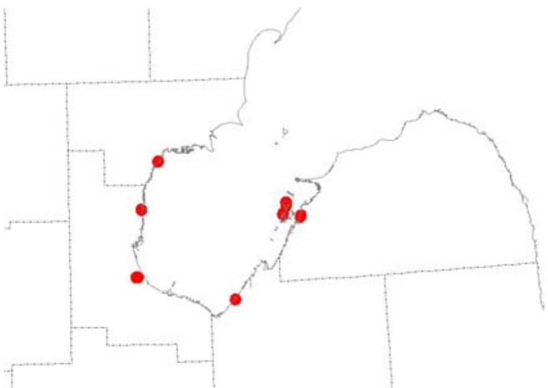
Swamp Forests of the Lake Huron Shoreline



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ABSTRACT

Although much of the Lake Huron shoreline was historically lined with swamp forests, many of the coastal swamp forests have been lost over the last 150 years through drainage or conversion to other wetland types as a result of intensive logging followed by agricultural and urban development. The loss of the historical swamp forests is most apparent along the southern part of the shoreline, where much of the landscape is under agricultural land cover. However, many coastal swamps remain in the northern part of the shoreline, where much of the landscape is forested. While numerous studies have been conducted in swamp forests of Michigan, data specific to the coastal swamp forests is lacking. The collection and analysis of baseline data specific to coastal swamp forests is needed to interpret trends in the composition and structure of their vegetation in relation to gradients in soil, hydrology, climate, and disturbance, thereby providing a sound basis for restoration activities along the shoreline. Therefore, in order to characterize the coastal swamp forests, including their hydrology, soil, vegetation, and landscape context, a total of 235 sample plots were established in 15 coastal swamps. Study sites were selected in Saginaw Bay, Alpena County, and the Les Cheneaux Islands and adjacent mainland to characterize the southern, central, and northern parts of the shoreline. All swamp forests of Saginaw Bay were dominated by hardwoods, while all but one of the swamps in Alpena County was dominated by conifers, and all swamps of the Les Cheneaux Islands were dominated by conifers. The hydrologic regime of the coastal swamps of Saginaw Bay, excluding a bedrock-influenced site on the islands of Wildfowl Bay, was characterized by complete inundation of the soil surface early in the growing season followed by a draw down of water below the soil surface later in the growing season. The substrate of all Saginaw Bay coastal swamps was mineral soil, and the soil pH was neutral at the surface and it became calcareous within the upper 100 cm. The major overstory dominants of the Saginaw Bay swamps were silver maple (*Acer saccharinum*) and red ash (*Fraxinus pennsylvanica*), with lesser amounts of American elm (*Ulmus americana*) and eastern cottonwood (*Populus deltoides*). Shrubs and small-tree-species were a minor component of the understory. The diversity and coverage of the ground-cover vegetation were relatively low due to inundation of the soil surface in combination with relatively high canopy coverage. In contrast to the coastal swamps of Saginaw Bay, the soil surface of the swamp forests of Alpena County and the Les Cheneaux Islands was saturated rather than inundated, and standing water was recorded only in small depressions. The only northern site where a large portion of the soil surface was inundated was a hardwood-dominated swamp in Alpena County, which was most likely historically a non-forested wetland. The substrate of all swamps of Alpena County and the Les Cheneaux Islands was sapric muck. As in Saginaw Bay, the soil pH was neutral at the surface and it became calcareous within the upper 100 cm. However, the soil pH was strongly acid (below 5.0) on hummocks within the northern swamps. In all conifer-dominated swamps of Alpena County and the Les Cheneaux Islands, northern white-cedar (*Thuja occidentalis*) was the dominant overstory species. Additional overstory species include balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*). Red ash was the dominant species of the hardwood-dominated site in Alpena County. Shrubs were a minor component of all northern swamps except the hardwood-dominated site, where speckled alder (*Alnus rugosa*) was abundant. An analysis of the land cover surrounding each of the study sites revealed a trend of decreasing agricultural cover and increasing forest cover from south to north. Although urban and agricultural land cover accounted for 26-79% of the land cover within 1 km of the study sites on the mainland of Saginaw Bay, their vegetation was not markedly different from that of similar sites on islands in Saginaw Bay, where there was no urban or agricultural land cover. To a large extent, the combined influence of inundation of the soil surface and relatively high canopy coverage prohibit many species from becoming established in the swamps, thereby minimizing the disturbance resulting from non-natural land cover adjacent to the swamps. Because the Saginaw Bay swamps were dominated by fast-growing tree species and few non-native species were present, restoration efforts mat be successful with a relatively low amount of effort. In Alpena County and the Les Cheneaux Islands, urban and agricultural land cover accounted for only 2-7% of the land cover within 1 km of the swamps, and the present vegetation was similar to the *circa* 1800 vegetation, as inferred from General Land Office survey records. However, due to excessive browsing by deer, the density of northern white-cedar seedlings was low in all swamps of Alpena County and the Les Cheneaux Islands. The lack of northern white-cedar regeneration may interfere with the long-term stability of these swamps.

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INTRODUCTION

An interpretation of General Land Office (GLO) survey records indicates that forested wetlands covered 15.4% of the state in the early part of the 19th century (Comer et al. 1995). At the time of the surveys, conifer-dominated swamps accounted for 97% of the forested wetland area, and hardwood-dominated swamps accounted for 3%. However, with intensive logging, agricultural development, mining, road construction, and urban development over the last 150 years, two-thirds of the conifer swamp coverage has been lost, either by drainage or conversion to other wetland types (Comer 1996). While the areal coverage of hardwood-dominated swamps has increased since the time of the surveys, primarily due primarily due to the conversion of other wetland types, the increase far from offsets the extraordinary loss of conifer-dominated swamps, and the total loss forested wetlands is high.

The loss of swamp forests is especially apparent along the shore of Lake Huron, where swamp forests once occupied a characteristic position inland of coastal marshes and adjacent to upland forests along much of the shoreline, from Saginaw Bay to the Upper Peninsula. Along the southern part of the shoreline, where extensive swamp forests once occupied much of the broad, flat, poorly drained terrain of the glacial lake plain, nearly all of the forests have been cleared to enable agricultural use of the land. The few remaining coastal swamp forests are relatively small in size and they are often surrounded by highly intensive land use. Farther north, agricultural land cover is less abundant, and a greater proportion of the swamp forests remain. In parts of the northern Lower Peninsula and the Upper Peninsula, coastal swamp forests are situated adjacent to extensive upland forests in a context that has not been highly altered by agricultural or urban development. Baseline data from swamp forests within a primarily natural landscape context may be useful in interpreting the conditions of swamp forests where the surrounding land cover has been markedly altered over the last 150 years.

Although there have been numerous studies of swamp forests in Michigan (Kost 2001b, Goforth et al. 2002, Barnes 1976, Baker and Barnes 1998, Sakai and Sulak 1985, Van Deelen et al. 1996, and many others), data specific to the physical site characteristics and the composition and structure of the vegetation in coastal swamp forests are lacking. Due to the unique environmental conditions along the shoreline and the characteristic location of the coastal swamps, between coastal marshes and upland forests, the remaining coastal swamp forests may be important to the maintenance of regional biodiversity and regulation of the flow of energy and materials between coastal marshes and inland ecosystems. Despite intensive land use adjacent to many of the remaining coastal swamps, many of the physical site factors and ecological processes may either remain intact, or restoration may be possible. Baseline data on the physical characteristics and the composition and structure of the vegetation of the coastal swamps is necessary for interpreting the effects of natural disturbances, such as lake-level fluctuations and major windthrow events. Baseline data is also necessary to interpret the effects of intensive human activities over the last 150 years, including logging, drainage, the input of nutrients, and the introduction of exotic species. Detailed studies of the coastal swamp forests can also provide the basis for shoreline protection and restoration.

The overall objective of this study was to compile and analyze baseline data on the physical site characteristics and vegetation of the swamp forests of the Lake Huron shoreline. Specific objectives were to:

(1) compare the physical site conditions and the composition and structure of vegetation among swamp forests of the southern, central, and northern portions of the Lake Huron shoreline,

(2) examine the present vegetation in relation to disturbance, as inferred from land cover of the surrounding landscape and changes from historical vegetation based on GLO survey records,

(3) compare coastal swamps to interior forested wetlands, and

(4) determine the potential for restoration and biodiversity management of the swamp forests.

STUDY AREA

To characterize swamp forests of the southern, central, and northern portions of the Lake Huron shoreline, fifteen sites were sampled in three major study areas: Saginaw Bay, Alpena County, and the Les Cheneaux Islands. Within each of the three major study areas, sites were selected to represent a wide range of disturbance conditions, as inferred from land cover of the landscape surrounding the swamp and comparisons with probable *circa* 1800 vegetation. When possible, hardwood- and conifer-dominated swamps were selected in each of the three major study areas. All swamp forests were located less than 1 km from the shore of Lake Huron on land owned by the State of Michigan, The Nature Conservancy, or other conservation organizations.

Saginaw Bay

Swamp forests were sampled at seven sites along Saginaw Bay: Wigwam Bay, Pinconning, Tobico Marsh, King Road, Pigeon Road, and Heisterman and Maisou Islands of Wildfowl Bay (Figure 1). On both of the Wildfowl Bay Islands, swamps were sampled in narrow swales and small depressions near the northern shore and on broad, flat terrain in the east-central part of the island. Because the swales and depressions on each island were more similar to each other in physiography, soil, and vegetation than they were to the broad, flat terrain on the same island, data from the islands were grouped by site type rather than by island. The broad, flat terrain of both islands was referred to as ‘Wildfowl Glade,’ because the overstory was composed of relatively small trees and the canopy coverage was lower than that of the other sites. The swales and depressions on both islands were referred to as ‘Wildfowl Swale.’ A total of 105 plots were sampled among the 7 sites as follows: 20 each at Wigwam Bay and Tobico Marsh; 15 each at Pinconning, King Road, and Pigeon Road; 12 at Wildfowl Glade; and 8 at Wildfowl Swale.

Hardwood forests dominated all of the sites, and no conifer-dominated swamps were identified in Saginaw Bay. However, GLO survey records suggest that the sites may have historically represented several different cover types. GLO survey records indicate that the shoreline in the western part of Saginaw Bay was primarily composed of mixed hardwood swamp and black ash swamp, with smaller areas of cedar swamp, shrub swamp/emergent marsh, and wet prairie (Comer et al. 1995) (Figure 1). Mixed conifer swamps were often located inland of the hardwood swamps. Along the southern and eastern portions of the Bay, extensive areas of shrub swamp/emergent marsh and wet prairie often extended several km inland. Low sand ridges within the emergent marshes and wet prairies were mapped as mixed oak savanna. Mixed hardwood swamps and black ash swamps were located inland of the emergent marshes and wet prairies, and mixed conifer swamps and cedar swamps were often situated inland of the hardwood swamps.

The *circa* 1800 vegetation of Wigwam Bay was mapped as a shrub swamp/emergent marsh (Comer et al. 1995) (Figure 1). Inland of Wigwam Bay there were large areas mapped as mixed hardwood swamp and cedar swamp to the north and south, respectively. In contrast, Pinconning was mapped as part of a long, narrow wet prairie located along the shoreline, with mixed hardwood swamp and black ash swamp immediately to the south. The forest at Tobico Marsh was mapped as a mixed conifer swamp, and it was bordered by black ash swamp and mixed hardwood swamp to the north, west, and south. King Road, located along the southeast shore of the Bay, was part of an extensive area mapped as shrub swamp/emergent marsh and wet prairie, with mixed oak savanna on low ridges and small sand dunes. Other than a small mixed hardwood forest located 4 km to the northeast of King Road, no forested wetlands were mapped within 2 km of the shoreline in the southeast part of the Bay. Pigeon Road was mapped as black ash swamp, and there were areas of mixed hardwood swamp, shrub swamp/emergent marsh, and mixed conifer swamp nearby. Wetlands on the islands of Wildfowl Bay were mapped as mixed hardwood swamp, and adjacent uplands were mapped as mixed oak savanna (Figure 1).

Alpena County

Three swamp forests were sampled in Alpena County: El Cajon Bay, Misery Bay, and Ossineke. Twenty plots were sampled at each site, 60 plots in all. The swamp forests at El Cajon Bay and Misery Bay were dominated by conifers. Although much of the swamp forest at Ossineke was dominated by conifers, sampling was conducted on hardwood-dominated portions of the site to provide data for comparisons to the conifer-dominated swamps of Alpena County and the hardwood-dominated swamps of Saginaw Bay.

GLO survey records indicate that conifer-dominated swamps covered almost the entire shoreline of Alpena County in the mid-1800s (Comer et al. 1995) (Figure 2a). El Cajon Bay and Misery Bay, in the northern part of the county, were located along part

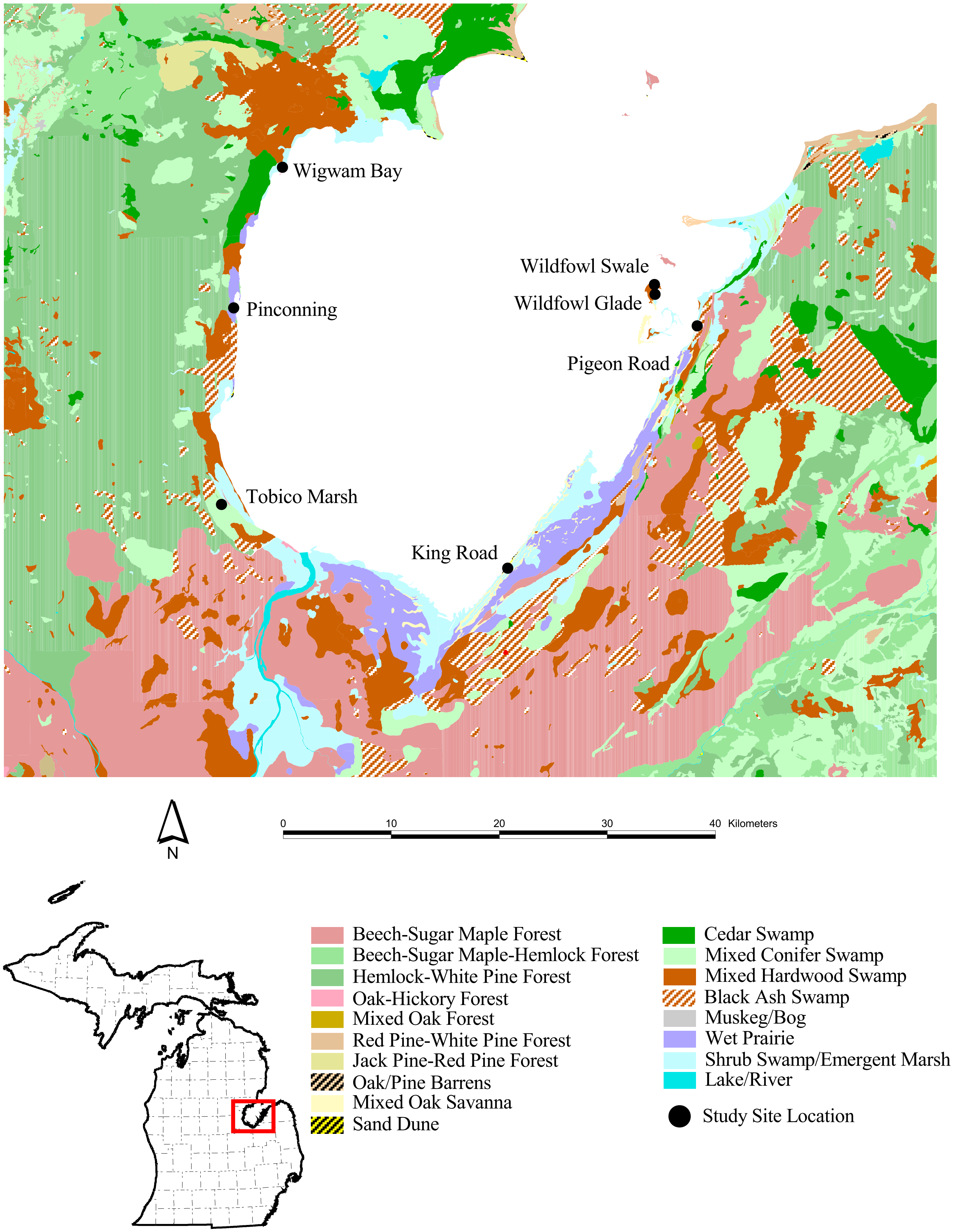


Figure 1. Location of seven swamp forests sampled in Saginaw Bay in relation to vegetation of Michigan circa 1800 (Comer et al. 1995).

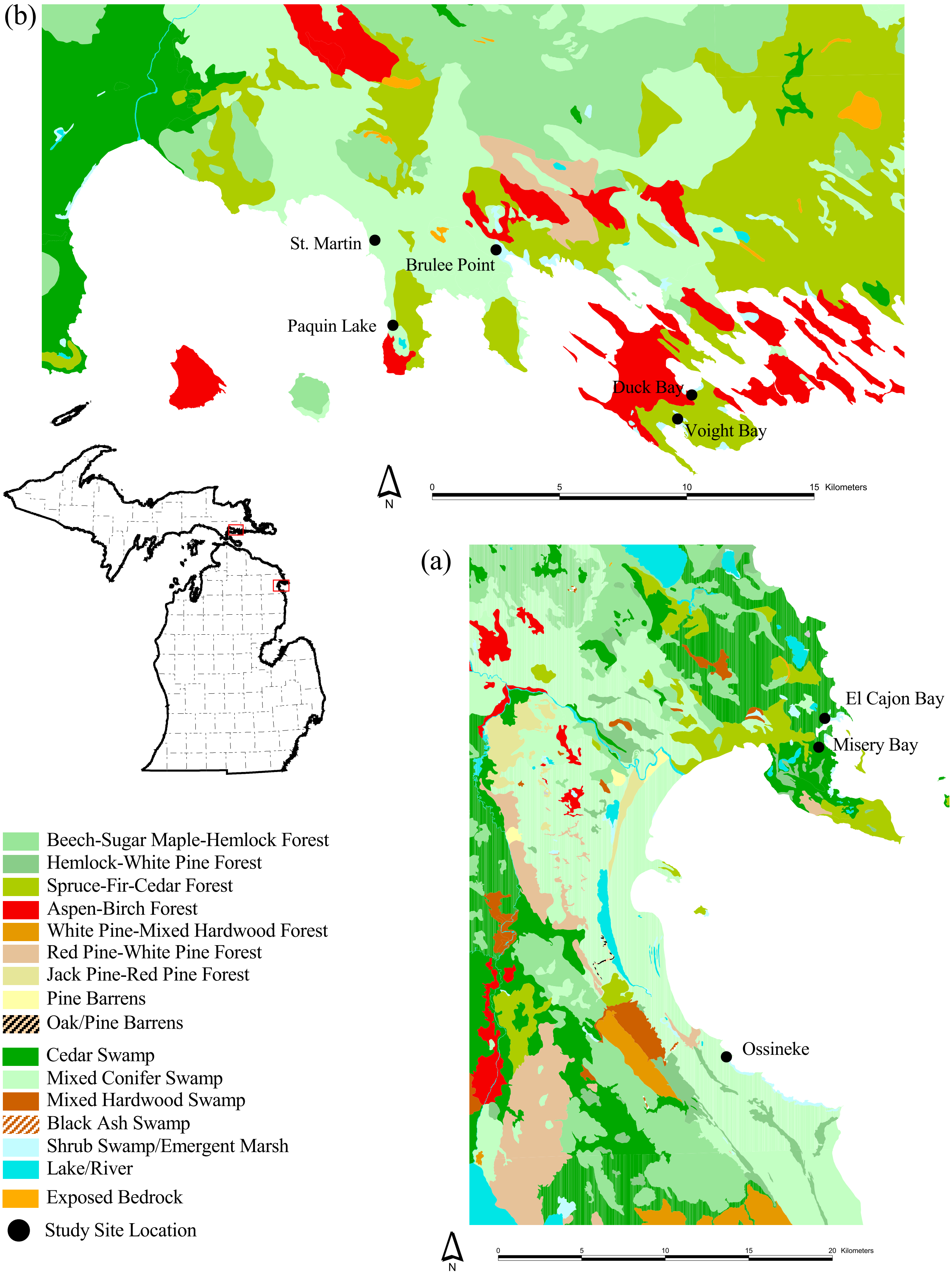


Figure 2. Location of swamp forests sampled in (a) Alpena County and (b) the Les Cheneaux Islands in relation to vegetation of Michigan circa 1800 (Comer et al. 1995).

of the shoreline mapped as cedar swamp. Adjacent uplands in the northern part of the county were mapped as spruce-fir-cedar forest. Ossineke was located in a large area mapped as mixed conifer swamp that extended 50 km southward along the shoreline into the central part of Alcona County. The majority of the sample plots at Ossineke were located within an area mapped as mixed conifer swamp, but several of the plots were located in an area mapped as shrub swamp/emergent marsh. Inland of the mixed conifer swamp, the uplands were dominated by either northern hardwoods or pines (Figure 2a).

