2)	--

[1] non-native species are in italics

Appendix H4. (continued)[1]

Species[1]	Ecosystem Type 3										Ecosystem Type 4
	Vanderbilt Park (n = 10)	Pigeon North (n = 20)	Lakeport (n = 20)	Weale Road (n = 25)	Bay Port Swale (n = 35)	Gotham Road (n = 15)	Kirk Road (n = 20)	BCSP Campground (n = 20)	Bradley-ville (n = 20)	Weale Train Tracks (n = 10)	Bay Port Saturated (n = 5)
GRAMINOIDS (continued)											
Glyceria striata	--	--	10 (0.2)	4 (0.0)	14 (0.1)	--	--	--	--	20 (0.3)	20 (0.2)
Phalaris arundinacea	--	--	--	--	--	7 (0.0)	5 (0.2)	--	--	--	--
FERNS											
Athyrium filix-femina	--	5 (0.3)	--	--	--	--	--	--	--	--	--

[1] non-native species are in italics

Appendix I1. Comparison of overstory species composition among seven swamp forests sampled along the southern Lake Huron shoreline in 2002 (percentages of total stem density and basal area are in parentheses).

	Ecosystem Type 3						Ecosytem Type 5
Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon South (n=15)	Wildfowl Swale (n=8)	Tobico Swamp (n=20)	Pin-conning (n=15)	Wildfowl Glade (n=12)
Acer saccharinum							
Stems/ha	250 (23)	593 (65)	307 (44)	225 (51)	185 (20)	487 (54)	33 (4)
BA (m^2/ha)	10.0 (19)	19.0 (52)	16.7 (44)	21.5 (53)	6.4 (16)	13.1 (47)	1.5 (7)
Avg dbh (cm)	20.2	20.9	22.9	30.6	20.9	17.1	22.6
Fraxinus pennsylvanica							
Stems/ha	537 (49)	215 (25)	300 (41)	381 (47)	405 (57)	267 (32)	746 (92)
BA (m^2/ha)	22.0 (47)	13.9 (38)	13.1 (41)	10.5 (41)	12.4 (50)	11.1 (36)	20.0 (90)
Avg dbh (cm)	20.9	29.5	23.9	17.6	18.8	21.2	17.2
Ulmus americana							
Stems/ha	237 (20)	53 (8)	60 (7)	6 (1)	108 (18)	7 (1)	13 (2)
BA (m^2/ha)	2.9 (6)	0.8 (2)	1.2 (4)	0.1 (0)	2.4 (14)	0.2 (1)	0.5 (2)
Avg dbh (cm)	12.1	13.0	17.5	16.7	15.2	15.4	22.8
Populus deltoides							
Stems/ha	83 (8)	--	10 (1)	--	25 (4)	43 (5)	--
BA (m^2/ha)	15.4 (26)	--	2.9 (7)	--	9.7 (20)	2.6 (9)	--
Avg dbh (cm)	49.6	--	60.4	--	65.4	24.5	--
Quercus bicolor							
Stems/ha	7 (1)	3 (0)	37 (5)	--	--	43 (7)	--
BA (m^2/ha)	0.7 (2)	0.1 (0)	1.3 (4)	--	--	1.4 (6)	--
Avg dbh (cm)	34.4	22.3	20.2	--	--	18.6	--
Fraxinus nigra							
Stems/ha	--	8 (1)	7 (1)	--	--	--	4 (1)
BA (m^2/ha)	--	0.2 (0)	0.2 (0)	--	--	--	0.0 (0)
Avg dbh (cm)	--	15.1	19.2	--	--	--	9.5
Quercus macrocarpa							
Stems/ha	--	8 (2)	--	--	--	--	13 (1)
BA (m^2/ha)	--	2.5 (7)	--	--	--	--	0.3 (1)
Avg dbh (cm)	--	68.0	--	--	--	--	14.8
Salix spp.							
Stems/ha	--	--	--	3 (1)	--	7 (1)	--
BA (m^2/ha)	--	--	--	1.9 (5)	--	0.3 (1)	--
Avg dbh (cm)	--	--	--	61.2	--	23.6	--
Tilia americana							
Stems/ha	--	--	3 (1)	--	--	--	--
BA (m^2/ha)	--	--	0.1 (0)	--	--	--	--
Avg dbh (cm)	--	--	13.4	--	--	--	--
Betula papyrifera							
Stems/ha	--	--	3 (1)	--	--	--	--
BA (m^2/ha)	--	--	0.1 (0)	--	--	--	--
Avg dbh (cm)	--	--	14.9	--	--	--	--
Populus tremuloides							
Stems/ha	--	--	--	--	3 (0)	--	--
BA (m^2/ha)	--	--	--	--	0.1 (1)	--	--
Avg dbh (cm)	--	--	--	--	26.7	--	--

Appendix I2. Comparison of large understory (1.6–9.0 cm dbh) species composition among seven swamp forests sampled along the southern Lake Huron shoreline in 2002 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 3						Ecosystem Type 5
Species	King Road (n = 15)	Wigwam Bay (n = 20)	Pigeon South (n = 15)	Wildfowl Swale (n = 8)	Tobico Swamp (n = 20)	Pin-conning (n = 15)	Wildfowl Glade (n = 12)
Fraxinus pennsylvanica	227 (22)	30 (6)	173 (30)	138 (79)	180 (44)	160 (51)	517 (99)
Ulmus americana	673 (67)	285 (58)	140 (24)	--	190 (46)	40 (13)	--
Acer saccharinum	103 (10)	143 (29)	213 (37)	38 (21)	42 (10)	103 (33)	4 (1)
Fraxinus nigra	--	20 (4)	33 (6)	--	--	--	--
Quercus bicolor	7 (1)	5 (1)	7 (1)	--	--	13 (4)	--
Thuja occidentalis	--	10 (2)	--	--	--	--	--
Carpinus caroliniana	--	--	7 (1)	--	--	--	--
TOTAL	1,010 (100)	493 (100)	573 (100)	175 (100)	413 (100)	317 (100)	521 (100)