Les Cheneaux Islands

On the Les Cheneaux Islands and the adjacent mainland, swamp forests were sampled at five sites: St. Martin Bay, Paquin Lake, and Brulee Point on the mainland, and Duck Bay and Voight Bay on Marquette Island. A total of 70 plots were sampled at the 5 sites: 20 plots each at St. Martin Bay and Paquin Lake, and 10 plots each at Brulee Point, Duck Bay, and Voight Bay. The forests at all sites were dominated by conifers. Based on GLO survey records, the Les Cheneaux Islands were mapped as aspen-birch forest, with a spruce-fir-cedar forest on the eastern half of Marquette Island, and shrub swamp/emergent marsh in the protected bays (Comer et al. 1995) (Figure 2b). The shoreline of the adjacent mainland was mapped as spruce-fir-cedar forest to the north and east of the islands and mixed conifer swamp to the west. An extensive part of the shoreline of the western part of St. Martin Bay was mapped as cedar swamp, but the study sites at St. Martin Bay, Paquin Lake, and Brulee Point, along the eastern part of the Bay, were mapped as mixed conifer swamp. The forests along Duck Bay and Voight Bay were mapped as spruce-fir-cedar forest and a small part of the Duck Bay site was mapped as aspen-birch forest (Comer et al. 1995) (Figure 2b).

METHODS

Vegetation Sampling

Overstory, understory, and ground-cover vegetation was sampled in a total of 235 plots established along transects in each of the 15 sites. Prior to sampling, field reconnaissance was conducted to identify gradients in soil and hydrologic characteristics. Where a gradient was perceived, a transect was run along the gradient. Where there was no apparent gradient, transects were oriented in a direction that would allow for the longest transect with the least influence of upland edge conditions. Depending on the shape of the site and gradients in hydrologic and soil conditions, transects were run parallel to each other or in directions that would ensure that the transects cover the majority of the site. When transects were run parallel to each other, a random number generator was used to determine the distance, in number of chains, between transects.

Five sample plots were established in each 20-chain section of the transect. A random number generator was used to determine the distance, in number of chains, from the start of the transect to the center of each plot. If a plot was located less than two chains from a previously selected plot, a new random number was selected until all plots were separated by a distance of at least two chains. Methods of plot location were modified at the smaller sites to ensure that the largest portion of the site was sampled with the least influence of upland edge conditions. At some of the smaller sites, plots were spaced every two chains along the transect. One-chain spacing was occasionally used between plots at the smallest sites. A Garmin 12XL Global Positioning System (GPS) receiver was used to record the location of each plot.

Each randomly selected point along the transect was the center of a 200 m^2 circular plot (radius 7.98 m) (Figure 3). Overstory vegetation (dbh > 9.0 cm) was sampled over the entire plot. The species and dbh, to the nearest 0.1 cm, was recorded for all live and standing dead overstory trees. Data from dead trees was analyzed separately from that of live trees. Understory vegetation (taller than 50 cm and up to 9.0 cm dbh) was sampled in a 100 m^2 circular subplot (radius 5.64 m) centered within the plot (Figure 3). For large-tree-species (species that could potentially occur in the overstory), the number of saplings (1.5-9.0 cm dbh) and seedlings (taller than 50 cm and less than 1.5 cm dbh) were tallied by species. For shrub species (species that typically do not reach overstory size), the number of stems was tallied by species, and areal coverage was estimated to the nearest percent. A rangefinder was used to determine whether or not overstory and understory trees were located within the plot. Ground-cover vegetation (all herbaceous vegetation and woody plants shorter than 50 cm) was sampled in a 1-m^2 square subplot, located with one corner, selected at random, at the center of the plot

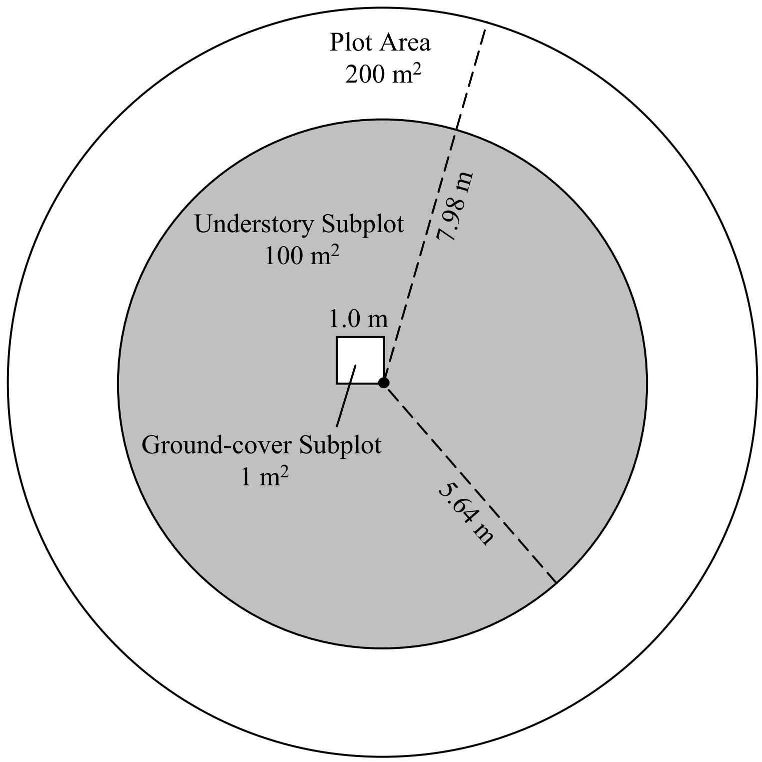


Figure 3. Diagram of a sample plot illustrating the location and relative size of understory and ground-cover subplots.

(Figure 3). Areal coverage of all woody and herbaceous species, as well as coarse woody debris (> 9.0 cm in diameter) and water, was estimated to the nearest percent. A 1x1-m frame composed of PVC tubes was used to delineate the ground-cover subplot. Smaller frames representing 5 and 20% coverage were used to standardize coverage estimates. When standing water was present, the water depth was measured to the nearest centimeter. When high-water marks (discolored bark on the lower part of the bole, resulting from inundation) could be detected on trees, the height of the high-water mark above the soil surface was measured to the nearest centimeter. At every fifth plot, an increment borer was used to core one dominant overstory tree. Trees were cored at breast height (137 cm) and the cores were read in the field. Four years were added to the age determined from the core to approximate the growth before it reached breast height.

Soil Sampling

Soil was sampled with a 100-cm long core, at every fifth plot along the transect. Soil auger borings were excavated to depths ranging from 60 to 100 cm depending on soil and hydrologic characteristics. In each boring, the substrate was classified as mineral or organic. For mineral soil, soil texture was determined in the field. Organic soil was classified as sapric (< 17% fibers), hemic (17-75% fibers), or fibric (> 75% fibers). In each boring, the depth of changes in substrate type and soil texture was recorded. A Hellige-Truogg soil reaction/pH kit was used to record soil pH at the soil surface and at depths of 20, 40, 60, 80, and 100 cm, or where there were distinct changes in soil properties. Soil pH was also recorded on the surface of hummocks at sites where microtopography was apparent. Data on coarse fraction, depth to the water table, and depth to bedrock were recorded where relevant.

Land-Cover Analysis

A Geographical Information System (GIS) was used to analyze the historical and present land cover along three major portions of the Lake Huron shoreline: (i) Saginaw Bay (Port Austin to Tawas City), (ii) the Northern Lower Peninsula (Harrisville to the Mackinac Bridge), and (iii) the Upper Peninsula (Mackinac Bridge to De Tour Village). A 1-km buffer was generated along each portion of the shoreline in GIS, and land cover within the inland portion of the buffer was calculated based on the *circa* 1800 vegetation map of Comer et al. (1995). Present land cover was calculated based on the 1978 Land Use/ Land Cover layer of the Michigan Resource

Information System (MIRIS) (MDNR, MNFI. 1978), classified following Andersen et al. (1976) level 4. The MIRIS data set is a raster data set with 30-m resolution that was interpreted from 1978 aerial photographs (1:24,000 scale). Land-cover classes for each of the two data sets (*circa* 1800 and 1978) were combined into the following nine classes: conifer-dominated swamp, hardwood-dominated swamp, non-forested wetland, upland forest/savanna, sand dune/beach/exposed rock, lake/river, urban, agriculture, and other. The areal and proportional coverage was calculated for each of the nine classes, and the change in area and the percent increase or decrease of each class from *circa* 1800 to 1978 was calculated.

In addition to calculations of land cover along three major portions of the Lake Huron shoreline, the present land cover within 1 km of each of the study sites was calculated based on the MIRIS 1978 data set (MDNR, MNFI 1978). To determine the land cover surrounding each of the study sites, the boundary of each swamp forest was digitized in Arcview (ESRI 2000). Boundaries were determined by plotting the location of each sample plot, obtained from GPS coordinates, and overlaying them on 7.5 minute United States Geological Survey (USGS) topographic maps. After the swamp boundaries were drawn, a 1-km buffer was generated around each site, and the proportional area of each land-cover class within the buffer was calculated from the MIRIS data set, classified following Andersen et al. (1976) level 2. Because all sites were located less than 1 km from Lake Huron, the cover class, 'lake,' accounted for a relatively large portion of the land cover at all sites. Because we were primarily interested in interpreting trends in the swamp forest vegetation in relation to land cover in the surrounding landscape, the class, 'lake,' was excluded from calculations of proportional land cover.

Although more recent imagery is available, the 1978 MIRIS data set was chosen because it was developed based on aerial photos. The more recent land-cover data is based on supervised classification of satellite imagery, and it contains classification errors that are likely to bias the analysis. For example, the marshes adjacent to the swamp forests were often classified as 'agricultural land' in the recent imagery, but they were classified as 'non-forested wetland' in the 1978 imagery. Although the 1978 imagery does not include the most recent land-cover changes, it does represent conditions that were present during the development of the present canopy trees, and it should be adequate for the analysis.

RESULTS AND DISCUSSION

Site Descriptions and Vegetation Composition and Structure

Saginaw Bay

Site Descriptions

Swamp forests of Saginaw Bay ranged in size from 2.1 ha at King Road to 15.3 ha at Tobico Marsh (Table 1). Tobico Marsh, Wigwam Bay, and Wildfowl Glade were located on broad, relatively flat terrain. They were relatively homogeneous in hydrology and soil characteristics, and there was little microtopography. Pigeon Road, King Road, and Wildfowl Swale occupied narrow swales, typically 15-30 m wide, situated between upland ridges. Pinconning was the most heterogeneous site. It included a variety of low rises within the swamp and higher upland ridges that were above the influence of the water table.

At all sites except Wildfowl Glade, either standing water was present at the time of sampling (Figure 4a), or high-water marks were apparent on the trees (Figure 4b). The greatest water depth, 37 cm, was recorded at Wildfowl Swale, and high-water marks up to 40 cm above the soil surface were recorded at Pigeon Road and King Road (Table 1). Water levels were slightly lower at Tobico Marsh and Pinconning, where maximum water levels at the time of sampling were 22 cm and 10 cm, respectively. High-water marks up to 30 cm above the soil surface were recorded at Pinconning. At Tobico Marsh, high-water marks were noted, but their height above the soil surface was not measured. However, with water levels 12 cm higher than those at Pinconning at the time of sampling, the high-water marks at Tobico Marsh were probably at least 12 cm higher than those of Pinconning. Although Wigwam Bay was sampled in mid June, within the same week as all other sites except King Road, standing water was only present in isolated small depressions. However, high-water marks up to 26 cm above the soil surface indicate that the entire soil surface at Wigwam Bay was inundated earlier in the year. King Road was sampled in late July, more than

Table 1. Comparison of site characteristics among seven swamp forests of Saginaw Bay.

Site Characteristic	King Road[1]	Wigwam Bay	Pigeon Road	Tobico Marsh	Pin-conning	Wildfowl Swale	Wildfowl Glade
Area (ha)	2.1	5.1	9.2	15.3	7.5	3.7	8.9
Number of Plots	15	20	15	20	15	8	12
Water							
Depth							
Mean (cm)	1	1	10	15	2	14	---
Maximum (cm)	0	3	21	22	10	37	---
Coverage							
Mean (%)	0	<1	73	93	21	48	---
Maximum (%)	0	10	100	100	100	100	---
High Water Mark							
Mean Height (cm)	29	19	31	---	22	---	---
Maximum Height (cm)	40	26	40	---	30	---	---
Soil							
Substrate[2]	MFS-FS over C	L-CL over C	MFS-FS over C	MFS-FS over C	MFS-FS over C	MFS over R	MFS over R
pH							
surface	7.4	7.2	7.2	7.0	6.5	7.4	7.2
20 cm	7.5	7.4	7.5	7.4	6.8	7.6	7.2
40 cm	7.8	7.8	7.5	7.5	7.2	7.8	7.2
60 cm	7.8	7.8	8.0	8.0	7.5	---	7.2
Dom Tree Age (yrs)	70-83	90-136	70-74	70-80	70-78	72-76	70-73
Overstory							
Density (stems/ha)	1,113	876	727	725	853	619	808
Basal Area (m^2/ha)	51.1	36.5	35.5	31	28.6	33.9	22.3
# of overstory species	5	6	8	5	6	4	5
Understory							
Trees							
Saplings/ha	1,010	493	573	413	317	13	101
# of sapling species	4	6	6	3	4	2	2
Seedlings/ha	397	15	237	285	123	213	451
# of seedling species	3	2	6	3	2	1	2
Shrubs							
Density (stems/ha)	373	19	367	550	547	13	158
Coverage (%)	1.0	1.0	2.1	2.5	2.0	0.1	0.4
# of shrub species	3	7	7	4	7	1	3

[1] King Road was sampled one month later than the other sites, which probably accounts for the lack of standing water

[2] MFS = Medium Fine Sand, FS = Fine Sand, C = Clay, L = Loam, CL = Clay Loam, R = Bedrock

(a)

Photo by Alan J. Tepley

(b)

Photo by Alan J. Tepley

Figure 4. Photographs of Wildfowl Swale, Huron Co., Michigan, illustrating (a) inundation of the soil surface and the lack of shrubs and ground-cover vegetation, and (b) high-water marks on the boles of red ash trees.


Photo by Joshua G. Cohen

Figure 5. Photograph of Wildfowl Glade, Huron Co., Michigan, illustrating the small tree size, low tree density, open canopy, and the abundance of graminoids.

one month later than the other sites. Although standing water was not present at the time of sampling, high-water marks up to 40 cm above the soil surface indicate that it was one of the wettest sites. Wildfowl Glade was the only site where standing water was not present at the time of sampling and there were no high-water marks on the trees (Figure 5, Table 1). The lack of standing water at Wildfowl Glade may be related to its broad, flat topographic shape and its location on small islands, where drainage from the upland features is likely to have a smaller influence on hydrology than on the mainland.

The substrate of all sites was mineral soil (Table 1). The mineral soil often contained high amounts of organic matter in the upper 20-30 cm, but muck was never encountered. At all sites on the mainland except Wigwam Bay, the soil was composed of medium-fine to fine sand over clay. The depth to the clay was highly variable, both within each site and between sites, but clay was always reached within 100 cm of the surface. Clay lenses 2-15 cm thick were often encountered within the sand. At Wigwam Bay, the texture of the surface soil was loam near the lakeshore and clay loam farther from the lake. Below the surface soil were layers of clay and medium-fine sand. At both sites on the islands of Wildfowl Bay, bedrock was encountered within 100 cm of the surface. Bedrock was generally 50-80 cm below the surface at Wildfowl Glade, and 30-60 cm below the surface at Wildfowl Swale (Table 1).

At all sites, the soil pH was cicrumneutral at the surface, and it became calcareous slightly below the surface. The pH at the soil surface ranged from 6.5 at Pinconning to 7.4 at Wildfowl Swale and King Road, and soil pH gradually increased with increasing depth, typically reaching 7.8-8.0 at depths of 40-60 cm (Table 1). At Pinconning, where there were many small rises and mounds that stood 10-30 cm above the soil surface, the soil pH on the mounds was not different from that of the general ground surface. The high pH on the mounds indicates the influence of ground water, otherwise a lower pH would be expected.

Overstory Vegetation

The age of the dominant overstory trees was within the range of 70-83 years at all sites except Wigwam Bay, where the dominant trees were 90-136 years old (Table 1). The present overstory trees at all sites were established after the drainage of much of inland parts of Saginaw Bay for agricultural purposes (Moon et al. 1938, Deeter and Matthews 1926). Overstory basal area ranged from 51.1 m^2/ha at King Road to 22.3 m^2/ha at Wildfowl Glade. In addition to the highest basal area, King Road also had the highest overstory stem density, 1,113 stems/ha, while that of all other sites was between 619 and 876 stems/ha (Table 1).

The major dominant overstory species in the swamps of Saginaw Bay were red ash (*Fraxinus pennsylvanica*), silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), and eastern cottonwood (*Populus deltoides*) (Figure 6, Appendix A). Other species were a minor component of the overstory at all sites. Together, red ash and silver maple accounted for 77-98% of the overstory stems and 66-95% of the overstory basal area at all sites except Wildfowl Glade, where red ash accounted for 92% of the overstory stems and 96% of the basal area. American elm was the only tree species except red ash and silver maple that was present at all sites. American elm trees were especially abundant at King Road, where they accounted for 20% of the overstory trees. Without the American elm trees, the overstory density of King Road would be similar to that of the other sites. Although live elm trees were recorded in the overstory of all sites, their average dbh was up to 13 cm lower than that of red ash and silver maple trees at all sites except Wildfowl Glade, where there was one large elm tree. Standing dead elm trees, that presumably died of Dutch Elm disease, were present at every site. Dead elm trees were most abundant at Tobico Marsh, where the density of dead elm trees, 95/ha, was almost as high as that of live elm trees, 105/ha (Appendix A). Despite the abundance of small overstory elm trees, the death of the elm trees due to Dutch Elm disease is likely to prevent American elm from becoming a large overstory species at any of the sites.

Large eastern cottonwood trees, with an average dbh more than twice that of the red ash or silver maple trees, were recorded at King Road, Tobico Marsh, and Pigeon Road (Appendix A). Eastern cottonwood trees only slightly larger than the red ash and silver maple trees were recorded at Pinconning. The cottonwood trees were typically located near the edge of an upland ridge or on small mounds that stood 10-30 cm above the general soil surface. Although cottonwood trees accounted for less than 8% of the overstory stems at all sites, the cottonwood trees were typically the largest trees present, and they made a large contribution to the overstory basal area. At King Road, where cottonwood trees more than 100 cm dbh were sampled, cottonwood accounted for 26% of the overstory basal area (Figure 6, Appendix A). Without the cottonwood trees the total overstory basal area at King Road would be similar to that of the other sites.

All other species combined accounted for less than 8% of the overstory stems and less than 8% of the basal area at all sites (Figure 6, Appendix A). Swamp white oak (*Quercus bicolor*) trees were present on small mounds or near the edge of the upland at Wigwam Bay, Pigeon Road, King Road, and Pinconning. Black ash (*Fraxinus nigra*) trees were present at sites, such as Wildfowl Glade, where the soil surface was not inundated and Wigwam Bay, where the period of inundation was shorter than that of the other sites. Black ash trees were also present near the boundary of the upland ridges at Pigeon Road, but not in lower parts of the swale, where the soil surface was deeply inundated during the early part of the growing season. Additional overstory species include bur oak (*Quercus macrocarpa*), willow (*Salix spp.*), basswood (*Tilia americana*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Besides bur oak, which was present at Wigwam Bay and Wildfowl Glade, and willow, which was present at Pinconning and Wildfowl Swale, none of the additional species were present at more than one site (Appendix A).

Understory Vegetation

At all sites, the composition of the sapling layer (1.5-9.0 cm dbh) was similar to that of the overstory, illustrating that the composition of the overstory is not likely to change dramatically in the absence of disturbance in the near future. The sapling density of the 5 sites on the mainland ranged from 317 to 573 saplings/ha (Table 1). At Wildfowl Swale, the wettest site, there were only 13 saplings/ha, while there were 101 saplings/ha at Wildfowl Glade. Together, red ash, silver maple, and American elm accounted for more than 90% of the saplings at the 5 mainland sites, and red ash and silver maple were the only sapling species recorded at both sites on the islands (Figure 7, Appendix B). At the mainland sites, the only other sapling species recorded were black ash, swamp white oak, northern white-cedar (*Thuja occidentalis*), and musclewood (*Carpinus caroliniana*). At each site where swamp white oak was present in the overstory, swamp white oak saplings were present in the understory. Northern white-cedar was only present at Wigwam Bay, where it was recorded in only one plot. Eastern cottonwood was the only dominant overstory species that was not present in the sapling layer (Figure 7, Appendix B). Eastern cottonwood is a short-lived, fast-growing species that is very intolerant of shade (Barnes and Wagner 1981), and in the absence of a major disturbance, such as a large blowdown, that would increase light levels on the forest floor, the current overstory cottonwood trees are unlikely to be replaced.

The number of tree seedlings (taller than 50 cm and less than 1.5 cm dbh) ranged from 15 seedlings/ha at Wigwam Bay, to 397 seedlings/ha at King Road

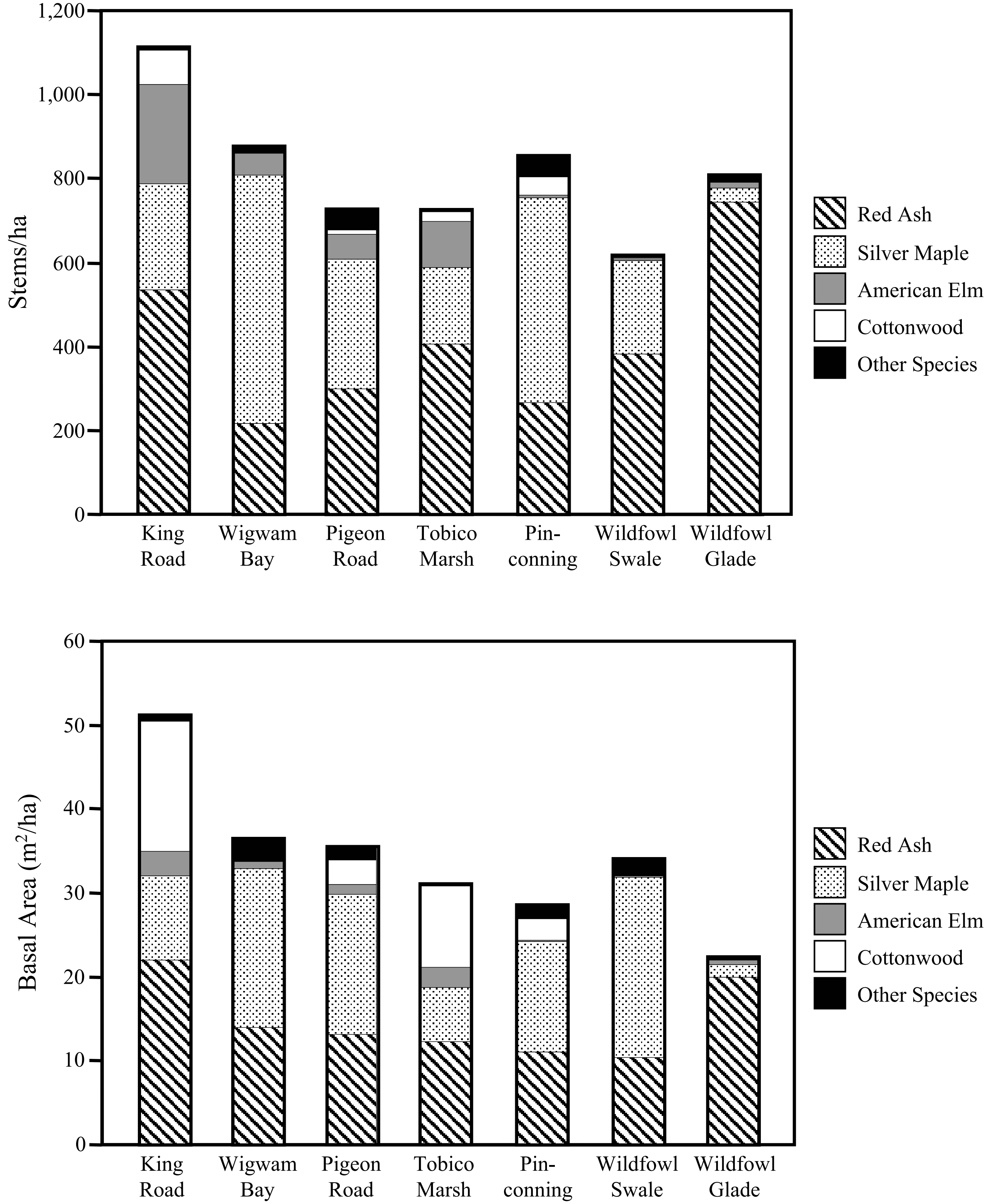
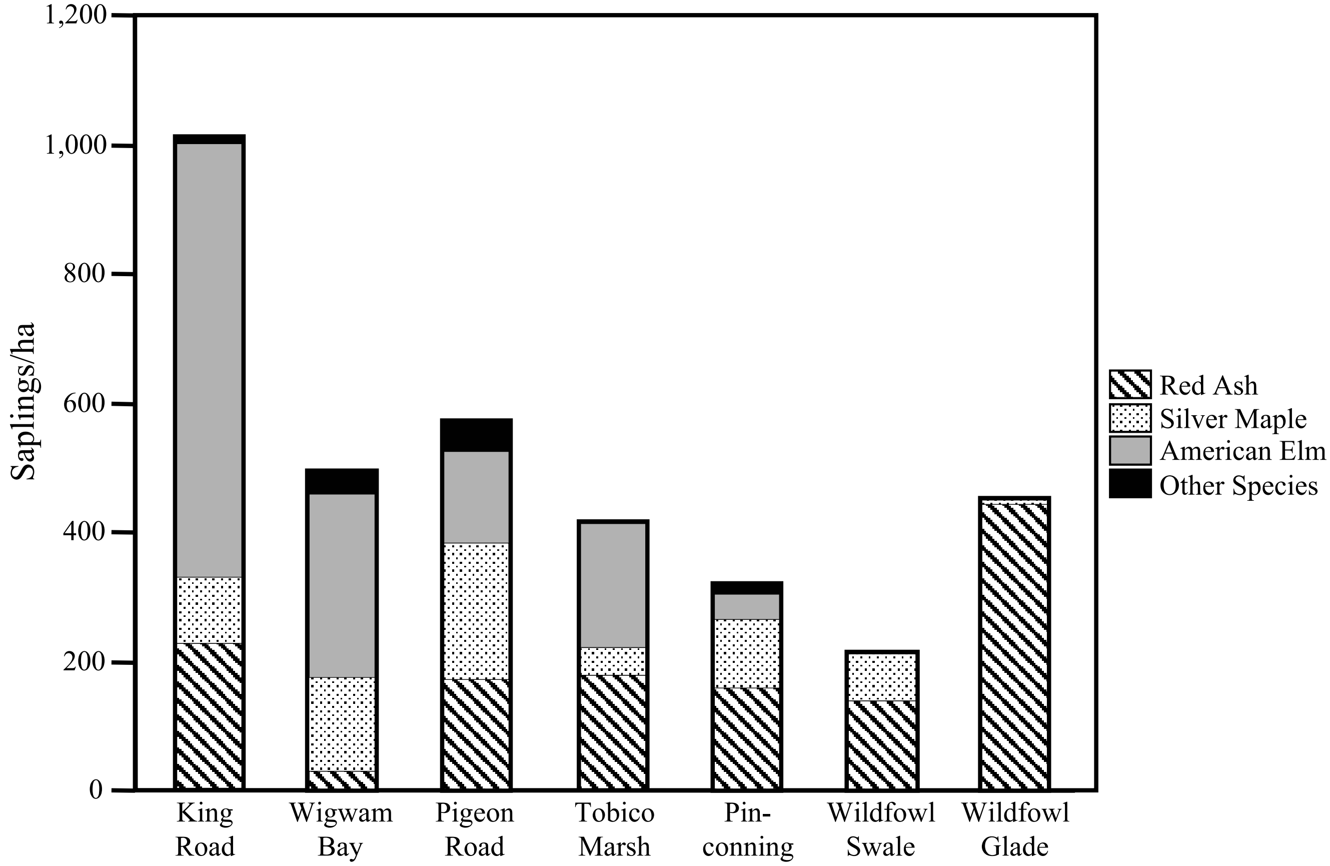


Figure 6. Comparison of overstory vegetation (dbh > 9.0 cm) among seven swamp forests of Saginaw Bay.



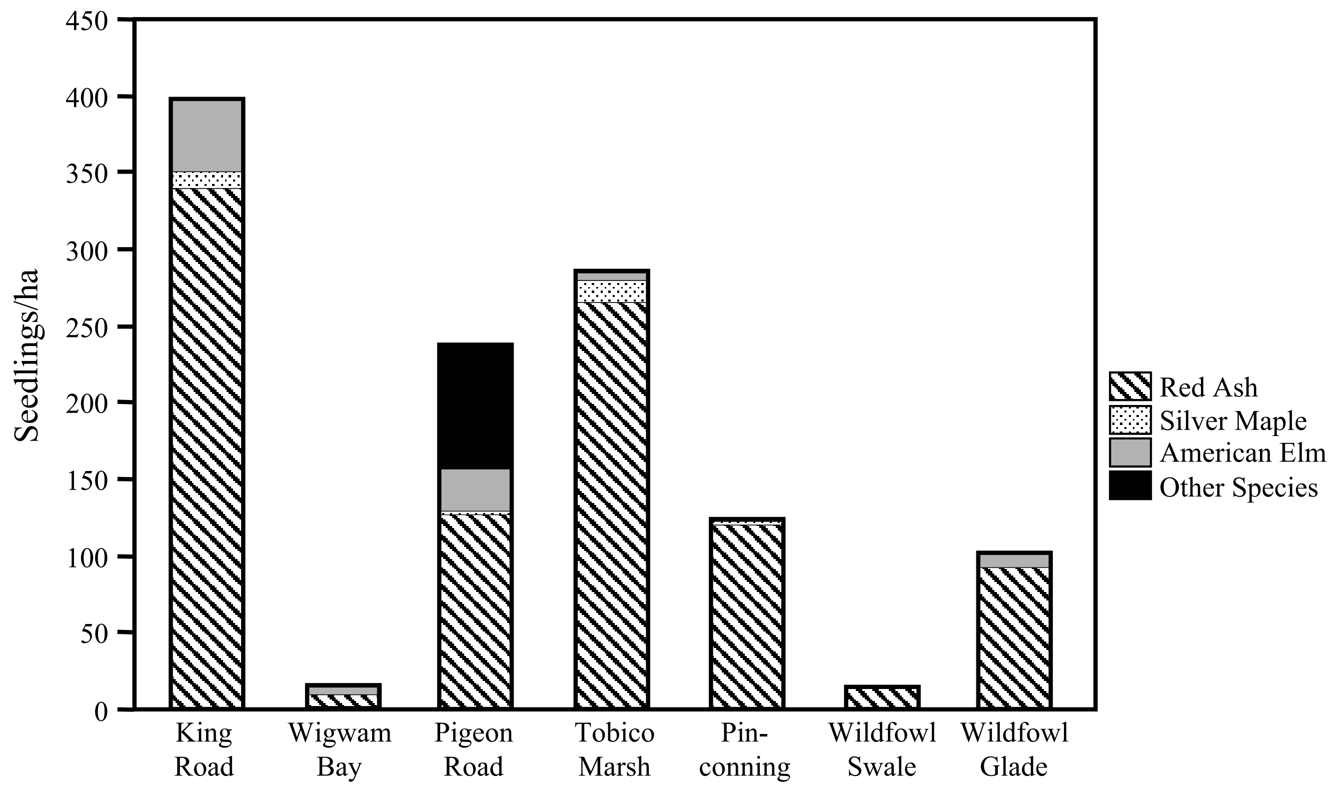


Figure 7. Comparison of species composition of the sapling (1.5-9.0 cm dbh) and seedling (taller than 50 cm and less than 1.5 cm dbh) layers among seven swamp forests of Saginaw Bay.

(Table 1). Red ash accounted for the majority of the seedlings at all sites (Figure 7, Appendix B). Although the abundance of silver maple saplings was often equal to or greater than that of red ash saplings, silver maple seedlings (taller than 50 cm) were absent from Wigwam Bay, Wildfowl Swale, and Wildfowl Glade, and there were few silver maple seedlings at the other sites. The ability of silver maple to form multiple-stemmed clumps probably accounts for the relatively high number of saplings despite the low number of seedlings. Many of the silver maple saplings were sprouts from the base of overstory trees that probably formed when conditions were more open following logging. The silver maple sprouts are probably able to persist in the shaded understory due to connections with the larger tree, but new seedlings that are not connected to an overstory tree probably require higher light levels to be recruited into the understory. Seedlings of few other species were present at any site except Pigeon Road, where black ash accounted for 28% of the seedlings. Despite the abundance of black ash seedlings at Pigeon Road, black ash only accounted for 8% of the saplings, indicating that the majority of the black ash seedlings probably die before reaching sapling size.

Shrubs were a minor component of the understory at all sites (Figure 4a), and the average shrub coverage ranged from 0.1% at Wildfowl Swale to 2.5% at Tobico Marsh (Table 1). Despite the low coverage of shrubs, a total of 16 shrub species were recorded in the swamp forests of Saginaw Bay (Appendix C). The most common shrub species were silky dogwood (*Cornus amomum*), nannyberry (*Viburnum lentago*), Michigan holly (*Ilex verticillata*), and common elder (*Sambucus canadensis*). Tatarian honeysuckle (*Lonicera tatarica*) was the only non-native shrubs species, and it was only recorded at one site, Tobico Marsh (Appendix C).

Ground-Cover Vegetation

With relatively high canopy coverage and inundation of the soil surface during the early part of the growing season at all sites except Wildfowl Glade, relatively few species were present in the ground cover. Although the coverage of the ground-cover layer was often high on dry microsites, ground-cover vegetation was often absent from low areas between microsites (Figure 4a). The total number of ground-cover species ranged from 11 at King Road to 44 at Tobico Marsh (Table 2). At Wildfowl Glade, where canopy coverage was lowest and the soil surface was not inundated, there was an average of 6.7 species per plot and the average coverage was 60%. At all other sites the average number of species per plot ranged from 1.9 at King Road to 5.0 at Tobico Marsh, and average coverage ranged from 7% at King Road to 34% at Tobico Marsh (Table 2).

A similar suite of ground-cover species was present at all sites where the soil surface was inundated during the early part of the growing season. The most characteristic species of the inundated sites were fowl manna grass (*Glyceria striata*), false nettle (*Boehmeria cylindrica*), jewelweed (*Impatiens capensis*), goldenrod (*Solidago spp.*), northern bugle weed (*Lycopus uniflorus*), common lake sedge (*Carex lacustris*), and Virginia wild rye (*Elymus virginicus*) (Appendix D). Seedlings of red ash and silver maple (shorter than 50 cm) were present at all sites, and seedlings of American elm and swamp white oak were often present. Although shrubs were often present in the ground cover, they were never abundant, and the average coverage of tall and short shrubs combined was 2.4% or lower at all sites (Table 2). Woody vines were common at all sites, and there were large vines of riverbank grape (*Vitis riparia*) at King Road, Tobico Marsh, and Wildfowl Swale. Aquatic plants including water-hemlock (*Cicuta maculata*), water-parsnip (*Sium suave*), water-plantain (*Alisma plantago-aquatica*), small duckweed (*Lemna minor*), and star duckweed (*Lemna trisulca*), were present at the wetter sites. Ferns were present at all sites except Pigeon Road, but the total coverage of ferns was relatively low at all sites (Table 2). Non-native plants were not abundant at any of the sites. With an average coverage of 3.8%, coverage of non-native species was highest at Tobico Marsh. Bittersweet nightshade (*Solanum dulcamara*) was the only abundant non-native plant at Tobico Marsh, and based on observations at other sites, it generally does not pose a threat to native vegetation.