Appendix I3. Comparison of small understory (taller than 50 cm and < 1.5 cm dbh) species composition among seven swamp forests sampled along the southern Lake Huron shoreline in 2002 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 3						Ecosytem Type 5
Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon South (n=15)	Wildfowl Swale (n=8)	Tobico Swamp (n=20)	Pin-conning (n=15)	Wildfowl Glade (n=12)
TREES							
Fraxinus pennsylvanica	340 (44)	127 (21)	120 (18)	265 (32)	10 (5)	108 (39)	13 (50)
Ulmus americana	47 (6)	27 (4)	--	5 (1)	5 (3)	8 (3)	--
Fraxinus nigra	--	67 (11)	--	--	--	--	--
Crataegus spp.	--	33 (6)	--	--	--	--	--
Acer saccharinum	10 (1)	3 (1)	3 (0)	15 (2)	--	--	--
Carpinus caroliniana	--	7 (1)	--	--	--	--	--
Quercus bicolor	--	7 (1)	--	--	--	--	--
SHRUBS							
Cornus amomum	40 (5)	33 (6)	380 (57)	130 (16)	15 (8)	125 (45)	--
Ilex verticillata	--	60 (10)	--	320 (38)	135 (71)	--	--
Cephalanthus occidentalis	293 (38)	13 (2)	--	--	--	--	13 (50)
Viburnum lentago	--	113 (19)	20 (3)	5 (1)	5 (3)	--	--
Rubus strigosus	--	--	73 (11)	--	5 (3)	8 (3)	--
Zanthoxylum americanum	--	60 (10)	--	--	--	--	--
Lonicera tatarica	--	--	--	55 (7)	--	--	--
Sambucus canadensis	--	7 (1)	33 (5)	--	5 (3)	--	--
Lindera benzoin	--	40 (7)	--	--	--	--	--
Cornus foemina	--	--	--	35 (4)	--	--	--
Rosa palustris	27 (3)	--	--	5 (1)	--	--	--
Rubus occidentalis	--	--	--	--	5 (3)	25 (9)	--
Rubus alleghaniensis	--	--	20 (3)	--	--	--	--
Ribes americana	--	--	13 (2)	--	5 (3)	--	--
Prunus virginiana	--	7 (1)	7 (1)	--	--	--	--
Spiraea alba	13 (2)	--	--	--	--	--	--
TOTALS	770 (100)	603 (100)	670 (100)	835 (100)	190 (100)	275 (100)	25 (100)

Appendix I4. Comparison of ground-cover species composition among seven swamp forests sampled along the southern Lake Huron shoreline in 2002 (values are frequency (%), average percent coverage is in parentheses).

	Ecosystem Type 3						Ecosystem Type 5
Species[1]	King Road (n = 15)	Wigwam Bay (n = 20)	Pigeon South (n = 15)	Wildfowl Swale (n = 8)	Tobico Swamp (n = 20)	Pin-conning (n = 15)	Wildfowl Glade (n = 12)
TREES							
Acer saccharinum	20 (0.8)	55 (0.6)	13 (0.3)	25 (0.4)	25 (0.9)	67 (0.9)	8 (0.8)
Fraxinus pennsylvanica	53 (3.0)	20 (0.8)	20 (0.2)	50 (5.5)	30 (1.1)	27 (0.6)	50 (0.6)
Quercus bicolor	13 (0.1)	5 (0.1)	--	--	--	13 (0.3)	--
Ulmus americana	13 (0.1)	10 (0.4)	--	13 (0.1)	--	7 (0.7)	--
TALL SHRUBS							
Cornus amomum	--	5 (0.5)	7 (0.7)	--	5 (0.8)	--	17 (0.9)
Lindera benzoin	--	--	13 (1.3)	--	--	--	--
Lonicera tatarica	--	--	--	--	10 (1.5)	--	--
SHORT SHRUBS							
Euonymus obovatus	--	--	7 (0.7)	--	--	--	--
Lonicera dioica	--	--	7 (0.7)	--	--	--	--
Ribes americanum	--	5 (0.2)	7 (0.7)	--	10 (0.1)	--	--
Ribes cynosbati	--	--	7 (0.3)	--	--	--	--
Rosa palustris	--	--	--	--	5 (0.3)	--	--
Rubus strigosus	--	--	--	13 (0.4)	--	--	8 (0.8)
WOODY VINES							
Menispermum canadense	--	--	13 (0.1)	--	--	--	--
Parthenocissus quinquefolia	7 (0.7)	--	27 (0.7)	--	5 (0.1)	--	8 (0.6)
Smilax tamnoides	--	--	--	--	--	7 (0.2)	--
Toxicodendron radicans	--	--	7 (0.7)	--	5 (0.2)	--	--
Vitis riparia	33 (0.4)	--	--	13 (0.1)	5 (0.5)	--	8 (0.8)
FORBS							
Alisma plantago-aquatica	--	--	--	--	5 (0.2)	--	--
Amphicarpaea bracteata	--	--	7 (0.7)	--	--	--	--
Arisaema triphyllum	--	--	--	13 (0.1)	5 (0.1)	--	--
Aster lateriflorus	--	25 (2.4)	27 (2.1)	13 (0.1)	20 (1.2)	20 (1.6)	--

[1] non-native species are in italics

Appendix I4. (continued)