At Wildfowl Glade, where the soil surface was not inundated and canopy coverage was lowest, the composition and coverage of the ground-cover layer was markedly different from that of the inundated sites. Graminoids accounted for a larger portion of the total ground-cover coverage at Wildfowl Glade than at any other site (Figure 5, Table 2). The most abundant graminoids were blue-joint grass (*Calamagrostis canadensis*), common lake sedge, and tussock sedge (*Carex stricta*) (Appendix D). Of these species, only common lake sedge was present at any of the other sites. Characteristic forbs at Wildfowl Glade include marsh vetchling (*Lathyrus palustris*), marsh skullcap (*Scutellaria galericulata*), and small bedstraw (*Galium triflorum*) (Appendix D). Such species are characteristic of open, sedge-dominated sites in southern Michigan (Kost 2001a).

Table 2. Comparison of groundcover data among seven coastal swamp forests of Saginaw Bay.

Ground Cover Variable	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Total # of Species	11	32	26	44	23	16	26
All Species							
Mean # species/plot	1.9	4.2	2.9	5.0	4.0	3.1	6.7
Mean coverage/plot	7.4	26.6	9.7	34.1	25.1	15.4	59.9
Woody Plants							
Mean # species/plot	1.4	1.2	1.3	1.2	1.3	1.1	1.0
Mean coverage/plot	4.5	2.4	3.7	7.2	2.3	6.5	2.3
Trees							
Mean # species/plot	1.0	0.9	0.3	0.6	1.1	0.9	0.6
Mean coverage/plot	4.1	1.9	0.5	2.0	1.9	6.0	0.7
Tall Shrubs							
Mean # species/plot	---	0.1	0.2	0.2	---	---	0.2
Mean coverage/plot	---	0.1	1.9	1.8	---	---	0.9
Short Shrubs							
Mean # species/plot	---	0.1	0.3	0.2	---	0.1	0.1
Mean coverage/plot	---	0.2	0.5	0.4	---	0.4	0.1
Vines							
Mean # species/plot	0.4	0.2	0.5	0.4	0.2	0.1	0.2
Mean coverage/plot	0.5	0.3	0.9	3.0	0.5	0.1	0.7
Herbaceous Plants							
Mean # species/plot	0.5	3.0	1.6	3.8	2.7	2.0	5.7
Mean coverage/plot	2.9	24.3	6.0	27.0	22.7	8.9	57.6
Forbs							
Mean # species/plot	0.3	1.7	1.0	3.0	1.6	1.8	2.9
Mean coverage/plot	1.5	9.2	4.0	11.3	10.2	3.6	7.9
Graminoids							
Mean # species/plot	---	1.2	0.6	0.8	0.9	0.1	2.6
Mean coverage/plot	---	13.2	2.0	15.7	12.3	5.0	46.8
Ferns							
Mean # species/plot	0.2	0.2	---	0.1	0.1	0.1	0.2
Mean coverage/plot	1.3	1.9	---	0.1	0.2	0.3	2.9
Native Plants							
Mean # species/plot	1.9	4.0	2.9	4.7	3.9	3.1	6.5
Mean coverage/plot	7.4	26.3	9.7	30.4	24.8	15.4	59.3
Non-native Plants							
Mean # species/plot	---	0.2	---	0.3	0.1	---	0.2
Mean coverage/plot	---	0.4	---	3.8	0.3	---	0.6

Alpena County

Site Descriptions

The swamp forests in Alpena County ranged in size from 2.7 ha at Ossineke to 8.1 ha at Misery Bay (Table 3). Sites on Misery Bay and El Cajon Bay were dominated by conifers. The Ossineke site was primarily dominated by conifers, but hardwood-dominated swamp was present in the following three areas within the study site: (i) long, narrow swales located between ridges, (ii) shallow depressions within the conifer-dominated swamp, and (iii) along the edge of an open meadow located inland of a beach ridge. Sampling was only conducted in hardwood-dominated portions of the site. Five plots were sampled in a swale, five plots were sampled in a shallow depression, and ten plots were sampled along the edge of the open meadow.

At both Misery Bay and El Cajon Bay, the majority of the trees were growing on hummocks that stood 10-50 cm above the general ground level (Figure 8a). The hummocks were most likely formed by tree tip ups, and they are often covered by sphagnum moss. High-water marks were not present on the trees and standing water was nearly absent. The only place where standing water was encountered was in several of the small depressions adjacent to hummocks. The maximum water depth was 4 cm at Misery Bay and only 1 cm at El Cajon Bay (Table 3). Average water coverage ranged from 4% at Misery Bay to less than 1% at El Cajon Bay. A small stream flowed through the swamp at El Cajon Bay. Low, upland ridges were present within the swamps at both Misery Bay and El Cajon Bay.

The hardwood-dominated portions of the Ossineke site were wetter than the conifer-dominated portions, and they were wetter than the conifer-dominated swamps at Misery Bay and El Cajon Bay (Figure 8b). The water level was highest in the swales, where almost the entire soil surface was inundated with water up to 23 cm deep, and high-water marks were recorded up to 50 cm above the soil surface (Table 3). The only areas that were not inundated were tussock sedge hummocks. Along the edge of the open meadow, water coverage ranged from 0 to 65%, water depth ranged from 0 to 7 cm, and high-water marks were recorded up to 35 cm above the soil surface. Tussock sedge hummocks were also abundant. The water table was lowest in the shallow depression, where water coverage ranged from 0 to 25% and the maximum water depth was only 6 cm. The highest high-water marks of the depression were only 14 cm above the soil surface.

The substrate at all sites was sapric muck, often with trace amounts of silt, over medium-fine to fine sand (Table 3). The depth of the sapric muck ranged from 8 to 20 cm, and it was a little bit deeper at Misery Bay and El Cajon Bay than Ossineke. At El Cajon Bay clay was encountered below the sand, at a depth of 60 cm. Although clay was not reached in the 80-cm deep auger borings at the other sites, clay was probably present below the sand. A cobble band was consistently encountered at depths between 28 and 45 cm in the swale and depression at Ossineke. The cobble band was probably a former cobble beach that has been covered by sand long ago. There were no cobble bands within 100 cm of the surface at El Cajon Bay or Misery Bay.

At all sites, the soil pH was circumneutral at the surface, and it gradually increased with depth, reaching 7.8 by depths of 40-60 cm (Table 3). The soil at the surface of the hummocks at both Misery Bay and El Cajon Bay was strongly acid, with a pH below 5.0, indicating that they are not strongly influenced by ground water. Such acid conditions were not encountered on the tussock sedge hummocks at Ossineke (Table 3). In general the height of the tussock sedge hummocks was similar to the level of the high-water mark on the trees, and the sedge hummocks were probably influenced by ground water, which transports calcareous material from deeper below the surface into the hummocks during periods of inundation.

Overstory Vegetation

The overstory trees of the conifer-dominated swamps most likely became established following logging of the previous forest in the late part of the 19th century, but the overstory trees of the hardwood-dominated swamps may have colonized sites that were not previously forested. The conifer-dominated swamps at Misery Bay and El Cajon Bay were older and denser than the hardwood-dominated swamps at Ossineke, and their basal area was higher. With dominant tree ages of 128-132 years at Misery Bay and 112-120 years at El Cajon Bay, the dominant trees of the conifer-dominated swamps were nearly twice as old as the dominant trees at Ossineke, where the dominant trees were 52-68 years old (Table 3). The overstory stem density at Misery Bay and El Cajon Bay, 1,840 and 1,748 stems/ha respectively, was roughly twice that of Ossineke, where there were only 913 stems/ha. With overstory basal areas of 62.2 m^2/ha and 59.8 m^2/ha respectively, the overstory basal area at Misery Bay and El Cajon Bay was nearly three times that of Ossineke, where the basal area was only 21.3 m^2/ha (Table 3). Although the low basal area at

Table 3. Comparison of site characteristics among three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands.

Site Characteristic	Alpena: Misery Bay	Alpena: El Cajon Bay	Alpena: Ossi-neke	Les Cheneaux: St. Martin	Les Cheneaux: Duck Bay	Les Cheneaux: Paquin Lake	Les Cheneaux: Voight Bay	Les Cheneaux: Brulee Point
Area (ha)	8.1	4.9	2.7	5.3	6.1	6.4	4.3	8.0
Number of Plots	20	20	20	20	10	20	10	10
Water								
Depth								
Mean (cm)	< 1	< 1	6	< 1	---	< 1	< 1	< 1
Maximum (cm)	4	1	23	4	---	4	2	3
Coverage								
Mean (%)	4	< 1	33	1	---	2	< 1	< 1
Maximum (%)	65	2	100	7	---	23	3	4
High Water Mark								
Mean Height (cm)	---	---	36	---	---	---	---	---
Maximum Height (cm)	---	---	50	---	---	---	---	---
Soil								
Substrate[1]	SM over MFS	SM over MFS-FS over C	SM over MFS-FS over Cob	SM over MFS-FS over C	SM over Si-SiL	SM over HM over MFS	SM over MFS-FS	SM over Si-SiL over C
pH								
Hummock	4.8	4.9	---	4.5	5.3	4.0	4.2	4.2
Surface	7.0	7.2	7.2	7.2	7.4	6.5	7.0	7.4
20 cm	7.0	7.6	7.4	7.3	7.6	7.0	7.2	7.6
40 cm	7.5	7.8	7.8	7.6	7.6	7.2	7.4	8.0
60 cm	7.8	7.8	7.8	7.6	8.0	7.6	7.5	8.0
Dom Tree Age (yrs)	128-132	112-120	52-68	89-152	96-164	85-91	106-112	88-110
Overstory								
Stems/ha	1,840	1,748	913	2,163	1,575	2,400	2,295	2,690
Ba (m^2/ha)	62.2	59.8	21.3	77.5	66.1	59.7	55.6	54.2
# of overstory species	9	14	13	9	8	9	9	6
Understory								
Trees								
Saplings/ha	300	718	683	540	610	765	1,280	1,490
# of sapling species	5	6	10	3	2	5	4	3
Seedlings/ha	115	915	305	5	410	5	470	20
# of seedlings species	3	7	6	1	4	1	2	1
Shrubs								
Stems/ha	---	25	11,205	---	---	10	120	490
Coverage (%)	---	0.4	22.2	---	---	0.1	0.3	0.8
# of shrub species	---	3	9	---	---	1	2	2

[1] SM = Sapric Muck, HM = Hemic Muck, MFS = Medium Fine Sand, FS = Fine Sand, C = Clay, Si = Silt, SiL = Silt Loam, Cob = Cobble Band

(a)

Photo by Alan J. Tepley

(b)

Photo by Joshua G. Cohen

Figure 8. Photographs of two swamp forests in Alpena Co., Michigan: (a) El Cajon Bay illustrating the occurrence of northern white-cedar trees on hummocks and the abundance of bulblet fern in the ground cover, and (b) a swale at Ossineke, illustrating dominance by relatively small red ash trees, the abundance of graminoids in the ground cover, and an upland ridge in the background on the right side of the photograph.

Ossineke may be accounted for, in part, by the relatively young trees, the low basal area was also due to the wetter conditions at Ossineke. Wet meadow or marsh vegetation may have persisted under such wet conditions until the middle part of the 20th century when the present overstory trees were established. The establishment of the trees may have followed a slight lowering of the water table or changes in the disturbance regime, such as a lack of fire.

At Misery Bay and El Cajon Bay, northern white-cedar was the dominant overstory species. Northern white-cedar trees accounted for 76-80% of the overstory stems and 78-79% of the overstory basal area of both sites (Figure 9, Appendix E). Balsam fir (*Abies balsamea*), which accounted for 6-8% of the overstory stems and 2-4% of the basal area, was the second most abundant species at both sites. Additional overstory species present at both sites include paper birch, black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera*), trembling aspen, eastern white pine (*Pinus strobus*), red ash, and red maple (*Acer rubrum*). White spruce (*Picea glauca*) was present at El Cajon Bay, black ash was present at Misery Bay, and striped maple (*Acer pensylvanicum*), sugar maple (*Acer saccharum*), and white ash (*Fraxinus americana*) were sampled in a plot at the edge of an upland ridge at El Cajon Bay (Appendix E).

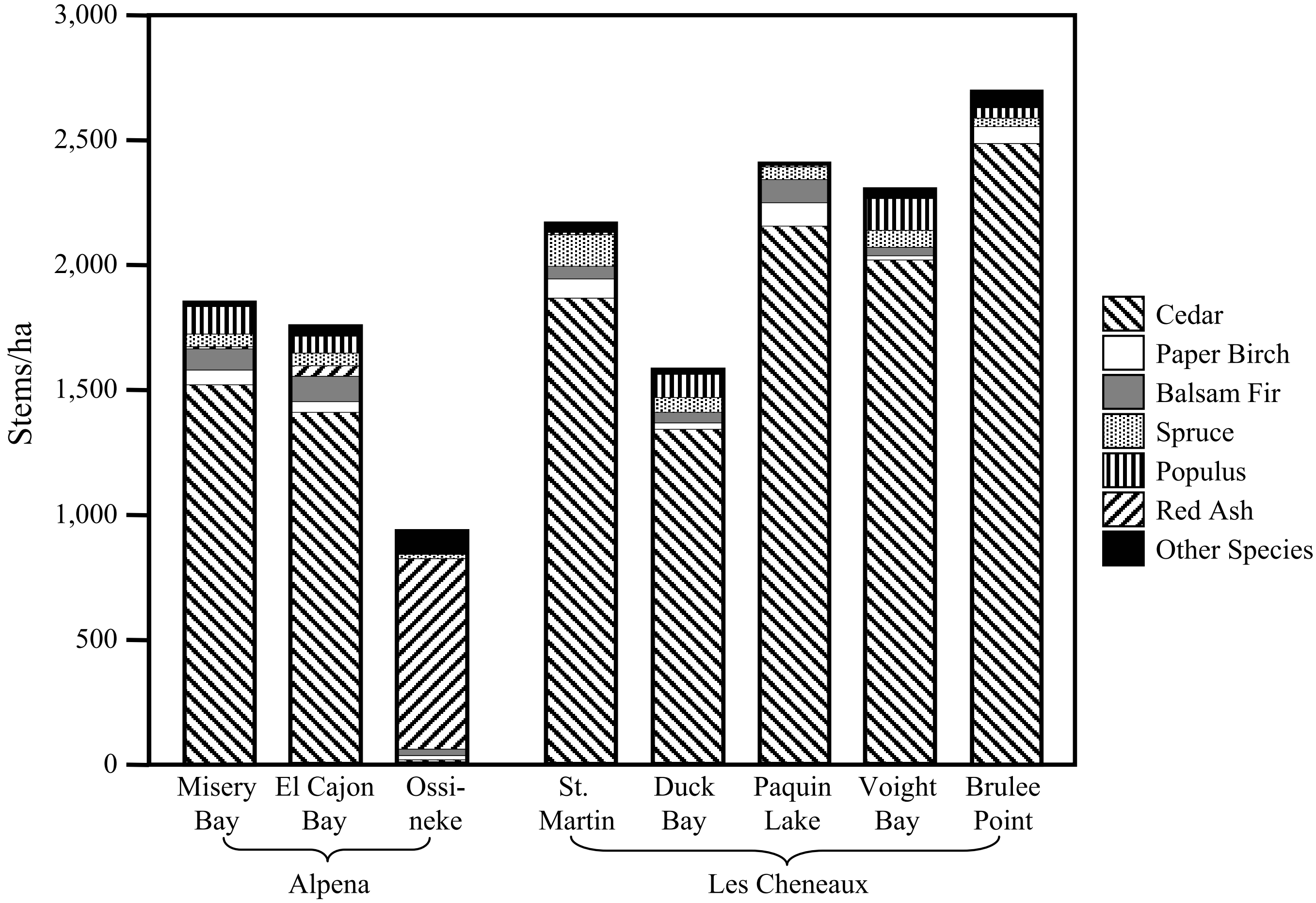
Red ash was the dominant overstory species at Ossineke, accounting for 79% of the overstory stems and 81% of the basal area (Figure 9, Appendix E). It was the only overstory species present in the swales, the wettest part of the site. Such dominance by red ash reflects the wetter conditions at Ossineke compared to those of the other sites. Red maple was the next most abundant overstory species, followed by balsam fir, paper birch, and black ash. The red maple and black ash trees were primarily located in the shallow depression, the area sampled at Ossineke that was least influenced by inundation of the soil surface during the growing season. Within the depression, balsam fir was only present around the edges of the depression, and on slightly elevated microsites above the high-water mark. Along the edge of the open meadow, tamarack (*Larix laricina*) and northern white-cedar trees were often present.

Understory Vegetation

The most abundant sapling (1.5-9.0 cm dbh) species at both conifer-dominated sites were northern white-cedar and balsam fir (Figure 10). Together these two species accounted for 87% of the saplings at Misery Bay and 93% of the saplings at El Cajon Bay (Appendix F). Despite similarities in the age, species composition, density, and basal area of the overstory trees between the two conifer-dominated sites, there were more than twice as many understory saplings at El Cajon Bay than Misery Bay (Table 3). The major difference in understory composition between the two sites is the abundance of balsam fir saplings, which was 520/ha at El Cajon Bay, but only 45/ha at Misery Bay. Such differences may reflect our sampling methods rather than differences in forest composition. Because the distribution of balsam fir saplings is highly contagious, with many saplings often aggregated under canopy gaps, the location of sample plots within dense patches of balsam fir saplings can have a strong influence on the average balsam fir sapling density for the site. At El Cajon Bay, the location of several of plots within such dense patches of balsam fir saplings resulted in a high average density of balsam fir, even though it was absent from many of the plots. At Misery Bay, the location of plots did not coincide with dense patches of balsam fir saplings. Additional sapling species include black ash, paper birch, and red maple at Misery Bay, and trembling aspen, tamarack, red ash, and silver maple at El Cajon Bay (Appendix F).

The composition of the seedling layer (taller than 50 cm and < 1.5 cm dbh) at both Misery Bay and El Cajon Bay was similar to the composition of the sapling layer, but northern white-cedar seedlings were absent from Misery Bay, and there were only 10 northern white-cedar seedlings per ha at El Cajon Bay (Figure 10, Appendix F). The absence of northern white-cedar seedlings is probably due to excessive browsing by deer (Van Deelen et al. 1996). The most abundant seedling species at both sites was balsam fir, which is not typically browsed by deer. The density of balsam fir seedlings at El Cajon Bay was ten times that of Misery Bay. At both sites, the abundance of trembling aspen seedlings was greater than that of trembling aspen saplings (Figure 10, Appendix F). Further examination indicated that most, if not all, of the trembling aspen seedlings were really sprouts from the roots of overstory trees. The abundance of trembling aspen in the seedling layer but the absence of aspen in the sapling layer illustrated that the sprouts were killed before reaching sapling size, and they are not likely to be recruited into larger size classes without a major disturbance to the overstory vegetation. Many of the trembling aspen sprouts were browsed by deer.