Species[1]	Ecosystem Type 3 King Road (n = 15)	Ecosystem Type 3 Wigwam Bay (n = 20)	Ecosystem Type 3 Pigeon South (n = 15)	Ecosystem Type 3 Wildfowl Swale (n = 8)	Ecosystem Type 3 Tobico Swamp (n = 20)	Ecosystem Type 3 Pin-conning (n = 15)	Ecosystem Type 5 Wildfowl Glade (n = 12)
FORBS (continued)							
Aster novae-angliae	--	--	--	--	--	--	8 (0.8)
Bidens spp.	--	--	--	--	5 (0.5)	--	--
Boehmeria cylindrica	--	20 (1.5)	--	50 (2.1)	10 (0.5)	27 (0.5)	8 (0.7)
Cicuta maculata	--	5 (0.2)	20 (1.7)	--	50 (2.7)	--	--
Circaea alpina	--	10 (0.2)	--	--	5 (0.2)	7 (0.3)	--
Cirsium arvense	--	--	--	--	--	--	17 (0.6)
Erechtites hieraciifolia	7 (0.7)	--	--	--	--	--	--
Erigeron philadelphicus	--	--	--	13 (0.1)	--	--	--
Galium aparine	--	--	7 (0.7)	13 (0.1)	--	--	25 (0.4)
Galium triflorum	--	10 (0.1)	--	--	10 (1.5)	13 (1.0)	75 (1.8)
Geum canadense	--	5 (0.4)	7 (0.2)	--	10 (0.4)	13 (1.7)	--
Impatiens capensis	--	35 (3.1)	7 (0.1)	13 (0.1)	15 (0.6)	47 (4.3)	8 (0.4)
Laportea canadensis	--	5 (0.5)	--	--	--	--	--
Lathyrus palustris	--	--	--	--	--	--	42 (0.8)
Lemna minor	--	--	--	--	25 (0.3)	7 (0.7)	--
Lemna trisulca	--	--	--	--	35 (0.4)	--	--
Lilium michiganense	--	--	7 (0.1)	--	--	--	--
Lycopus americanus	--	5 (0.5)	--	--	--	--	--
Lycopus uniflorus	13 (0.5)	--	--	38 (0.4)	5 (0.5)	--	8 (0.8)
Lysimachia ciliata	--	--	7 (0.7)	--	--	--	--
Lysimachia nummularia	--	5 (0.5)	--	--	--	--	--
Lysimachia thyrsiflora	--	--	--	--	5 (0.1)	--	17 (0.8)
Maianthemum canadense	--	--	--	13 (0.3)	--	--	--
Mentha arvensis	--	--	--	--	5 (0.5)	--	--
Phryma leptostachya	--	--	--	--	5 (0.3)	--	--
Pilea pumila	--	15 (0.3)	--	--	--	--	--
Polygonum amphibium	--	--	--	--	--	--	17 (0.3)
Ranunculus flabellaris	--	--	--	--	5 (0.5)	--	--
Rubus pubescens	--	--	--	--	--	7 (0.3)	--
Sanicula gregaria	--	5 (0.4)	--	--	5 (1.0)	--	--

[1] non-native species are in italics

Appendix I4. (continued)

Species[1]	Ecosystem Type 3						Ecosystem Type 5
	King Road (n = 15)	Wigwam Bay (n = 20)	Pigeon South (n = 15)	Wildfowl Swale (n = 8)	Tobico Swamp (n = 20)	Pin-conning (n = 15)	Wildfowl Glade (n = 12)
FORBS (continued)							
Scutellaria galericulata	7 (0.1)	--	--	--	--	--	50 (1.8)
Scutellaria lateriflora	7 (0.8)	--	--	--	5 (0.5)	--	--
Smilacina stellata	--	5 (0.2)	7 (0.7)	--	--	--	--
Solanum dulcamara	--	15 (0.3)	--	--	20 (2.7)	13 (0.3)	--
Solidago gigantea	--	--	--	--	--	7 (0.5)	--
Thalictrum dasycarpum	--	--	7 (0.7)	--	--	7 (0.4)	--
Unknown	--	5 (0.1)	--	--	5 (0.5)	--	--
Unknown aquatic plant #1	--	--	--	--	40 (0.9)	--	--
Unknown aquatic plant #2	--	--	--	--	5 (0.5)	--	--
Urtica dioica	--	--	--	--	--	--	17 (0.3)
Viola pubescens	--	10 (0.4)	--	--	--	--	--
Viola sorroria	--	--	--	13 (0.3)	5 (0.9)	--	--
Viola spp.	--	5 (0.5)	--	--	10 (0.4)	7 (0.2)	--
Zizia aurea	--	--	--	--	5 (0.5)	--	--
GRAMINOIDS							
Calamagrostis canadensis	--	--	--	--	5 (0.3)	--	83 (24.5)
Carex amphibola	--	5 (0.3)	--	--	--	--	--
Carex blanda	--	--	7 (0.7)	--	--	--	--
Carex gracillima	--	10 (0.3)	--	--	--	--	--
Carex intumescens	--	--	13 (0.2)	--	--	--	--
Carex lacustris	--	--	--	--	10 (4.4)	27 (2.7)	75 (6.0)
Carex muskingumensis	--	--	7 (0.2)	--	5 (0.5)	--	--
Carex oligosperma	--	10 (0.4)	--	--	--	--	--
Carex spp. # 1	--	5 (0.3)	--	--	5 (0.5)	--	--
Carex spp. # 2	--	--	--	--	5 (0.5)	20 (2.5)	8 (6.3)
Carex stipata	--	10 (0.6)	--	--	15 (0.4)	--	--
Carex stricta	--	--	--	--	--	--	75 (8.2)
Elymus virginicus	--	20 (0.4)	20 (0.6)	--	10 (4.0)	--	--
Glyceria striata	--	55 (11.5)	13 (0.9)	13 (5.0)	20 (6.5)	33 (5.7)	8 (0.6)

[1] non-native species are in italics

Appendix I4. (continued)

	Ecosystem Type 3						Ecosystem Type 5
Species[1]	King Road (n = 15)	Wigwam Bay (n = 20)	Pigeon South (n = 15)	Wildfowl Swale (n = 8)	Tobico Swamp (n = 20)	Pin-conning (n = 15)	Wildfowl Glade (n = 12)
GRAMINOIDS (continued)							
Juncus balticus	--	--	--	--	--	13 (1.4)	--
Phalaris arundinacea	--	--	--	--	--	--	8 (1.3)
FERNS							
Athyrium filix-femina	--	--	--	13 (0.3)	--	--	--
Dryopteris cristata	20 (1.3)	--	--	--	--	--	--
Equisetum fluviatile	--	--	--	--	5 (0.5)	--	--
Onoclea sensibilis	--	15 (1.8)	--	--	--	--	8 (2.8)
Osmunda regalis	--	--	--	--	--	7 (0.7)	--
Thelypteris palustris	--	5 (0.1)	--	--	--	7 (0.1)	8 (0.2)

[1] non-native species are in italics

Appendix J1. Comparison of overstory species composition among eight swamp forests sampled along the eastern Lake Michigan shoreline in 2003 (percentages of total stem density and basal area are in parentheses).

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species	Betsie River (n = 20)	Manistee River (n = 20)	Pere Marquette River (n = 15)	Big Sable River (n = 4)	Manistee River (n = 4)	Betsie River (n = 4)	Muskegon River (n = 20)	Kalamazoo River (n = 20)
Fraxinus pennsylvanica								
Stems/ha	702 (72)	508 (88)	240 (46)	--	25 (2)	88 (7)	183 (42)	103 (16)
BA (m^2/ha)	17.9 (72)	17.5 (62)	9.8 (43)	--	0.8 (2)	3.1 (9)	4.3 (16)	11.4 (25)
Avg dbh (cm)	16.6	19.2	20.4	--	19.2	19.2	16.5	32.1
Acer saccharinum								
Stems/ha	120 (12)	50 (9)	270 (48)	--	--	--	205 (54)	500 (74)
BA (m^2/ha)	4.8 (18)	10.1 (36)	15.0 (55)	--	--	--	40.8 (82)	32.0 (71)
Avg dbh (cm)	19.0	43.8	24.1	--	--	--	43.2	24.9
Ulmus americana								
Stems/ha	5 (1)	2 (0)	13 (2)	--	--	25 (2)	25 (4)	45 (7)
BA (m^2/ha)	0.1 (0)	0.0 (0)	0.2 (1)	--	--	0.3 (1)	0.6 (2)	1.1 (2)
Avg dbh (cm)	13.0	12	13.8	--	--	12.3	17.0	17.0
Thuja occidentalis								
Stems/ha	13 (1)	--	--	663 (44)	925 (79)	750 (62)	--	--
BA (m^2/ha)	0.2 (1)	--	--	14.4 (28)	29.2 (78)	25.9 (69)	--	--
Avg dbh (cm)	13.7	--	--	16.1	18.9	20.1	--	--
Fraxinus nigra								
Stems/ha	118 (12)	12 (2)	20 (4)	200 (12)	75 (7)	225 (16)	--	--
BA (m^2/ha)	1.9 (8)	0.4 (1)	0.3 (1)	5.0 (9)	0.8 (2)	5.0 (12)	--	--
Avg dbh (cm)	13.3	17.3	12.9	17.3	11.5	15.9	--	--
Acer rubrum								
Stems/ha	--	--	--	163 (12)	113 (8)	13 (1)	--	--
BA (m^2/ha)	--	--	--	7.8 (15)	4.9 (11)	0.4 (1)	--	--
Avg dbh (cm)	--	--	--	24.3	22.4	19.1	--	--
Betula alleghaniensis								
Stems/ha	3 (0)	--	--	113 (7)	--	88 (7)	--	--
BA (m^2/ha)	0.1 (0)	--	--	3.6 (7)	--	1.8 (5)	--	--
Avg dbh (cm)	27.2	--	--	19.1	--	15.8	--	--

Appendix J1. (continued)

Species	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
	Betsie River (n = 20)	Manistee River (n = 20)	Pere Marquette River (n = 15)	Big Sable River (n = 4)	Manistee River (n = 4)	Betsie River (n = 4)	Muskegon River (n = 20)	Kalamazoo River (n = 20)
Betula papyrifera								
Stems/ha	--	--	--	--	13 (1)	38 (3)	--	--
BA (m^2/ha)	--	--	--	--	0.6 (1)	1.1 (3)	--	--
Avg dbh (cm)	--	--	--	--	24.0	18.6	--	--
Larix laricina								
Stems/ha	--	--	--	50 (2)	--	13 (1)	--	--
BA (m^2/ha)	--	--	--	2.8 (5)	--	0.2 (0)	--	--
Avg dbh (cm)	--	--	--	26.6	--	14.8	--	--
Tsuga canadensis								
Stems/ha	--	--	--	325 (23)	50 (4)	--	--	--
BA (m^2/ha)	--	--	--	18.5 (36)	3.4 (7)	--	--	--
Avg dbh (cm)	--	--	--	25.0	26.0	--	--	--
Tilia americana								
Stems/ha	8 (1)	--	--	--	--	13 (1)	--	--
BA (m^2/ha)	0.1 (0)	--	--	--	--	0.2 (1)	--	--
Avg dbh (cm)	10.9	--	--	--	--	15.0	--	--
Alnus rugosa								
Stems/ha	5 (0)	--	--	--	--	--	--	--
BA (m^2/ha)	0.0 (0)	--	--	--	--	--	--	--
Avg dbh (cm)	10.3	--	--	--	--	--	--	--
Cephalanthus occidentalis								
Stems/ha	--	--	3 (0)	--	--	--	--	--
BA (m^2/ha)	--	--	0.0 (0)	--	--	--	--	--
Avg dbh (cm)	--	--	9.4	--	--	--	--	--
Viburnum lentago								
Stems/ha	3 (0)	3 (1)	--	--	--	--	--	--
BA (m^2/ha)	0.0 (0)	0.0 (0)	--	--	--	--	--	--
Avg dbh (cm)	9.7	10	--	--	--	--	--	--