The most abundant sapling species at Ossineke were red ash and balsam fir, which accounted for a combined total of 89% of the saplings (Figure 10, Appendix F). Red ash accounted for 47% of the saplings, and 42% of the saplings were balsam fir. Red ash saplings were abundant in the swales, depressions, and along the edge of the open meadow.



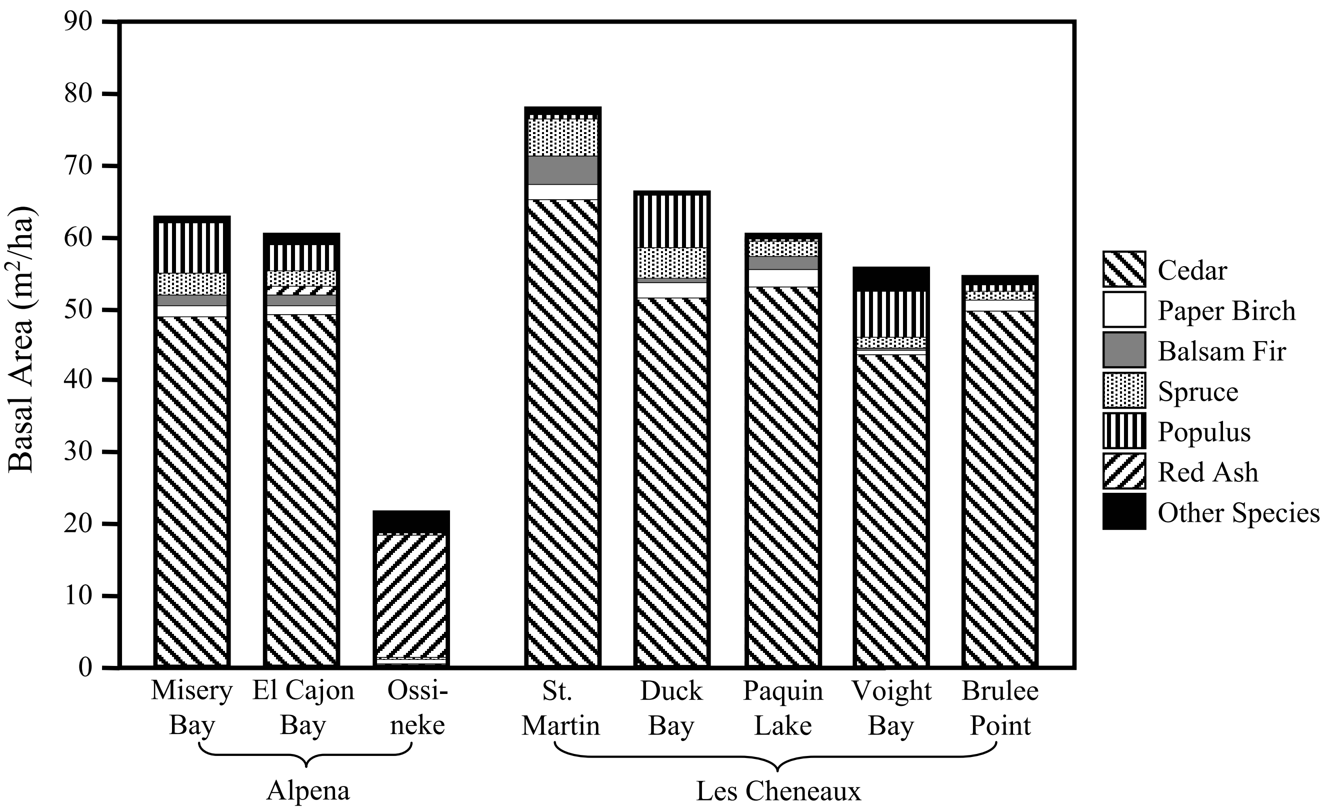


Figure 9. Comparison of overstory vegetation (dbh > 9.0 cm) among three swamp forests of Alpena County and 5 swamp forests of the Les Cheneaux Islands (Spruce includes black spruce and white spruce, Populus includes balsam poplar and trembling aspen).

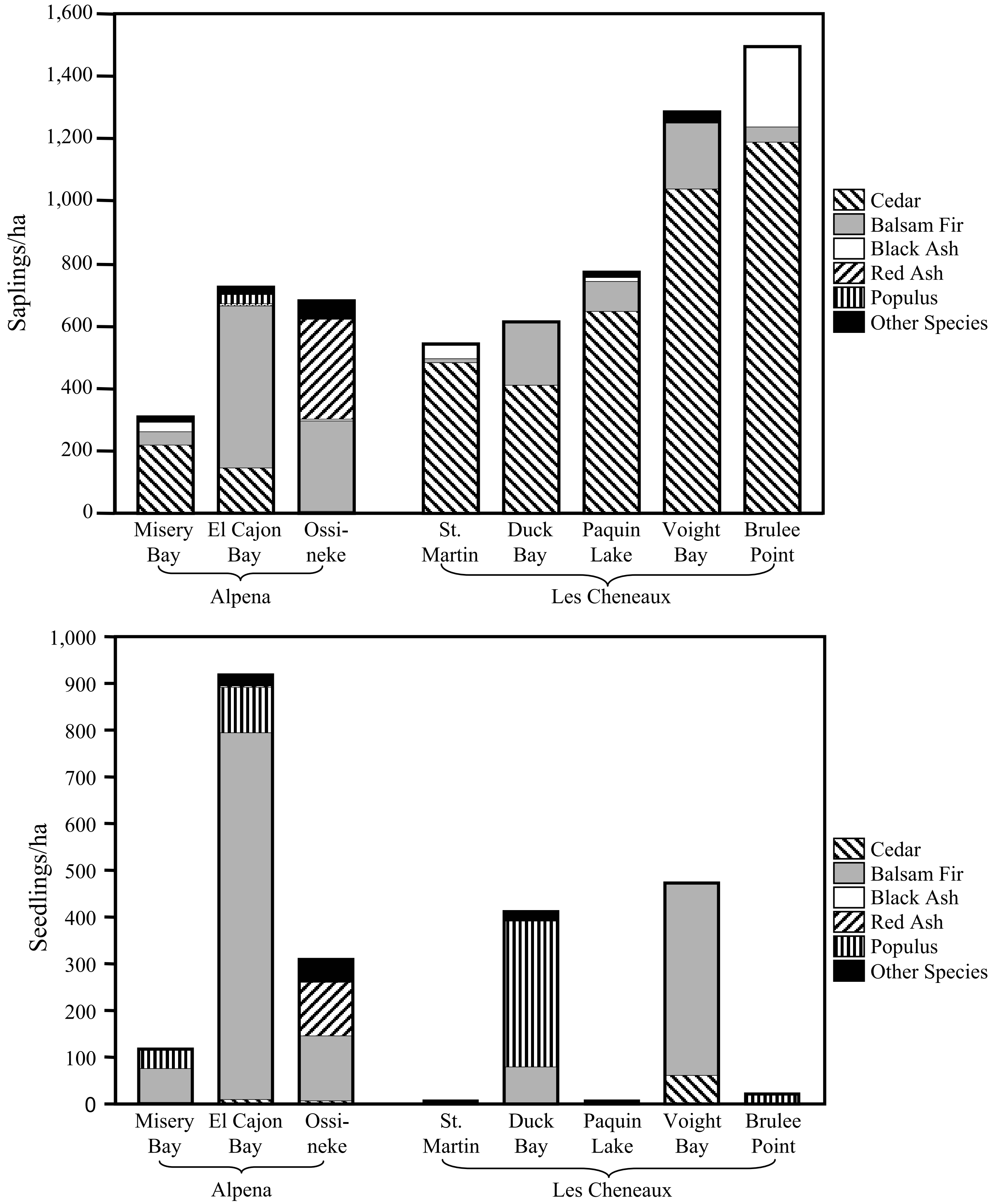


Figure 10. Comparison of species composition of the sapling (1.5-9.0 cm dbh) and seedling (taller than 50 cm and less than 1.5 cm dbh) layers among three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands (Populus includes balsam poplar and trembling aspen).

In contrast, almost all of the balsam fir saplings were located in the shallow depression, where balsam fir regeneration was often dense around the edge of the depression and on microsites that were elevated above the high-water marks. Additional sapling species include black spruce, red maple, eastern white pine, black ash, northern white-cedar, paper birch, tamarack, and silver maple (Appendix F).

The composition of the seedling layer at Ossineke was similar to that of the sapling layer (Figure 10). Red ash and balsam fir were the most abundant species, and the two species were present in nearly equal proportions. However, red ash was present in all sites, while balsam fir was only present in the relatively dry microsites of the depression. Addition seedling species include tamarack, eastern white pine, black spruce, and northern white-cedar (Appendix F).

Shrubs were only a minor component of the conifer-dominated swamps of Alpena County. No shrub species were recorded in the understory at Misery Bay. The density of shrubs at El Cajon Bay was only 25/ha, and the average coverage was only 0.4% (Appendix G). The shrub species present at El Cajon Bay were serviceberry (*Amelanchier sp.*), mountain maple (*Acer spicatum*), and round-leaved dogwood (*Cornus rugosa*).

In contrast to the conifer-dominated swamps where shrubs were sparse or absent, shrubs were abundant in the hardwood-dominated swamp at Ossineke. The shrub density at Ossineke, 11,205 stems/ha, was greater than the density of overstory trees and understory seedlings and saplings. The most abundant shrubs were speckled alder (*Alnus rugosa*), meadowseet (*Spiraea alba*), and bog birch (*Betula pumila*) (Appendix G). Speckled alder was abundant in all parts of the hardwood swamp. Meadowsweet and bog birch were most abundant along the edge of the open meadow. The large number of shrubs at Ossineke and the abundance of shrubs species such as meadowsweet and bog birch, which typically grow under open conditions, suggests that the site might not have previously been forested.

Ground-Cover Vegetation

Ground-cover species composition varied between the conifer- and hardwood-dominated sites. Balsam fir was the most abundant tree seedling in the ground cover of the conifer-dominated swamps, but red ash was the most abundant tree seedling in the ground cover at Ossineke (Appendix H). Shrubs were a minor component of the conifer-dominated swamps, where the average coverage of tall and short shrubs combined was only 1.4% at El Cajon Bay and 0.1% at Misery Bay (Table 4). At Ossineke, the average coverage of tall and short shrubs combined was 6.1%. Short shrubs including meadowsweet and bog birch were abundant in the wet swale and adjacent to the open meadow. Woody vines were absent from all sites. Characteristic forbs of the conifer-dominated swamps include colt's foot (*Petasites frigidus*), large-leaved aster (*Aster macrophyllus*), and Canada mayflower (*Maianthemum canadense*), while dwarf raspberry (*Rubus pubescens*), whorled loosestrife (*Lysimachia thyrsiflora*), and northern bugle weed were the most abundant forbs at Ossineke. The presence of acidifiles, such as Canada mayflower, illustrates the importance of the tree-base hummocks in regulating species composition at the conifer-dominated swamps. Characteristic sedge species of the conifer-dominated swamps (*Carex eburnea* and *Carex deweyana*) were different from those of the hardwood-dominated swamp, where tussock sedge was the most abundant sedge species. Two additional sedge species (*Carex intumescens* and *Carex trisperma*) were present in the hardwood-dominated swamp but absent from the conifer-dominated swamps. Ferns were common at all sites, but fern species composition differed between the conifer- and hardwood-dominated sites. Rattlesnake fern (*Botrichyium virginianum*), bulblet fern (*Cystopteris bulbifera*), and oak fern (*Gymnocarpium dryopteris*) were the most abundant ferns of the conifer-dominated sites, while sensitive fern *(Onoclea sensibilis*) and marsh fern (*Thelypteris palustris*) were the most abundant ferns at Ossineke (Appendix H).

The composition of the ground-cover layer also varied between the two conifer-dominated sites. With a total of 54 species, an average of 7.2 species per plot, and an average of 41% cover, the ground cover of El Cajon Bay was much more diverse than that of Misery Bay, where there were 32 total species, an average of 4.0 species per plot, and an average coverage of 13% (Table 4). Forbs including twinflower (*Linnaea borealis*), dwarf bishop's cap (*Mitella nuda*), gay-wings (*Polygala paucifolia*), goldthread (*Coptis trifolia*), and ground dogwood (*Cornus canadensis*) were abundant at El Cajon Bay, but they were not sampled at Misery Bay (Appendix H). Bulblet fern was common at El Cajon Bay, especially near the stream channel, but it was not present at Misery Bay.

Non-native plants were a minor component of the ground cover at all sites. There were no non-native species present at Ossineke, and the average coverage of non-native species was only 2% at Misery Bay and 0.6% at El Cajon Bay (Table 4). The only non-native species present were bull thistle (*Cirsium vulgare*), dandelion (*Taraxacum officionale*), and helleborine (*Epipactis helleborine*) (Appendix H). Based on observations at other sites, these species generally do not pose a threat to native vegetation.

Table 4. Comparison of ground-cover data among three coastal swamp forests of Alpena County and five coastal swamp forests of the Les Cheneaux Islands.

Species	Alpena			Les Cheneaux Islands				
	Misery Bay (n=20)	El Cajon Bay (n=20)	Ossi-nike (n=20)	St. Martin (n=20)	Duck Bay (n=10)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)
Total # of Species	32	54	46	48	27	33	37	48
All Species								
Mean # species/plot	4.0	7.2	10.4	8.0	4.7	4.7	7.6	12.4
Mean coverage/plot	12.8	41.3	57.3	19.4	15.7	12.4	25.7	43.6
Woody Plants								
Mean # species/plot	1.1	2.1	2.6	1.4	0.7	1.3	2.1	2.4
Mean coverage/plot	2.1	6.4	7.8	1.5	0.8	2.2	4.7	6.0
Trees								
Mean # species/plot	1.0	1.7	1.3	1.1	0.4	0.8	1.0	1.0
Mean coverage/plot	2.0	5.0	1.7	1.2	0.5	0.9	2.0	1.3
Tall Shrubs								
Mean # species/plot	0.1	0.2	0.4	0.3	0.3	0.3	0.3	0.8
Mean coverage/plot	0.1	0.5	0.9	0.3	0.3	1.0	0.4	3.3
Short Shrubs								
Mean # species/plot	---	0.2	0.8	---	---	0.2	0.7	0.6
Mean coverage/plot	---	0.9	4.7	---	---	0.3	2.2	1.4
Vines								
Mean # species/plot	---	---	---	---	---	---	---	---
Mean coverage/plot	---	---	---	---	---	---	---	---
Herbaceous Plants								
Mean # species/plot	2.9	5.2	7.8	6.6	4.0	3.4	5.5	10.0
Mean coverage/plot	10.7	35.0	49.5	17.9	14.9	10.2	21.0	37.6
Forbs								
Mean # species/plot	1.8	3.8	4.7	4.6	2.7	1.9	4.4	6.9
Mean coverage/plot	5.0	11.1	12.3	9.9	7.9	4.4	12.8	17.8
Graminoids								
Mean # species/plot	0.7	1.0	2.5	1.4	0.5	1.3	0.9	1.6
Mean coverage/plot	3.6	13.2	31.8	6.2	1.7	5.4	6.0	7.1
Ferns								
Mean # species/plot	0.4	0.5	0.9	0.7	0.8	0.2	0.3	1.5
Mean coverage/plot	2.1	10.7	5.9	1.9	5.3	0.5	0.3	12.7
Native Plants								
Mean # species/plot	6.7	6.9	10.4	8.0	4.5	4.6	7.1	12.2
Mean coverage/plot	10.8	40.8	57.3	19.4	14.6	12.2	25.1	43.3
Non-native Plants								
Mean # species/plot	0.4	0.4	---	---	0.2	0.1	0.5	0.2
Mean coverage/plot	2.0	0.6	---	---	0.1	0.2	0.6	0.3

Les Cheneaux Islands

Site Descriptions

The swamp forests of the Les Cheneaux Islands and the adjacent mainland ranged in size from 4.3 ha at Voight Bay to 8.0 ha at Brulee Point (Table 3). The swamps at St. Martin and Paquin Lake were a series of long, narrow swales situated between upland ridges. Brulee Point was located on broad, flat terrain adjacent to a marsh, and a stream flowed through the swamp. The Duck Bay swamp, on the north side of Marquette Island, was located on a narrow groundwater seepage situated between the marsh and the base of the slope to the upland. At Voight Bay, on the south side of Marquette Island, there was a long, gradual slope from the marsh to the upland. Areas of fen and swamp forest were located between the marsh and the upland forest.

The swamps at all Les Cheneaux sites were dominated by conifers, and the majority of the trees were growing on hummocks that stood 10-50 cm above the general ground level. The hummocks were most likely formed by tree tip ups, and they were often covered by sphagnum moss. Standing water was rarely present at any of the sites, and there were no high-water marks on the trees. The average coverage of water ranged from 0% at Duck Bay to 2% at Paquin Lake (Table 3). At St. Martin and Paquin Lake, transects were run along several different swales. Typically there was no standing water, but water 23 cm deep was recorded in a depression within one of the swales at Paquin Lake. At St. Martin, water 7 cm deep was recorded in a small depression (Table 3).

The soil near the surface at all sites was sapric muck, and it often contained traces of silt (Table 3). The depth of the muck ranged from 18 to 80 cm, but it was usually less than 30 cm deep. Below the muck was mineral soil, and the texture was medium-fine to fine sand at all sites except Duck Bay and Brulee Point, where the soil texture was silt to silt loam. At Brulee Point, clay was encountered below the silt, at a depth of 50 cm. At St. Martin, clay was consistently encountered below the sand, at depths ranging from 35 to 50 cm. In one of the swales at Paquin Lake, the upper 40 cm was sapric muck, and there were layers of sapric and hemic muck from 40 to 80 cm below the surface (Table 3).

At all sites the soil was circumneutral at the surface, and the pH gradually increased with increasing depth, reaching 7.5-8.0 within 60 cm of the surface (Table 3). The soil at the surface of the hummocks was strongly acid, with a pH ranging from 4.0 to 5.3. The acid conditions on the hummocks indicate that they are not strongly influenced by ground water.