Appendix J2. Comparison of large understory (1.6–9.0 cm dbh) species composition among eight swamp forests sampled along the eastern Lake Michigan shoreline in 2003 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species	Betsie River (n = 20)	Manistee River (n = 20)	Pere Marquette River (n = 15)	Big Sable River (n = 4)	Manistee River (n = 4)	Betsie River (n = 4)	Muskegon River (n = 20)	Kalamazoo River (n = 20)
TREES								
Fraxinus pennsylvanica	1,110 (33)	430 (41)	73 (19)	--	275 (21)	425 (20)	50 (25)	40 (13)
Acer saccharinum	120 (4)	--	80 (21)	--	--	--	10 (5)	140 (44)
Ulmus americana	10 (0)	--	7 (2)	--	--	25 (1)	10 (5)	25 (8)
Fraxinus nigra	160 (5)	20 (2)	--	--	150 (12)	725 (35)	--	--
Carpinus caroliniana	--	--	--	--	--	--	--	--
Tilia americana	20 (1)	--	--	--	--	--	--	--
Thuja occidentalis	10 (0)	--	--	250 (83)	100 (8)	700 (34)	--	--
Tsuga canadensis	--	--	--	25 (8)	50 (4)	--	--	--
Acer spicatum	--	--	--	--	--	75 (4)	--	--
Betula alleghaniensis	--	--	--	25 (8)	--	--	--	--
SHRUBS								
Alnus rugosa	770 (23)	473 (45)	133 (34)	--	725 (56)	--	--	--
Cornus amomum	425 (12)	97 (9)	--	--	--	--	--	--
Viburnum lentago	205 (6)	13 (1)	7 (2)	--	--	--	--	--
Vitis riparia	25 (1)	7 (1)	27 (7)	--	--	125 (6)	80 (40)	95 (30)
Cephalanthus occidentalis	--	--	47 (12)	--	--	--	50 (25)	--
Ilex verticillata	340 (10)	--	13 (3)	--	--	--	--	--
Cornus foemina	10 (0)	20 (2)	--	--	--	--	--	--
Toxicodendron radicans	--	--	--	--	--	--	--	20 (6)
Cornus stolonifera	130 (4)	--	--	--	--	--	--	--
Sambucus canadensis	24 (1)	--	--	--	--	--	--	--
Viburnum trilobum	20 (1)	--	--	--	--	--	--	--
Rosa palustris	20 (1)	--	--	--	--	--	--	--
TOTAL	3,404 (100)	1,060 (100)	387 (100)	300 (100)	1,300 (100)	2,075 (100)	200 (100)	320 (100)

Appendix J3. Comparison of small understory (taller than 50 cm and < 1.5 cm dbh) species composition among eight swamp forests sampled along the eastern Lake Michigan shoreline in 2003 (values are stems/ha, percentage of total stem density is in parentheses).

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species	Betsie (n = 20)	Manistee (n = 20)	Pere Marquette (n = 15)	Big Sable (n = 4)	Manistee (n = 4)	Betsie (n = 4)	Muskegon (n = 20)	Kalamazoo (n = 20)
TREES								
Fraxinus pennsylvanica	480 (25)	27 (3)	7 (4)	--	25 (1)	1,375 (40)	--	150 (38)
Acer saccharinum	5 (0)	--	--	--	--	--	--	15 (4)
Ulmus americana	5 (0)	--	--	--	--	--	--	5 (1)
Fraxinus nigra	--	--	--	--	--	1,175 (34)	--	--
Thuja occidentalis	--	--	--	--	--	450 (13)	--	--
Larix laricina	--	--	--	--	550 (23)	--	--	--
Betula alleghaniensis	--	--	--	--	--	50 (1)	--	--
Pinus strobus	--	--	--	50 (25)	--	--	--	--
Acer rubrum	--	--	--	--	--	25 (1)	--	--
Acer spicatum	--	--	--	--	--	25 (1)	--	--
Fagus grandifolia	--	--	--	150 (75)	--	--	--	--
SHRUBS								
Alnus rugosa	495 (26)	470 (56)	140 (81)	--	1,425 (60)	--	--	--
Cephalanthus occidentalis	--	10 (1)	27 (15)	--	--	--	225 (100)	180 (46)
Cornus amomum	500 (26)	80 (10)	--	--	--	--	--	--
Ilex verticillata	170 (9)	--	--	--	--	50 (1)	--	--
Cornus stolonifera	65 (3)	--	--	--	--	50 (1)	--	--
Berberis thunbergii	--	147 (18)	--	--	325 (14)	--	--	--
Ribes americana	5 (0)	--	--	--	--	100 (3)	--	--
Rubus strigosus	--	--	--	--	--	100 (3)	--	--
Viburnum lentago	65 (3)	--	--	--	--	--	--	--
Vitis riparia	20 (1)	20 (2)	--	--	--	25 (1)	--	--
Sambucus canadensis	33 (2)	--	--	--	25 (1)	--	--	--
Rosa palustris	35 (2)	--	--	--	--	--	--	--
Prunus virginiana	--	--	--	--	--	25 (1)	--	--
Lonicera tatarica	--	80 (10)	--	--	--	--	--	--
Lindera benzoin	--	--	--	--	25 (1)	--	--	--
Parthenocissus quinquefolia	15 (1)	3 (0)	--	--	--	--	--	--
Rosa multiflora	--	--	--	--	--	--	--	20 (5)
Toxicodendron radicans	--	--	--	--	--	--	--	20 (5)
Viburnum trilobum	5 (0)	--	--	--	--	--	--	--
TOTAL	1,898 (100)	837 (100)	173 (100)	200 (100)	2,375 (100)	3,450 (100)	225 (100)	390 (100)

Appendix J4. Comparison of ground-cover species composition among eight swamp forests sampled along the eastern Lake Michigan shoreline in 2003 (values are frequency (%), average percent coverage is in parentheses).

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species[1]	Betsie River (n = 100)	Manistee River (n = 150)	Pere Marquette River (n = 75)	Betsie River (n = 20)	Manistee River (n = 20)	Big Sable River (n = 20)	Muskegon River (n = 100)	Kalamazoo River (n = 100)
TREES								
Acer rubrum	--	--	--	5 (0.5)	65 (0.7)	75 (0.8)	--	--
Acer saccharinum	12 (0.2)	27 (0.3)	1 (0.1)	--	--	--	27 (0.3)	25 (0.3)
Betula alleghaniensis	--	--	--	5 (0.5)	--	20 (0.2)	--	--
Betula papyrifera	--	--	--	--	25 (0.3)	5 (0.5)	--	--
Fraxinus nigra	--	--	--	35 (1.3)	--	5 (0.5)	--	--
Fraxinus pennsylvanica	16 (0.4)	15 (0.2)	8 (0.8)	10 (0.2)	50 (0.6)	15 (0.3)	6 (0.7)	10 (0.2)
Larix laricina	--	--	--	--	5 (0.1)	--	--	--
Pinus strobus	--	--	--	--	--	15 (0.2)	--	--
Prunus serotina	--	--	--	5 (0.5)	--	30 (0.3)	--	--
Quercus rubra	--	1 (0.7)	--	--	15 (0.2)	40 (0.4)	--	--
Quercus velutina	--	--	--	--	--	10 (0.1)	--	--
Thuja occidentalis	--	--	--	20 (1.0)	15 (0.2)	10 (0.1)	--	--
Tsuga canadensis	--	--	--	--	5 (0.5)	50 (0.6)	--	--
Ulmus americana	6 (0.1)	1 (0.7)	3 (0.3)	5 (0.5)	--	--	6 (0.6)	17 (0.2)
TALL SHRUBS								
Acer spicatum	--	--	--	30 (0.4)	15 (0.2)	--	--	--
Alnus rugosa	4 (0.4)	3 (0.3)	1 (0.4)	--	10 (0.2)	5 (0.5)	--	--
Amelanchier spp.	--	--	--	--	5 (0.5)	5 (0.5)	--	--
Cephalanthus occidentalis	--	1 (0.3)	--	--	--	--	3 (0.4)	3 (0.1)
Cornus amomum	13 (1.1)	5 (0.1)	--	--	--	--	--	--
Cornus stolonifera	2 (0.2)	--	--	35 (0.7)	--	--	--	--
Elaeagnus umbellata	--	--	--	--	--	5 (0.1)	--	--
Ilex verticillata	6 (0.3)	--	--	5 (0.5)	--	5 (0.5)	--	--
Lindera benzoin	--	--	--	--	10 (0.3)	20 (0.2)	--	1 (0.1)
Lonicera canadensis	--	1 (0.7)	--	15 (0.2)	5 (0.1)	--	--	--
Sambucus canadensis	7 (0.2)	4 (0.3)	--	--	--	--	--	1 (0.2)
Viburnum lentago	2 (0.3)	1 (0.2)	--	--	--	--	--	--
Viburnum trilobum	1 (0.6)	--	--	--	5 (0.1)	--	--	--

[1] non-native species are in italics

Appendix J4. (continued)

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species[1]	Betsie River (n = 100)	Manistee River (n = 150)	Pere Marquette River (n = 75)	Betsie River (n = 20)	Manistee River (n = 20)	Big Sable River (n = 20)	Muskegon River (n = 100)	Kalamazoo River (n = 100)
SHORT SHRUBS								
Berberis thunbergii	--	2 (0.9)	--	--	25 (0.4)	--	--	--
Ribes americanum	5 (0.1)	--	--	15 (0.3)	--	--	--	--
Ribes cynosbati	--	--	--	5 (0.1)	--	--	--	--
Rosa multiflora	--	--	--	--	--	--	--	1 (0.2)
Rosa palustris	4 (0.1)	--	--	--	--	--	--	--
Vaccinium myrtilloides	--	--	--	--	--	5 (0.1)	--	--
WOODY VINES								
Parthenocissus quinquefolia	8 (0.1)	13 (0.3)	--	5 (0.5)	5 (0.1)	--	2 (0.2)	--
Toxicodendron radicans	--	10 (0.2)	5 (0.5)	--	--	--	23 (0.3)	37 (0.8)
Vitis riparia	3 (0.5)	7 (0.5)	8 (0.9)	--	--	--	6 (0.8)	10 (0.1)
FORBS								
Amphicarpaea bracteata	--	4 (0.2)	--	--	--	--	--	--
Anemone canadensis	22 (0.4)	15 (0.9)	--	--	--	--	--	8 (0.1)
Aralia nudicaulis	--	--	--	20 (0.4)	15 (0.3)	--	--	--
Arisaema dracontium	--	--	--	--	--	--	--	1 (0.3)
Arisaema triphyllum	--	--	--	10 (0.2)	10 (0.2)	--	--	2 (0.2)
Asclepias incarnata	--	1 (0.1)	--	--	--	--	--	--
Asclepias syriaca	--	5 (0.5)	--	--	--	--	--	--
Aster ciliolatus	--	--	--	--	--	5 (0.5)	--	--
Aster lateriflorus	14 (0.6)	23 (0.7)	--	35 (0.4)	25 (0.4)	30 (0.4)	7 (0.1)	50 (2.2)
Aster macrophyllus	--	--	--	10 (0.2)	--	--	--	--
Barbarea vulgaris	--	1 (0.5)	--	--	--	--	--	--
Bidens connatus	--	--	--	--	5 (0.1)	25 (0.4)	--	--
Bidens coronata	--	--	--	--	5 (0.5)	--	--	--
Bidens frondosus	--	--	--	--	--	5 (0.1)	--	--
Boehmeria cylindrica	38 (1.4)	57 (3.5)	32 (2.6)	--	--	--	71 (8.9)	71 (8.4)
Calla palustris	1 (0.2)	--	--	--	--	--	--	--
Campanula aparinoides	--	1 (0.1)	--	--	--	--	--	--

[1] non-native species are in italics

Appendix J4. (continued)