Overstory Vegetation

The forests of the Les Cheneaux Islands and the adjacent mainland were cut in the late part of the 19th century or the early part of the 20th century, and the age of the dominant overstory trees at each site reflects regeneration following logging. Several older trees that were left uncut during the logging operations remained at St. Martin and Duck Bay, where trees 152 and 164 years old, respectively, were cored (Table 3). At the other three sites, the oldest trees, 112 years old, were encountered at Voight Bay, and the youngest, 85 years old, at Paquin Lake. Basal area at St. Martin and Duck Bay, 77.5 and 66.1 m^2/ha respectively, was greater than that of the other sites, which ranged from 54.2 to 59.7 m^2/ha in overstory basal area. St. Martin, Paquin Lake, Voight Bay, and Brulee Point were similar to each other in overstory stem density, which ranged from 2,163 to 2,690 stems per ha. However, the overstory stem density at Duck Bay, 1,575 stems per ha, was markedly lower than that of the other sites (Table 3). With better drainage conditions than the other sites due to its location on a gently sloping groundwater seepage rather than in swales or on flat terrain, Duck Bay supported the largest northern white-cedar trees (Appendix E). The occurrence of large northern white-cedar trees at Duck Bay is reflected in its high basal area despite a lower stem density than the other sites.

Northern white-cedar was the dominant overstory species at all sites. It accounted for 84-91% of the overstory stems and 77-91% of the basal area (Figure 9, Appendix E). Paper birch and balsam poplar were also present in the overstory of all sites, and balsam fir and white spruce were present at all sites except Brulee Point. Black spruce was present at all sites except Duck Bay. Additional overstory species include trembling aspen, black ash, tamarack, yellow birch (*Betula alleghaniensis*), eastern white pine, mountain ash (*Sorbus americana*), and striped maple (Appendix E).

Understory Vegetation

Northern white-cedar was the most abundant sapling (1.5-9.0 cm dbh) species at all sites (Figure 10, Appendix F). The majority of the northern white-cedar saplings were formed by layering or tipping of overstory trees. Few, if any, were truly derived from seedlings. At Duck Bay, Paquin Lake, and Voight Bay, balsam fir was the second most abundant sapling species. Black ash was the second most abundant species at St. Martin and Brulee Point. The only other species present in the sapling layer were black spruce, tamarack, and paper birch (Appendix F).

The seedling (taller than 50 cm and < 1.5 cm dbh) density was very low at St. Martin, Paquin Lake, and Brulee Point, where there were only 5-20 seedlings/ha (Figure 10, Appendix F). There were many more seedlings at Duck Bay and Voight Bay, where seedlings density ranged from 410 to 470 seedlings/ha. Balsam fir was the only seedling species at St. Martin, and balsam poplar was the only seedling species at Paquin Lake and Brulee Point. With 270 seedlings/ha, balsam poplar was the most abundant seedling species at Duck Bay. Balsam fir, trembling aspen, and white spruce were also present. At Voight Bay, there were 410 balsam fir seedlings per ha. In addition to balsam fir, northern white-cedar seedlings were present at Voight Bay (Figure 10, Appendix F). The northern white-cedar seedlings were slightly taller than 50 cm, probably just below the snow line. All northern white-cedar seedlings taller than 60-75 cm had been browsed by deer. The absence of northern white-cedar from the seedling layer of all sites except Voight Bay reflects the impact of deer browsing on cedar regeneration.

Shrubs were a minor component of the understory at all swamps, and the shrubs showed a trend of increasing stem density and coverage with decreasing overstory basal area. At all sites the average shrub coverage was less than 1% (Table 3). No shrub species were recorded in the understory at St. Martin and Duck Bay, the sites where overstory basal area was highest, and canopy coverage was probably greatest. Speckled alder was the only shrub species present at Paquin Lake (Appendix G). Meadowsweet and shrubby cinquefoil were present in plots where the canopy was relatively open at Voight Bay. Speckled alder and alder-leaved buckthorn (*Rhamnus alnifolia*) were the only shrub species present at Brulee Point, and they were recorded in plots near the edge of the marsh, where canopy coverage was relatively low (Appendix G).

Ground-Cover Vegetation

The total number of species recorded in the ground cover ranged from 27 at Duck Bay to 48 at St. Martin and Brulee Point (Table 4). With an average of 12.4 species per plot and an average coverage of 44%, the ground-cover species diversity at Brulee Point was greater than that of all other sites, where the average number of species per plot ranged from 4.7 to 8.0 and the average coverage ranged from 12 to 26% (Table 4).

Seedlings (shorter than 50 cm) of balsam fir, paper birch, black ash, northern white-cedar, and balsam poplar were present at most sites (Appendix H). With an average combined coverage of tall and short shrubs of 4.7% or lower at all sites, shrubs were a minor component of the ground cover (Table 4). Low light levels on the forest floor due to the dense canopy of northern white-cedar trees was probably a major factor contributing to the low abundance of shrubs in the ground cover. Shrub coverage was highest at Voight Bay, where canopy coverage was relatively low. The coverage of shrubs decreased with increasing overstory basal area, and probably also with increasing canopy coverage. In contrast to Saginaw Bay, where vines were present at every site, woody vines were absent from all sites of the Les Cheneaux Islands (Table 4).

Characteristic forb species of the Les Cheneaux swamps include large-leaved aster, small bedstraw, twinflower, Canada mayflower, dwarf bishop's cap, colt's foot, gay-wings, dwarf raspberry, and starflower (*Trientalis borealis*) (Appendix H). The greatest diversity of forbs was recorded at St. Martin, Brulee Point, and Voight Bay. The coverage of graminoids was between 5.4 and 7.1% at all sites except Duck Bay, where the coverage of graminoids was only 1.7% (Table 4). Several sedges (*Carex eburnea, Carex disperma*, and *Carex pedunculata*) were present at most sites. Horsetail (*Equisetum spp.*) and ferns were common at all sites, and they were especially abundant at St. Martin, Duck Bay, and Brulee Point (Table 4). The most abundant fern species include crested wood fern, rattlesnake fern, and oak fern (Appendix H).

Non-native species were a minor component of the ground cover at all sites. The average cover of non-native species was less than 1% at all sites, and the only non-native species present were hawkweed (*Hieracium spp.*), dandelion, and helleborine (Appendix H). Based on observations at other sites, these species do not generally pose a threat to native vegetation.

Comparisons Among Major Study Areas

Physical Site Characteristics

The conifer-dominated swamps of Alpena County and the Les Cheneaux Islands were similar to each other in physical site characteristics, but their physical site characteristics were markedly different from those of the hardwood-dominated swamps of Saginaw Bay and Ossineke. In the conifer-dominated swamps, standing water was only recorded in small, shallow depressions, the majority of the overstory trees were growing on hummocks that stood 10-50 cm above the general ground level, and high-water marks were never present on the trees. In contrast, at all hardwood-dominated swamps except Wildfowl Glade, almost the entire soil surface was inundated during the early part of the growing season and high-water marks were present on the trees. Inundation of the soil surface in the hardwood-dominated portion of the Ossineke site, but not in parts of the site that were dominated by conifers, suggests that differences in canopy composition were related to hydrologic conditions rather than recent disturbances. However, the young age of the trees and the abundance of shrubs at Ossineke suggest that the hardwood-dominated parts of the sites may have previously supported shrub swamp or open meadow vegetation.

The substrate of all sites in Saginaw Bay was mineral soil, but the substrate was muck in all swamps of Alpena County and the Les Cheneaux Islands. Although the majority of the soil surface of the Saginaw Bay swamps was inundated during the early part of the growing season, the water table fell well below the soil surface later in the summer. The regular soil aeration due to the draw down of water provides favorable conditions for rapid decomposition, preventing the accumulation of organic matter. Within the conifer-dominated swamps, the soil surface remained saturated throughout the growing season but the water table does not fluctuate widely, as it does in Saginaw Bay. Decomposition is slow due to the constant saturation of the soil surface, and muck has accumulated in all conifer-dominated sites. Although standing water was present at Ossineke, the water level probably does not draw down to the same extent that it does in Saginaw Bay, resulting in slower decomposition and the accumulation of a relatively shallow layer of sapric muck.

The soil texture at the surface of all sites in Saginaw Bay except Wigwam Bay, and below the muck at all conifer-dominated sites except Duck Bay and Brulee Point was medium-fine to fine sand. The sand was deposited, either by streams or by differential erosion of surface sediments, into the proglacial lakes that previously covered all sites. Then it was redeposited by wave action along the margins of the proglacial lakes as they receded to their present levels. The silty material of Wigwam Bay, Duck Bay, and Brulee Point was probably deposited in local ponded areas. Clay was encountered within the upper 100 cm at almost all sites. At Ossineke, Misery Bay, Duck Bay, and Voight Bay, where clay was not encountered, it was probably present deeper below the surface. Clay was present near the surface in marsh transects at Misery Bay, Duck Bay, and Voight Bay (Dennis Albert, personal communication). At Wildfowl Glade and Wildfowl Swale, where bedrock was present within 100 cm of the surface, there was no clay below the sand. At Ossineke, there was a cobble band, probably a buried cobble beach below the sand, and clay was not encountered.

The soil pH of all sites was circumneutral at the soil surface, and the soil pH gradually increased with increasing depth, becoming calcareous within the upper 50 cm. The cycling of calcareous material in the ground water is an important process that leads to the high soil pH. At all conifer-dominated swamps, the soil pH on the surface of the hummocks was strongly acid, indicating that the hummocks are not strongly influenced by ground water. Sphagnum moss was also present on many of the hummocks, probably contributing directly to the acid conditions. The soil pH of the low rises in several of the swamps of Saginaw Bay and the tussock sedge hummocks at Ossineke was similar to that of the general ground surface, indicating that ground water maintains the calcareous conditions on the low rises and tussock sedge hummocks, where the soil surface is regularly inundated.

Vegetation

The age of the dominant overstory trees in the conifer-dominated swamps of Alpena County was similar to that of the swamps in the Les Cheneaux Islands, but the dominant overstory trees in Saginaw Bay were much younger than those of the northern sites. The present canopy trees of the conifer swamps of Alpena County and the Les Cheneaux Islands probably established following cutting of the previous forests in the late part of the 19th century. Several of the trees in the Les Cheneaux sites were probably present in the previous forest prior to cutting and were left uncut. For wetland forests on calcareous soil of the lake plain that were cut in the late 19th Century (Deeter and Matthews 1926), successful regeneration by northern white-cedar has resulted in few changes from the previous forest composition (Albert 1995). Although many of the swamp forests of Saginaw Bay were cleared and drained for agriculture in the middle and late parts of the 19th century, swamps located on sandy soil close to the shoreline were not as useful for agricultural purposes and they were not cut until the early part of the 20th century. Dominant overstory trees at Ossineke were slightly younger than the overstory trees of Saginaw Bay, and they were much younger than the trees in the conifer-dominated swamps of Alpena County. The young age of the overstory trees, and the abundance of sedges and shrubs suggest that the trees may have recently colonized sites that supported shrub swamp or sedge meadow vegetation rather than forest.

Stem density and basal area of the overstory trees of the conifer-dominated swamps in Alpena County were within the range of density and basal area of the swamps of the Les Cheneaux Islands. However, density and basal area of the overstory trees in the hardwood-dominated swamps was often less than half that of the conifer-dominated swamps. At Ossineke, the overstory stem density was within the range of overstory density of the swamps of Saginaw Bay, but the overstory basal area was slightly lower than that of all Saginaw Bay Swamps except Wildfowl Glade. The overstory basal area of Ossineke, 21.3 m^2/ha, was almost the same as that of Wildfowl Glade 22.3 m^2/ha. Although the younger age of the overstory trees at Ossineke than those of Saginaw Bay partially accounts for the lower basal area, differences in basal area are probably also influenced by differences in hydrologic conditions and substrate. The water level falls well below the surface in late summer at all sites in Saginaw Bay, but the soil surface remains saturated throughout the growing season at Ossineke, resulting in accumulation of muck and reduced rates of tree growth. The low basal area at Wildfowl Glade is most likely related to shallow rooting because the bedrock is close to the surface and the soil above the bedrock is probably saturated throughout much of the growing season.

The composition of the understory and ground-cover vegetation revealed trends among the three major study areas. At all sites the major overstory dominants were also the most abundant species in the sapling layer, indicating that major changes in overstory composition are unlikely in the absence of major disturbance in the near future. However, the low abundance of northern white-cedar seedlings in all of the conifer-dominated swamps, due primarily to excessive deer browsing (Zasada 1952, Van Deelen et al. 1996), indicates that under the present deer population, the relative abundance of northern white-cedar is likely to gradually decrease in these swamps.

Shrubs were a minor component of the swamp forest at all sites except Ossineke. The abundance of shrubs at Ossineke was probably related to the relatively open canopy conditions, and the high abundance of shrubs may indicate that it was previously a shrub swamp. Despite the inundation of the soil surface in the swamps of Saginaw Bay and Ossineke, the swamps of Saginaw Bay were characterized by higher canopy coverage due to accelerated rates of tree growth when water levels fall in the late part of the growing season.

Woody vines were abundant in all swamps of Saginaw Bay, but there were no woody vines in the swamp forests of Alpena County or the Les Cheneaux Islands. Many woody vines cannot tolerate the low light levels of the conifer-dominated swamps, and woody vines are often restricted to large river valleys in the northern part of the state. While there were few ferns in the swamps of Saginaw Bay, ferns were abundant in the swamps of Alpena County and the Les Cheneaux Islands, where they accounted for up to one-third of the total coverage of the ground-cover layer. The low soil pH on the hummocks in the conifer-dominated swamps plays an important role in regulating species composition. Acidifiles, such as creeping-snowberry (*Gaultheria hispidula*) and Canada mayflower, were restricted to the hummocks in the conifer-dominated swamps, and acidifiles were not present in the hardwood-dominated swamps. The occurrence of acid hummocks within swamps where the pH of the general ground surface is circumneutral promotes a high species diversity, where acidifiles and calcifiles grow adjacent to each other.

Non-native species were not abundant in any of the swamps. Although there is undoubtedly a large seed pool for non-native species in Saginaw Bay, the combination of inundation of the soil surface and the relatively high canopy coverage probably limits the establishment and growth of non-native species. The canopy coverage of the conifer-dominated swamps was higher than that of the hardwood-dominated swamps. Although most of the soil surface in the conifer-dominated swamps was not inundated in the early part of the summer, low light levels on the forest floor due to higher canopy coverage are probably the dominant factor leading to the low abundance of non-native species. In addition, the seed pool for non-native species in northern Michigan is relatively low, compared to that of southern Michigan. At Ossineke, where no non-native species were recorded, the lack of non-native species may be due to the combined influence of standing water throughout much of the growing season and a relatively small seed pool for non-native species.

Land-Cover Change Along the Lake Huron Shoreline

Land cover along the Lake Huron shoreline has changed dramatically over the last 150 years. Along the Saginaw Bay shoreline in the early 1800s, non-forested wetland was the most abundant land-cover type, followed by upland forest/savanna, and nearly equal proportions of conifer- and hardwood-dominated swamp (Table 5). While all types of forested and non-forested wetland accounted for a combined total of 18,409 ha along the Bay in the early 1800s, only 9,702 ha of wetland remained in 1978. The 7,139-ha increase in agricultural land cover since the early 1800s accounts for much of the total wetland loss. Draining of swamps and burning of their organic soil to allow for agricultural land use probably accounts for the majority of the loss of conifer-dominated swamps and a large portion of the loss of non-forested wetlands (Deeter and Matthews 1926). Despite a loss of nearly all of the conifer-dominated swamps and 59% of the non-forested wetlands, the area of hardwood-dominated swamps along Saginaw Bay has increased by 35% over the last 150 years. The increase in hardwood-dominated swamps is most likely due to conversion of non-forested wetlands to hardwood dominated swamps, either through a lack of fire or a lowering of the water table by artificial drainage. In addition to losses of conifer-dominated swamp and non-forested wetlands along the Bay, 68% of the upland forest and savanna has been lost. The area of upland forest/savanna lost is nearly identical to the increase in urban land cover. While agricultural development in Saginaw Bay largely took place in wetlands where the soil organic matter content was high, urban development primarily took place in the uplands where drainage was not necessary.

In the early 1800s, the Lake Huron shoreline in the Northern Lower Peninsula was dominated by nearly equal proportions of upland forest/savanna (while the joint upland class of forest/savanna was utilized in the analysis, forest rather than savanna was prevalent along the shoreline) and conifer-dominated swamp (Table 5). Additional land-cover classes were a minor component of the shoreline. However, by 1978, three-quarters of the conifer-dominated swamp had been lost while the area of upland forest/savanna remained nearly unchanged. Logging of the conifer-dominated swamps undoubtedly led to large increases in hardwood-dominated swamp and non-forested wetland. In addition to the conversion of conifer-dominated swamps to other wetland types, many of the conifer-dominated swamps were probably converted to urban land cover. The combined increase in the area of hardwood-dominated swamp, non-forested wetland, and urban land cover, 10,898 ha, is nearly identical to the decrease in coverage of conifer-dominated swamp, 11,003 ha. In contrast to Saginaw Bay, where 29% of the shoreline was under agricultural land cover in 1978, only 1.5% of the shoreline in the Northern Lower Peninsula was under agricultural land cover in 1978 (Table 5).

In the Upper Peninsula, the Lake Huron shoreline was dominated by upland forest and conifer-dominated swamp in the early 1800s (Table 5). By 1978, there had been little change in the extent of upland forest, but two-thirds of the conifer-dominated swamp had been lost. Much of the decrease in conifer-dominated swamp can be accounted for by increases in hardwood-dominated swamp, non-forested wetland, and urban land cover. As in the Northern Lower Peninsula, agricultural land cover was only a minor component of the Lake Huron shoreline in the Upper Peninsula in 1978.

Several major trends in land-cover change occurred along the shoreline from the early 1800s to 1978. While considerable losses of conifer-dominated swamp occurred in all three portions of the shoreline, the largest proportional loss was along Saginaw Bay, and the proportional losses of conifer-dominated swamp progressively decreased toward the northern part of the shoreline. The loss of conifer-dominated swamp was accompanied by an increase in hardwood-dominated swamp in all parts of the shoreline. In the Northern Lower Peninsula and the Upper Peninsula, where non-forested wetland was previously a minor component of the shoreline, the loss of conifer-dominated swamp was accompanied by an increase in non-forested wetland. In Saginaw Bay, where non-forested wetland was the most abundant land-cover type in the early 1800s, 59% of the non-forested wetland had been lost by 1978. The total loss of wetlands in Saginaw Bay can largely be accounted for by an increase in agricultural land cover. In the Northern Lower Peninsula and the Upper Peninsula, where agricultural land cover is not abundant along the lakeshore, much of the wetland loss can be accounted for by increases in urban land cover. While the areal extent of upland forest remained largely unchanged in the Upper Peninsula and Northern Lower Peninsula, 68% of the upland forest/savanna has been lost along Saginaw Bay. Upland forests of Saginaw Bay were cleared for both urban and agricultural

Table 5. Comparison of ~1800 and 1978 land cover within 1 km of the Lake Huron shoreline in Saginaw Bay (Port Austin to Tawas City), the Northern Lower Peninsula (Harrisville to the Mackinac Bridge), and the Upper Peninsula (Mackinac Bridge to De Tour Village).