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species[1]	Betsie River (n = 100)	Manistee River (n = 150)	Pere Marquette River (n = 75)	Betsie River (n = 20)	Manistee River (n = 20)	Big Sable River (n = 20)	Muskegon River (n = 100)	Kalamazoo River (n = 100)
FORBS (continued)								
Chelone glabra	--	2 (0.3)	--	--	--	--	--	--
Cicuta bulbifera	--	2 (0.2)	--	--	--	--	--	--
Cicuta maculata	--	1 (0.2)	--	--	5 (0.2)	--	--	--
Circaea alpina	--	--	--	5 (0.5)	10 (0.1)	--	--	--
Circaea lutetiana	--	1 (0.5)	--	10 (0.2)	--	--	--	--
Cirsium arvense	--	3 (0.7)	--	--	--	--	--	--
Cirsium muticum	--	--	--	5 (0.5)	--	--	--	--
Clematis virginiana	--	--	--	45 (1.5)	10 (0.2)	--	--	--
Convolvulus arvensis	--	1 (0.7)	--	--	--	--	--	--
Coptis trifolia	--	--	--	--	75 (2.9)	60 (5.5)	--	--
Cornus canadensis	--	--	--	10 (0.2)	--	--	--	--
Cryptotaenia canadensis	--	--	--	--	--	--	--	2 (0.6)
Cuscuta gronovii	--	--	--	--	--	--	--	2 (0.3)
Cypripedium calceolus	--	--	--	--	--	5 (0.5)	--	--
Echinocystis lobata	--	--	--	--	--	--	(0.1)	--
Epilobium sp.	--	1 (0.7)	--	--	--	5 (0.5)	--	--
Erechtites hieraciifolia	--	1 (0.2)	--	--	--	--	--	--
Eupatorium maculatum	2 (0.8)	1 (0.4)	--	--	5 (0.1)	--	--	--
Fragaria virginiana	--	--	--	50 (0.8)	5 (0.1)	--	--	--
Galium triflorum	--	19 (0.4)	--	20 (0.2)	60 (0.8)	45 (0.7)	--	--
Geum canadense	--	3 (0.1)	--	10 (0.2)	--	--	--	1 (0.2)
Glechoma hederacea	--	--	--	--	--	--	2 (0.5)	1 (0.2)
Hackelia virginiana	--	1 (0.5)	--	--	--	--	--	--
Impatiens capensis	3 (0.6)	17 (0.4)	1 (0.3)	25 (1.8)	--	--	4 (0.1)	1 (0.1)
Irisi virginica	16 (0.6)	14 (0.9)	1 (0.8)	--	--	--	1 (0.1)	2 (0.3)
Laportea canadensis	2 (0.9)	7 (0.3)	--	--	--	--	5 (0.9)	30 (2.0)
Lathyrus palustris	--	--	--	--	10 (0.1)	--	--	--
Lemna minor	1 (0.3)	5 (0.2)	--	--	--	--	--	--
Linnaea borealis	--	--	--	--	5 (0.5)	--	--	--

[1] non-native species are in italics

Appendix J4. (continued)

Species[1]	Ecosystem Type 6: Betsie River (n = 100)	Ecosystem Type 6: Manistee River (n = 150)	Ecosystem Type 6: Pere Marquette River (n = 75)	Ecosystem Type 7: Betsie River (n = 20)	Ecosystem Type 7: Manistee River (n = 20)	Ecosystem Type 7: Big Sable River (n = 20)	Ecosystem Type 8: Muskegon River (n = 100)	Ecosystem Type 8: Kalamazoo River (n = 100)
FORBS (continued)								
Lycopus americanus	--	--	--	--	5 (0.1)	--	--	--
Lycopus uniflorus	7 (0.2)	15 (0.2)	1 (0.3)	5 (0.1)	45 (1.3)	25 (0.4)	1 (0.1)	4 (0.1)
Lysimachia ciliata	3 (0.6)	5 (0.3)	--	15 (0.4)	50 (1.1)	10 (0.2)	--	30 (0.8)
Lysimachia nummularia	--	7 (1.7)	--	--	--	--	2 (0.2)	40 (7.8)
Lysimachia thyrsiflora	3 (0.6)	11 (0.3)	--	--	20 (0.5)	--	--	--
Maianthemum canadense	--	--	--	40 (0.5)	70 (0.8)	45 (0.6)	--	--
Mentha arvensis	2 (0.6)	7 (0.3)	--	--	--	--	--	--
Mitchella repens	--	--	--	10 (0.1)	--	5 (0.5)	--	--
Mitella diphylla	--	--	--	65 (1.4)	--	--	--	--
Mitella nuda	--	--	--	60 (1.1)	60 (1.4)	55 (2.5)	--	--
Myosotis scorpioides	18 (1.6)	11 (1.4)	--	--	--	--	20 (2.3)	--
Peltandra virginica	--	--	7 (0.2)	--	--	--	36 (1.9)	6 (0.2)
Physostegia virginiana	--	--	--	--	--	--	--	13 (0.3)
Pilea fontana	--	--	--	--	--	--	--	11 (0.4)
Pilea pumila	5 (0.6)	23 (0.5)	15 (0.2)	5 (0.5)	--	10 (0.7)	32 (0.6)	10 (0.3)
Polygala paucifolia	--	--	--	--	--	15 (0.2)	--	--
Polygonum amphibium	--	1 (0.1)	--	--	--	--	--	--
Polygonum hydropiperoides	3 (0.5)	1 (0.2)	--	--	--	--	--	--
Prenanthes	--	--	--	--	5 (0.1)	--	--	--
Prunella vulgaris	--	--	--	5 (0.5)	--	10 (0.2)	--	--
Pyrola asarifolia	--	--	--	--	--	35 (0.5)	--	--
Ranunculus hispidus	--	1 (0.1)	--	--	--	--	--	1 (0.1)
Ranunculus recurvatus	1 (0.3)	--	--	--	--	10 (0.2)	--	--
Rubus pubescens	3 (0.4)	1 (0.1)	--	95 (3.0)	60 (1.6)	35 (0.6)	--	--
Rumex orbiculata	--	1 (0.5)	--	--	--	--	--	--
Sagittaria latifolia	--	--	--	--	--	--	2 (0.6)	--
Sanicula gregaria	--	--	--	--	--	--	--	1 (0.1)
Saururus cernuus	--	--	32 (2.5)	--	--	--	46 (7.8)	43 (6.2)
Scutellaria galericulata	--	12 (0.4)	--	--	--	--	--	--

[1] non-native species are in italics

Appendix J4. (continued)