	~1800		1978		Change	
Land Cover	ha	%	ha	%	ha	%
Saginaw Bay						
Conifer-Dominated Swamp	4,001	16.3	11	0.0	-3,990	-99.7
Hardwood-Dominated Swamp	4,041	16.5	5,460	22.4	+1,419	+35.1
Non-Forested Wetland	10,367	42.2	4,231	17.3	-6,136	-59.2
Upland Forest/Savanna	5,913	24.1	1,866	7.6	-4,047	-68.4
Sand Dune/Beach	80	0.3	102	0.4	+22	+28.2
Lake/River	140	0.6	448	1.8	+308	+220.3
Urban	---	---	3,944	16.2	+3,944	+>100
Agriculture	---	---	7,139	29.3	+7,139	+>100
Other	---	---	1,190	4.9	+1,190	+>100
TOTAL	24,542	100.0	24,391	100.0		
Northern Lower Peninsula						
Conifer-Dominated Swamp	14,631	47.6	3,628	11.2	-11,003	-75.2
Hardwood-Dominated Swamp	293	1.0	5,203	16.0	+4,910	+1,674.5
Non-Forested Wetland	396	1.3	2,304	7.1	+1,908	+481.9
Upland Forest/Savanna	14,893	48.5	15,004	46.2	+111	+0.7
Sand Dune/Beach/Exposed Rock	31	0.1	449	1.4	+418	+1,344.1
Lake/River	462	1.5	499	1.5	+38	+8.2
Urban	---	---	4,080	12.6	+4,080	+>100
Agriculture	---	---	499	1.5	+499	+>100
Other	---	---	807	2.5	+807	+>100
TOTAL	30,706	100.0	32,472	100.0		
Upper Peninsula						
Conifer-Dominated Swamp	4,603	28.8	1,541	9.4	-3,062	-66.5
Hardwood-Dominated Swamp	---	---	586	3.6	+586	+>100
Non-Forested Wetland	332	2.1	904	5.5	+572	+172.4
Upland Forest	10,869	68.0	10,728	65.8	-141	-1.3
Lake/River	72	0.5	101	0.6	+29	+39.9
Urban	---	---	1,543	9.5	+1,543	+>100
Agriculture	---	---	457	2.8	+457	+>100
Other	108	0.7	451	2.8	+343	+317.6
TOTAL	15,983	100.0	16,311	100.0		

development, with urban or residential development accounting for the greater part.

Present Land Cover Surrounding the Study Sites

The 1978 land cover surrounding each of the study sites provides a representative example of the characteristic land cover in each part of the shoreline. The trend of decreasing agricultural land cover and increasing forest land cover from south to north is apparent based on the land cover surrounding each of the study sites (Figure 11). The swamp forests of Saginaw Bay are located in a landscape dominated by agricultural land cover (Figure 11a). The swamp forests of Alpena County are surrounded by forest, and there is a large area of agricultural land inland of Ossineke, several km from the study site (Figure 11b). The City of Alpena is a large urban area located just over 5 km from the swamp forests at El Cajon Bay and Misery Bay. A large industrial site where concrete is produced is located on the east side of the city, closest to the study sites. In the Les Cheneaux Islands and the adjacent mainland, forest is the predominant land-cover type (Figure 11c). Urban and agricultural land cover account for only a very small portion of the land surrounding the swamp forests of the Les Cheneaux Islands.

Saginaw Bay

In Saginaw Bay, agricultural land cover is abundant within 1 km of all swamp forests except the two sites on the islands of Wildfowl Bay. Non-natural land-cover classes accounted for the following proportions of the land cover within 1 km of the Saginaw Bay sites: Pinconning, 79%; Wigwam Bay, 65%; King Road, 62%; Tobico Marsh, 53%; and Pigeon Road, 26% (Table 6). Deciduous forest, forested wetland, and non-forested wetland were the only land-cover types within 1 km of Wildfowl Glade and Wildfowl Swale. Agricultural land cover was abundant within 1 km of all other sites, and urban land cover was present within 1 km of all sites except King Road (Table 6).

Despite the abundance of non-natural land cover surrounding the majority of the swamps, the direct effects of disturbance on vegetative composition were not evident within the swamps. Red ash, silver maple, American elm, and sometimes eastern cottonwood, were the dominant species at all sites, and the proportions of these species were similar at all sites except Wildfowl Glade, which was a nearly pure stand of red ash (Figure 6). In other studies of similar forested wetlands on the lake plain, silver maple, American elm, bur oak, and red ash were the dominant species in an old-growth forest in northwestern Ohio (Boerner and Cho 1987), and red ash, eastern cottonwood, and silver maple were the dominant species in swamps on islands and along the shore of Lake Erie (Boerner 1984). Similarities in overstory species composition between the coastal swamp forests of Saginaw Bay and those of Lake Erie suggest that the present canopy species are characteristic of the conditions along the coast of the Great Lakes in southern Michigan. However, in both areas, similar highly intensive land-use history makes historic change analysis difficult.

At all sites, red ash, silver maple, and American elm accounted for the majority of the understory saplings and few other sapling species were present (Figure 7). The similarities between the composition of the overstory and understory indicate that the overstory species composition is unlikely to change markedly in the absence of disturbance. One exception is the gradual loss of eastern cottonwood, which was absent from the understory at all sites. Eastern cottonwood is a fast-growing, very intolerant species (Barnes and Wagner 1981) that is relatively common along Great Lakes shorelines. It most likely established under the open conditions that resulted following logging of the swamps forests. Regeneration of eastern cottonwood is unlikely at these sites without major disturbances, such as large-scale windthrow events. Such large-scale windthrow events were commonly recorded in GLO survey records along Saginaw Bay in the early part of the 19th century.

The low abundance of shrubs is probably related to inundation of the soil surface during the early part of the growing season and the relatively high canopy coverage. A relatively low number of shrub species can tolerate inundation of the soil surface during the growing season, and shrubs that can tolerate such conditions typically require high light levels. For example, buttonbush (*Cephalanthus occidentalis*) is a characteristic species of sites where the soil surface is inundated most of the growing season, but it was never abundant in the swamp forests of Saginaw Bay. The relatively high canopy coverage of the swamp forests in Saginaw Bay probably accounts for the low abundance of buttonbush, which generally requires open conditions (Barnes and Wagner 1981). The low abundance of non-native species, despite a large seed pool in Saginaw Bay, is probably also related to the combination of inundation of the soil surface during the growing season and relatively high canopy coverage.

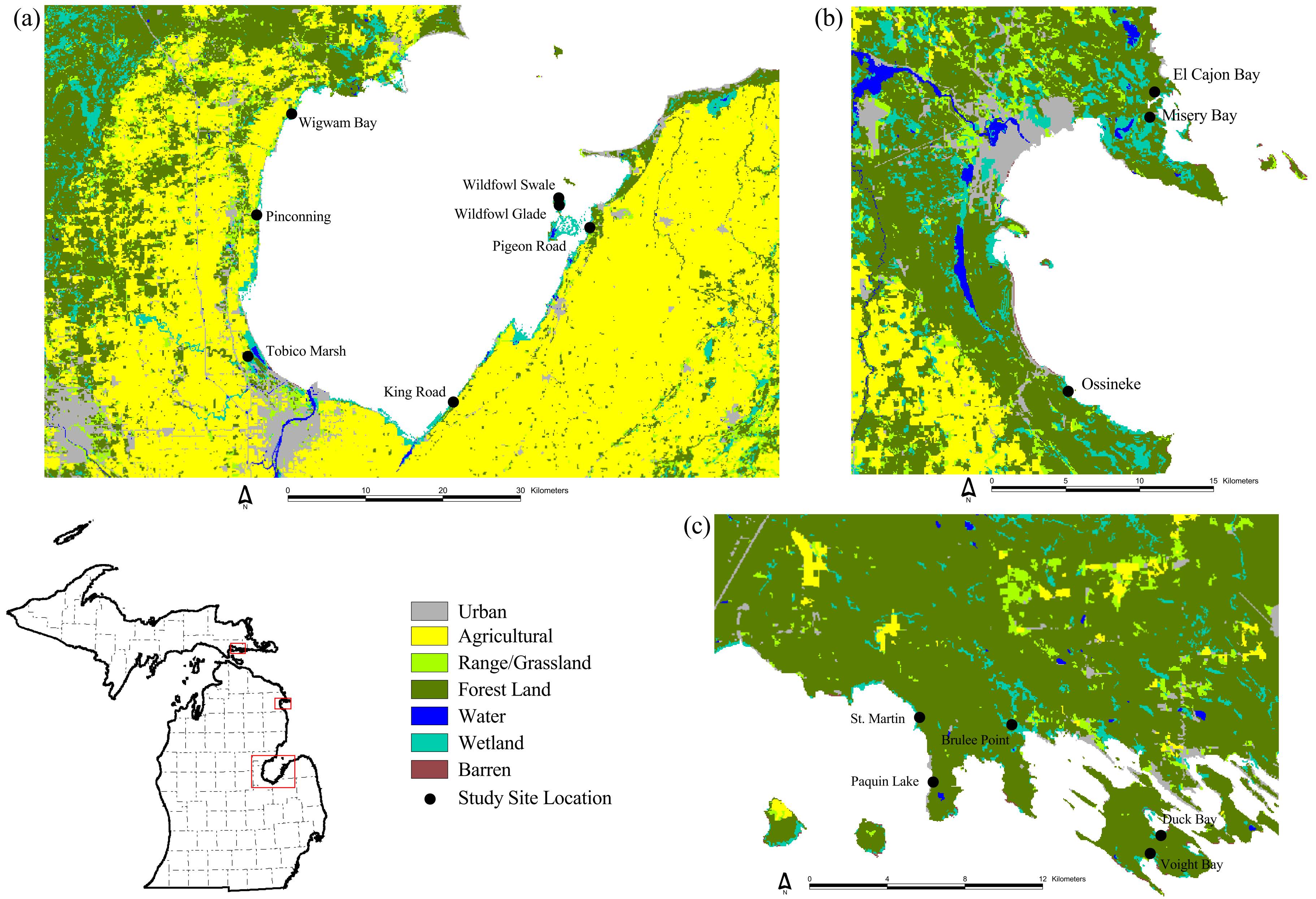


Figure 11. Location of study sites in (a) Saginaw Bay, (b) Alpena, and (c) Les Cheneaux Islands in relation to 1978 land cover (Land cover classification is based on Andersen et al. 1976, level 1).

Table 6. Comparison of land cover within a 1-km buffer of seven swamp forests in Saginaw Bay (land cover is based on an Andersen Level 2 classification of 1978 MIRIS Data, with lake excluded)

	Wildfowl Swale		Wildfowl Glade		Pigeon Road		Tobico Marsh		King Road		Wigwam Bay		Pin-conning	
Land Cover	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Natural Land Cover														
Deciduous Forest	82	32	22	25	181	58	85	19	76	31	31	14	25	9
Coniferous Forest	---	---	---	---	---	---	4	1	---	---	---	---	---	---
Forested Wetland	74	29	35	39	---	---	56	13	4	2	35	16	6	2
Nonforested Wetland	102	39	32	36	51	16	66	15	12	5	14	6	18	7
River	---	---	---	---	---	---	---	---	---	---	---	---	6	2
SUBTOTAL	258	100	89	100	233	74	211	47	91	38	80	35	55	21
Non-Natural Land Cover														
Residential	---	---	---	---	12	4	4	1	---	---	1	1	23	9
Commercial	---	---	---	---	1	1	---	---	---	---	---	---	---	---
Transportation	---	---	---	---	---	---	5	1	---	---	---	---	1	1
Other Urban/Built Up	---	---	---	---	---	---	9	2	---	---	---	---	---	---
Cropland, Pasture	---	---	---	---	23	7	164	37	142	59	81	36	34	13
Herbaceous Rangeland	---	---	---	---	8	2	5	1	---	---	20	9	72	27
Shrub Rangeland	---	---	---	---	31	10	50	11	7	3	44	20	67	26
Permanent Pasture	---	---	---	---	---	---	---	---	---	---	---	---	6	2
Open Land	---	---	---	---	6	2	---	---	2	1	---	---	5	2
SUBTOTAL	---	---	---	---	80	26	237	53	150	62	147	65	207	79
TOTAL	258	100	89	100	312	100	448	100	241	100	227	100	262	100

The relatively low species diversity and coverage of the ground-cover layer in the swamp forests of Saginaw Bay is probably also related to the same two factors: inundation the growing season and relatively high canopy coverage. Low diversity is not necessarily the result of human-induced disturbance. Despite differences in the land cover surrounding each swamp, there was a relatively narrow range in the number of species per plot and average coverage among the sites. At King Road, which was characterized by the lowest average number of species per plot and the lowest average coverage of the ground-cover layer, the total coverage of the natural land-cover classes (38%) accounted for a larger proportion of the land cover within 1 km of the site than natural land-cover classes at Wigwam Bay (35%) and Pinconning (21%), where there were more species per plot and a higher coverage of the ground-cover layer (Tables 2 and 5). However, cropland, the most intensive type of agricultural land cover, accounted for 59% of the land cover within 1 km of the King Road site. Also, the King Road site was smaller than the other sites, resulting in a greater proportion of edge conditions. Although the low species diversity and coverage of the ground-cover vegetation at the King Road site may be related to its small size and the abundance of cropland near the site, the average number of species per plot and the average coverage of the ground-cover layers was only slightly higher at Wildfowl Swale, where there was no non-natural land cover within 1 km of the site (Tables 2 and 5). In addition, cropland was the dominant land-cover type surrounding Tobico Marsh (Table 6), but the average number of species per plot and the average coverage of the ground-cover layer at Tobico Marsh was greater than that of all other sites except Wildfowl Glade, where canopy coverage was lowest and standing water was not present (Table 2).

Although the land cover and hydrology of the sites on the islands of Wildfowl Bay has not been dramatically altered in recent time, the sites are not useful as a baseline for determining the effects of disturbance at other sites. With bedrock less than 100 cm below the soil surface, the physical conditions of the sites on the islands were markedly different from those of the mainland. Due to the lack of standing water or high-water marks on the trees at Wildfowl Glade, it is not useful for comparisons to sites on the mainland, where the soil surface was inundated. Although the swales on the islands of Wildfowl Bay were similar to swales on the mainland, a low number of plots were sampled at Wildfowl Swale due to the small area of the swale. With a much smaller sample at Wildfowl Swale than at similar sites on the mainland, it is difficult to identify meaningful relationships in the data.

Alpena County and the Les Cheneaux Islands

In contrast to the Saginaw Bay sites, where non-natural land-cover classes dominated the land cover within 1 km of most sites, the proportion of non-natural land cover within 1 km of the Alpena County and Les Cheneaux sites was 7% or less at all sites (Table 7). With such a small proportion of altered land cover adjacent to the swamps and so little evidence of disturbance in the composition and structure of the vegetation, it is difficult to interpret trends in the present vegetation that relate to land cover in the surrounding landscape. Paquin Lake was located adjacent to M-134 and an area of 21 ha (7%) within 1 km of the site was under residential land cover, but the composition and structure of the overstory and understory vegetation was similar to that of the other conifer-dominated sites. Although the average number of ground-cover species per plot and the average coverage of the ground-cover vegetation at Paquin Lake were lower than that of any other site in the Les Cheneaux Islands, the ground-cover characteristics of Paquin Lake were similar to those of Misery Bay, where there was very little residential land cover in the 1-km buffer (Table 7). Although Duck Bay is located on an island and there is no residential land cover within 1 km of the swamp, the ground-cover species diversity and coverage at Duck Bay were only slightly higher than those of Paquin Lake (Table 4).

Although the present vegetation at Ossineke is probably different from the *circa* 1800 vegetation, almost all of the land surrounding the Ossineke site was under a natural land-cover class, and the differences between current and historical vegetation are probably related to changes in disturbance regimes rather than changes in land cover. Occasional years of high water levels in the swamps associated with high water levels in Lake Huron, or occasional wildfires, may have promoted marsh vegetation at the parts of the Ossineke site where hardwood-dominated swamps now occur. However, because the physical site conditions at Ossineke are markedly different from those of the other sites in Alpena County and those of the Les Cheneaux Islands, it is difficult to interpret the influence of disturbance on the present vegetation.

Changes from *circa* 1800 Conditions

Saginaw Bay

At many of the sites in Saginaw Bay, the present vegetation is different from the *circa* 1800 vegetation,

Table 7. Comparison of land cover within a 1-km buffer surrounding three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands (land cover is based on an Andersen level 2 classification of 1978 MIRIS data, with lake excluded).

	Alpena						Les Cheneaux									
	Ossi-neke		Misery Bay		El Cajon Bay		St. Martin		Voight Bay		Duck Bay		Brulee Point		Paquin Lake	
Land Cover	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Natural Land Cover																
Deciduous Forest	82	28	101	32	132	38	131	34	93	25	96	56	94	24	101	35
Coniferous Forest	156	54	89	28	132	38	228	60	242	66	63	37	218	55	165	57
Forested Wetland	6	2	100	31	18	5	14	4	6	2	3	2	31	8	---	---
Nonforested Wetland	41	14	20	6	52	15	5	1	22	6	5	3	38	10	---	---
SUBTOTAL	285	99	310	97	334	97	378	99	363	99	167	97	380	97	266	93
Non-Natural Land Cover																
Residential	---	---	7	2	6	2	2	1	---	---	---	---	3	1	21	7
Herbaceous Rangeland	1	1	---	---	4	1	2	1	2	1	---	---	8	2	---	---
Shrub Rangeland	---	---	3	1	---	---	---	---	---	---	---	---	3	1	---	---
Beach	1	1	---	---	1	1	---	---	2	1	5	3	---	---	---	---
Open Land	1	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---
SUBTOTAL	4	3	10	3	11	4	4	2	4	2	5	3	14	3	21	7
TOTAL	287	100	320	100	345	100	381	100	367	100	172	100	393	100	287	100

as interpreted from GLO survey records (Comer et al. 1995) (Figure 1). However, because most of the sites are relatively small and they are not located along section lines, site-specific historical data is usually lacking. In addition, the surveyors often did not distinguish between species of ash or maple. Much of what the surveyors referred to as 'black ash' may have been red ash, and what the surveyors referred to as 'soft maple' was either red maple or silver maple. Although GLO survey records provide highly valuable information for interpreting trends in the historical vegetation over broad areas, they should not be used as the only source of information in interpreting the history of the vegetation of small sites that are not located along section lines.

Although GLO survey records indicate that most of the wetlands near the King Road site were not forested at the time of the surveys, the presence of an area described as "wet ash swamp" within 1 km of the study site indicates that the site may also have been forested. In the southeast portion of the Bay, where King Road is located, wetlands along the shoreline were mapped as shrub swamp/emergent marsh, and they extended inland to low ridges mapped as mixed oak savanna (Comer et al. 1995) (Figure 1). Wetlands located inland of the ridges were mapped as wet prairie. In this portion of the shoreline no forested wetlands were mapped until at least 2 km inland from the shore. Because the King Road site is not located along a section line, site specific information on the vegetation at the time of the surveys is lacking. However, the surveyors described a 100-m wide portion of the section line 1 km to the east of the King Road site as "wet ash swamp," and they recorded black ash trees 10 and 14 inches in diameter and an elm tree 14 inches in diameter. Although this area was not included as a forested wetland in the map of Comer et al. (1995), the presence of such a swamp in close proximity to the King Road site illustrates that the King Road site may have been forested at the time of the surveys. If the trees that the surveyors referred to as 'black ash' were really red ash trees, the overstory composition of the swamp was probably similar to the present overstory at King Road.