Species[1]	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
	Betsie River (n = 100)	Manistee River (n = 150)	Pere Marquette River (n = 75)	Betsie River (n = 20)	Manistee River (n = 20)	Big Sable River (n = 20)	Muskegon River (n = 100)	Kalamazoo River (n = 100)
FORBS (continued)								
Scutellaria lateriflora	1 (0.1)	9 (0.5)	--	--	25 (0.3)	20 (0.3)	8 (0.1)	11 (0.3)
Sium suave	4 (0.1)	1 (0.7)	--	--	--	--	--	--
Smilacina stellata	--	--	--	20 (0.3)	--	--	--	--
Solanum dulcamara	29 (1.1)	7 (0.1)	1 (0.1)	10 (0.1)	--	--	10 (0.1)	--
Solidago altissima	--	--	--	--	5 (0.1)	--	--	--
Solidago canadensis	--	--	--	10 (0.3)	--	--	--	--
Solidago flexicaulis	--	--	--	5 (0.1)	--	--	--	--
Solidago gigantea	3 (0.2)	1 (0.4)	--	10 (0.2)	5 (0.1)	--	--	--
Solidago patula	--	--	--	35 (0.7)	20 (0.3)	--	--	--
Solidago rugosa	--	--	--	5 (0.1)	25 (0.5)	--	--	--
Symplocarpus foetidus	--	44 (7.6)	41 (5.7)	--	25 (0.4)	--	1 (0.3)	--
Taraxacum officionale	--	--	--	--	--	5 (0.1)	--	1 (0.1)
Thalictrum dasycarpum	2 (0.4)	5 (0.2)	--	--	--	--	--	--
Trientalis borealis	--	--	--	10 (0.1)	10 (0.1)	25 (0.3)	--	--
Trillium grandiflora	--	--	--	--	10 (0.1)	--	--	--
Urtica dioica	--	6 (0.3)	--	--	--	--	2 (0.3)	--
Veronica officionalis	--	--	--	5 (0.2)	--	--	--	1 (0.6)
Viola spp.	6 (0.9)	13 (0.2)	4 (0.7)	--	50 (0.9)	40 (0.5)	2 (0.2)	15 (0.3)
GRAMINOIDS								
Brachyeletrum erectum	--	--	--	--	5 (0.2)	--	--	--
Calamagrostis canadensis	37 (7.7)	25 (5.2)	--	--	--	--	--	2 (0.3)
Carex arctata	--	--	--	--	5 (0.2)	40 (1.9)	--	--
Carex bebbii	2 (0.3)	11 (0.7)	--	--	--	--	--	--
Carex eburnea	--	--	--	--	25 (1.2)	5 (0.2)	--	--
Carex gracillima	--	--	--	50 (1.1)	25 (0.3)	--	--	--
Carex grayi	--	--	--	--	--	--	--	3 (0.6)
Carex intumescens	3 (0.7)	4 (0.4)	--	--	--	15 (0.3)	--	--
Carex lacustris	80 (21.9)	66 (26.8)	12 (1.4)	--	25 (0.7)	--	1 (0.3)	--
Carex leptalea	--	--	--	--	--	15 (4.7)	--	--

[1] non-native species are in italics

Appendix J4. (continued)

	Ecosystem Type 6			Ecosystem Type 7			Ecosystem Type 8	
Species[1]	Betsie River (n = 100)	Manistee River (n = 150)	Pere Marquette River (n = 75)	Betsie River (n = 20)	Manistee River (n = 20)	Big Sable River (n = 20)	Muskegon River (n = 100)	Kalamazoo River (n = 100)
GRAMINOIDS (continued)								
Carex pedunculata	--	--	--	5 (0.1)	--	25 (0.7)	--	--
Carex stipata	1 (0.1)	8 (0.8)	--	--	--	--	--	--
Carex stricta	25 (7.5)	19 (2.7)	--	--	--	--	--	--
Carex trisperma	--	--	--	10 (0.2)	5 (0.1)	25 (4.3)	--	--
Carex vulpinoidea	--	1 (0.3)	--	--	--	--	--	--
Cinna arundinacea	--	--	--	--	--	10 (0.1)	--	5 (0.8)
Elymus virginicus	3 (0.8)	14 (2.9)	--	--	--	--	--	2 (0.3)
Glyceria canadensis	--	1 (0.1)	--	--	--	--	--	--
Glyceria striata	9 (0.5)	7 (1.2)	1 (0.3)	45 (5.6)	20 (0.3)	15 (0.2)	--	--
Leersia oryzoides	2 (0.8)	19 (2.8)	--	--	40 (1.2)	--	19 (2.4)	27 (0.7)
Panicum spp.	1 (0.1)	1 (0.1)	--	--	--	10 (0.1)	--	--
Phalaris arundinacea	2 (0.1)	35 (4.8)	100 (62.7)	--	--	--	89 (39.6)	2 (0.6)
Scirpus atrovirens	--	1 (0.3)	--	--	--	--	--	--
Unknown grass	--	1 (0.2)	--	--	--	--	--	--
FERNS								
Athyrium filix-femina	--	--	1 (0.4)	25 (2.2)	5 (0.2)	--	--	--
Botrichyium virginianum	--	--	--	--	5 (0.5)	--	--	--
Dryopteris cristata	--	--	--	15 (0.4)	50 (2.3)	5 (0.2)	--	--
Equisetum arvense	--	1 (0.3)	--	50 (2.1)	30 (0.8)	--	--	--
Gymnocarpium dryopteris	--	--	--	10 (0.2)	10 (0.3)	35 (1.7)	--	--
Matteuccia struthiopteris	--	--	3 (0.9)	--	--	--	--	--
Onoclea sensibilis	60 (18.6)	2 (0.2)	--	45 (6.3)	40 (2.9)	15 (0.2)	--	3 (0.9)
Osmunda cinnamomea	--	--	--	5 (0.1)	65 (25.5)	80 (23.2)	--	--
Osmunda regalis	--	--	--	--	5 (0.1)	5 (0.1)	--	--
Thelypteris palustris	--	1 (0.7)	--	25 (0.5)	20 (0.6)	25 (0.6)	--	--

[1] non-native species are in italics