The swamp forest at Tobico Marsh is located in an area where the *circa* 1800 vegetation was mapped as mixed conifer swamp (Comer et al. 1995) (Figure 1), but it is now dominated by hardwoods. Although the swamp may have been converted from a conifer-dominated swamp to a hardwood-dominated swamp as a result of human-induced disturbances within the last 200 years, it is difficult to be conclusive about the historical vegetation due to the low amount of historical information. Early soil surveys from Tuscola County (Deeter and Matthews 1926) describe the clearing of conifer swamps and burning of the organic soil to improve their suitability for agriculture. However, the sites where such practices were described in Tuscola County were located several km inland on clay or marl soil. The sand soil at Tobico Marsh was of less value for farming, and drainage of sites along the lakeshore was probably more difficult than sites further inland. Thus, the lack of an organic substrate at Tobico Marsh is probably a natural condition rather than the result of the purposeful burning to improve conditions for agriculture.

Although the land surveyors recorded tamarack trees at the half-section mark and at the northwest corner of the section line to the west of the Tobico study site, they also recorded soft maple and black ash trees in an area mapped as black ash swamp, located 1 km to the northwest of the site (Figure 1). The tamarack trees were recorded adjacent to upland ridges. Observations during field reconnaissance revealed that there were often areas 20-200 m wide adjacent to the upland ridges where the soil surface was saturated, or the water table was slightly below the surface, but standing water was not present, as it was in the areas where sampling was conducted. Although the Tobico Marsh site was located within a relatively large area mapped as mixed conifer swamp, it may have been a mosaic of conifer- and hardwood-dominated swamps where the conifer-dominated swamps occupied the higher areas near the upland ridges and hardwood-dominated swamps occupied lower areas where the soil surface was inundated. The slightly higher areas are now dominated by trembling aspen, with some red ash and silver maple. The lower, wetter areas, where sampling was conducted, are dominated by red ash, silver maple, and cottonwood, and their overstory composition may be similar to the *circa* 1800 vegetation.

Although the present overstory composition of several of the swamp forests of Saginaw Bay may be similar to that of the *circa* 1800 forest, the introduction of Dutch Elm disease and the subsequent loss of American elm as a dominant overstory tree is major disturbance that has influenced the overstory composition of all sites. American elm trees were frequently recorded by the land surveyors in areas mapped as mixed hardwood swamp and black ash swamp, but the elm trees recorded in the present survey occurred in the subdominant overstory and the understory rather than the dominant overstory. In sites where there are relatively few dominant species because factors of the physical environment (moisture in the case of the Saginaw Bay swamps) are restrictive, the loss of a dominant species may be expected to result in sudden and striking changes in overstory composition. Barnes (1976) noted a shift toward increasing abundance of black ash following the death of American elm in kettle swamps of the inland portion of southeastern Michigan, and Huenneke (1983) noted the establishment of dense patches of shrubs that may inhibit tree regeneration in gaps created by the death of more than one overstory elm tree. Although such striking changes were noted in depressional swamps where transpiration of the overstory trees play a strong role in regulating the hydrologic regime, the changes were probably less drastic in the coastal swamps, where the hydrologic regime is more strongly regulated by the water level in Lake Huron. Because few species can tolerate the inundated conditions in the swamp forests of Saginaw Bay, the loss of American elm as a dominant overstory tree has probably led to few changes other than a shift toward greater dominance by red ash and silver maple. Due to the low number of shrubs in the understory and ground cover of the swamps of Saginaw Bay, the formation of patches of shrubs dense enough to inhibit tree regeneration is unlikely in these swamps.

Alpena County and the Les Cheneaux Islands

With the exception of Ossineke, the present vegetation of the swamp forests of Alpena County and the Les Cheneaux Islands closely resembles the *circa* 1800 vegetation, as inferred from GLO survey records (Comer et al. 1995) (Figure 2). Misery Bay and El Cajon Bay, which were both mapped as cedar swamp (Figure 2a), are now dominated by northern white-cedar trees (Figure 9). Although the *circa* 1800 vegetation of the sites on Marquette Island was mapped as spruce-fir-cedar forest and that of the sites on the adjacent mainland was mapped as mixed conifer swamp, all sites of the Les Cheneaux Islands are now dominated by northern white-cedar in similar proportions to the cedar swamps of Alpena County. Due to the overlap among tree species of the spruce-fir-cedar forest, mixed conifer swamp, and cedar swamp cover types and the low number of trees that the surveyors recorded on Marquette Island and along the shore of the adjacent mainland, distinctions among these three cover types based on GLO survey records are not always reliable. However, similarities between our sample plot data in the Les Cheneaux Islands and the Alpena County cedar swamps illustrate that the previous cover type at all Les Cheneaux sites was most likely cedar swamp. Many of the overstory species that are now present in low numbers in cedar-dominated swamps of Alpena County and the Les Cheneaux Islands, such as black spruce, white spruce, balsam fir, tamarack, paper birch, balsam poplar, and trembling aspen, were often recorded by the surveyors in areas mapped as cedar swamp.

Northern white-cedar is reported to have regenerated successfully following logging on the calcareous soil of northern Michigan, resulting in the formation of second-growth forests where the species composition closely resembles that of the previous forest (Albert 1995). Such regeneration by northern white-cedar following late 19th century logging of Misery Bay, El Cajon Bay, and the study sites of the Les Cheneaux Islands probably accounts for the similarities between the present forest and the regionally common *circa* 1800 types. In an analysis of permanent sample plots in conifer-dominated swamps on muck soil in Northern Lower Michigan, Sakai and Sulak (1985) found that the present population of trees was most strongly influenced by conditions at the time of establishment, and events since then have been of minor importance, except on sites where large-scale windthrow events have occurred. There was no evidence of large-scale disturbance events at any of the study sites, and the present forest composition is probably strongly related to the conditions at the time of establishment.

Although northern white-cedar trees have regenerated successfully following logging in the late 19th century, the age of extant mature cedar trees in northern Michigan indicate establishment during a period of low deer populations, and such successful regeneration should not be expected following additional logging under the present, higher deer populations (Van Deelen et al. 1996). Following logging of conifer-dominated swamps in the Upper Peninsula in the middle 20th century, when deer populations were undoubtedly higher than those of the late 19th century, the proportion of northern white-cedar in the new stands has dropped, and the proportion of balsam fir and hardwoods has increased on all soil types (Zasada 1952). Likewise, in deer yards of northern Michigan, woody species that are palatable to deer and intolerant of browsing have decreased while species that are unpalatable to deer or tolerant of browsing have increased relative to their historical abundances, as inferred from GLO survey records (Van Deelen et al. 1996).

Even though the *circa* 1800 vegetation of the Ossineke site was mapped as part of a large mixed conifer swamp with small amounts of shrub swamp/ emergent marsh near the lakeshore (Comer et al. 1995) (Figure 2a), some of the sites where sampling was conducted might not have been forested. Sampling was conducted in a small swale, a depression, and along the edge of an open meadow. Although these sites were not located along section lines and they were probably too small to include as a different cover type on the map, their vegetation at the time of the surveys was probably different from that of the areas that are now dominated by conifers due to the higher water levels in the hardwood-dominated sites. The wet swale was mapped as shrub swamp/emergent marsh. Red ash was the only overstory species in the swale, and the trees were much younger (52-68 years old) than the overstory trees at the other sites of Alpena County (112-132 years old). The young age of the overstory trees indicates that their establishment may be related to favorable physical conditions, such as low water levels, rather than establishment resulting from logging-related changes. In addition, the open meadow was included within the area mapped as mixed conifer swamp, but the present conditions suggest it was most likely also an open meadow at the time of the surveys. The narrow, hardwood-dominated swamp that was sampled along the edge of the meadow may have also been an open meadow or shrub swamp at the time of the GLO surveys. The small depression was probably forested, but it is unclear whether it was dominated by hardwoods or conifers.

GENERAL DISCUSSION

Interrelationships Among Physical Site Characteristics and Vegetation

Hydrology and Soil

The different responses of tree species to saturated and inundated conditions undoubtedly had a strong influence on the differences in species composition between the hardwood- and conifer-dominated swamps. Although all sites were poorly drained, the soil surface of the hardwood-dominated swamps was inundated while that of the conifer-dominated swamps was saturated, with inundation of the soil surface only occurring in small depressions between the hummocks. Greenhouse studies indicate that seedlings of silver maple, red ash, American elm, and eastern cottonwood, the dominant trees of the inundated swamps of Saginaw Bay, were among the most tolerant species to inundation, and they were able to recover rapidly when water was drawn down (Hosner 1960). Silver maple seedlings exhibited the greatest tolerance to inundation, with all seedlings surviving 30 days of inundation and recovering rapidly when water was drawn down. In contrast, red maple seedlings exhibited a lower tolerance to inundation. Red maple seedlings that survived 10 days of inundation recovered moderately, and none of the red maple seedlings were still alive after 20 days of inundation (Hosner 1960). However, in a study of the response of seedlings to saturated conditions, all red maple seedlings survived 32 days and recovered rapidly after water was drawn down (McDermott 1954). Red maple was not present in any of the inundated swamps of Saginaw Bay, but it was often present in both of the conifer-dominated swamps studied in Alpena County. It was also present on slightly elevated microsites in the depression at Ossineke, but it was absent from the swale, where high-water marks were recorded up to 50 cm above the soil surface. Common species of the conifer-dominated swamps, including northern white-cedar, balsam fir, white spruce, black spruce, and eastern white pine, may be similar to red maple in their ability to tolerate saturated but not inundated conditions.

Based on GLO survey records, most of the shoreline of Saginaw Bay was lined with hardwood-dominated swamp, shrub swamp/emergent marsh, or wet prairie (Comer et al. 1995). Where the shrub swamp/emergent marsh and wet prairie were located along the shore, hardwood-dominated swamps were typically located immediately inland of them. Conifer-dominated swamps were typically located inland of the hardwood-dominated swamps. With hydrological conditions within sites close to the lakeshore strongly associated with water levels of Lake Huron, cycles of inundation of the soil surface and draw down of the water level were probably common. Such conditions probably prevented the accumulation of muck soil and supported the regeneration of species such as red ash, silver maple, American elm, and eastern cottonwood, which are tolerant of inundation. In sites farther from the shore, hydrological conditions were probably more strongly influenced by ground water than by Lake Huron, and the magnitude of fluctuations of the water level was probably less than that of sites closer to the shore. Swamps further from the shore were probably saturated, but not inundated, favoring the accumulation of muck soil and the regeneration of conifer species and hardwood species such as red maple, that are tolerant of saturation but not inundation. There is a strong correlation between the distribution of the *circa* 1800 conifer-dominated swamps of Tuscola County (Comer et al. 1995) and the distribution of muck soil (Deeter and Matthews 1926). However, almost all of the conifer-dominated swamps have been cleared and drained, and their organic matter has been burned to facilitate agricultural use of the land.

GLO survey records indicate that north of Saginaw Bay, most of the forested wetlands along Lake Huron shoreline were dominated by conifers in the mid-1800s, and hardwood-dominated swamps were virtually absent from the shoreline (Comer et al. 1995) (Table 5). While the substrate was mineral soil at all sites in Saginaw Bay, it was muck at all sites in Alpena County and the Les Cheneaux Islands. Because hydrological conditions of the coastal swamp are closely associated with lake-level fluctuations, hydrological conditions in the northern part of the shoreline are not likely to be different from those of Saginaw Bay. However, the shorter growing season, colder temperatures, and greater snow accumulation in the northern part of the shoreline may have resulted in slower decomposition, favoring the accumulation of muck on top of the mineral soil. The muck remains saturated throughout the growing season, but it is only inundated in localized depressions. The saturated rather than inundated conditions probably favor the growth of conifer species.

Comparison of Saginaw Bay Coastal Swamps to Interior Swamps of Southern Michigan

Recent studies have been conducted in non-coastal swamp forests of southern Michigan, including floodplain forests (Goforth et al. 2001 and 2002) and depressional wetlands of ice-contact terrain and outwash plain landforms (Kost 2001b). Such studies provide the basis for comparisons of interior swamp forests to the Saginaw Bay coastal swamp forests, which are presented below.

Coastal Swamps and Floodplain Forests

Inundation of the soil surface during the early part of the growing season followed by a draw down of water levels later in the growing season is an important characteristic of both river floodplain forests and the coastal swamp forests of Saginaw Bay that leads to similarities in vegetation composition and structure between the two types of swamps. However, inundation by fast moving water due to over-the-bank flooding in floodplain forests leads to much greater spatial heterogeneity than that of the coastal swamps. Such spatial heterogeneity, favors the occurrence of many species in floodplain forests that were absent from coastal swamps. Likewise, the structure of the vegetation on microsites within floodplains is often markedly different from that of coastal swamps.

While the coastal swamp forests were relatively homogeneous sites, where most, if not all, of the soil surface was inundated throughout much of the growing season, the process of over-the-bank flooding and related patterns of erosion and deposition leads to the development of a characteristic pattern of fluvial landforms in the floodplain forests, each with a characteristic topographic shape and soil properties, and each is associated with a particular suite of vegetation. Floodwaters deposit their coarsest sediments adjacent to the river channel, resulting in the formation of relatively high natural levees (Brinson 1990). Soil of the levee is typically coarser in texture than that of other parts of the floodplain, and soil drainage and aeration are better (Buchholz 1981). After flooding over the levee, stream deposits thin rapidly and become finer in texture with increasing distance from the river (Hosner and Minckler 1963). A low, flat, poorly drained first bottom typically occurs adjacent to the levee. In general, as distance from the river increases surface elevation gradually decreases and progressively finer materials are deposited, resulting in the formation of a low, poorly drained backswamp (Barnes et al. 1998). Soil texture of the first bottom is typically silt loam to silty clay while that of the levee is loam or sandy loam. Due to lateral migration of the meandering stream channel, former channels, point bars, levees, and backswamps are cut off and abandoned, resulting in local relief of ridges, swales, and oxbows (Brinson 1990). In many river valleys, a series of typically drier bottoms is situated adjacent to the first bottom, and each bottom is flooded progressively less frequently and for a shorter time (Barnes et al. 1998). Such diversity of fluvial landforms in floodplain forests contrasts with coastal swamps where extremes in drainage conditions are represented in the inundated swamp and the adjacent excessively drained ridges, but additional sites characterized by drainage conditions between the two extremes are typically absent.

The first bottom of the floodplain forests is most similar to the coastal swamps in the composition and structure of the overstory and understory vegetation, but the additional fluvial landforms of the floodplain promotes the occurrence of a greater diversity of overstory species and a different vegetation structure in parts of the floodplain. With the exclusion of King Road, where basal area was unusually high (51.5 m^2/ha) due to the occurrence of several very large eastern cottonwood trees, the basal area of the coastal swamps, 22.3-36.5 m^2/ha (Table 1), was similar to that of inundated first bottoms of floodplain forests in southern Michigan 17.3-35.8 m^2/ha (Goforth et al. 2002). Major overstory dominants of the coastal swamps, red ash, silver maple, American elm, and eastern cottonwood, were also the dominant overstory species of southern Michigan floodplain forests. Although few additional overstory species were present in the coastal swamp forests, where physical site conditions are relatively homogeneous, a variety of overstory species, including basswood (*Tilia americana*), shagbark hickory (*Carya ovata*), bitternut hickory (*Carya cordiformis*), black walnut (*Juglans nigra*), butternut (*Juglans cinerea*), and hackberry (*Celtis occidentalis*), were common to floodplain forests. Many of the additional floodplain tree species are typically restricted to fluvial landforms such as levees, high microsites within the first bottom, and second bottoms, where the duration of inundation is shorter than that of the first bottom.

In both coastal swamps and the first bottom of floodplain forests, the understory stem density is typically low and there are few shrub species. Likewise, woody vines such as riverbank grape are common to both types of swamp. However, understory stem density is typically higher on the slightly drier levee of the floodplain forests, where light levels are high due to its location adjacent to the river channel and shrubs and small-tree-species, including musclewood, prickly-ash (*Zanthoxylum americanum*), nannyberry, spicebush (*Lindera benzoin*), redbud (*Cercis canadensis*), and dogwood species, are often abundant (Goforth et al. 2002).

Despite similarities between coastal swamps and the first bottom of floodplain forests in the composition and structure of the overstory and understory vegetation, floodplain forests are characterized by a greater diversity and coverage of the ground-cover layer than that of coastal swamps. There was an average of 6.5 species per 1-m^2 plot and the average coverage of the ground-cover layer was 42% in the floodplain forests (Goforth et al. 2002), but across all coastal swamps of Saginaw Bay the average number of species per plot was 4.0 and the average coverage was only 25% (Table 2). Across all coastal swamps excluding Wildfowl Glade, where the diversity and coverage of the ground-cover layer were higher than that of all other Saginaw Bay coastal swamps due to the low canopy coverage and the lack of inundation of the soil surface, the average number of species per plot, 3.5, and the average coverage of the ground-cover layer, 20%, were markedly lower than that of floodplain forests. Characteristic ground-cover plants of floodplain forests include false nettle, wood nettle (*Laportea canadensis*), wild ginger (*Asarum canadense*), tall meadow rue (*Thalictrum dasycarpum*), Virginia wild rye, jewelweed, late goldenrod (*Solidago gigantea*), skunk cabbage (*Symplocarpus foetidus*), and swamp buttercup (*Ranunculus hispidus*) (Goforth et al. 2002). While several of these species, such as false nettle and jewelweed, were among the most abundant species in the coastal swamps, most of them were absent. The absence of many of the characteristic floodplain species from coastal swamps is probably related to a shorter duration of inundation in floodplain forests, and the occurrence of a wide variety of microsites where the duration of inundation is further reduced. In addition, the common occurrence of bare mineral soil in floodplains due to the disruption of the litter layer and deposition of new soil by floodwater may facilitate the establishment of many species.

In contrast to coastal swamps, where non-native species were never abundant, non-native species were abundant in most floodplain forests of southern Michigan (Goforth et al. 2001 and 2002). A total of only five non-native species were recorded among the seven coastal swamps, but a wide variety of non-native species including Japanese barberry (*Berberis thunbergii*), multiflora rose (*Rosa multiflora*), garlic mustard (*Alliaria petiolata*), dame's rocket (*Hesperis matronalis*), bittersweet nightshade, moneywort (*Lysimachia nummularia*), dandelion, and burdock (*Arctium minor*) were common to many southern Michigan floodplain forests. The spatial heterogeneity and the regularity of disturbance in floodplain forests may facilitate the establishment and dispersal of non-native species. Due to the common occurrence of ice or woody debris in the floodwaters, over-the-bank flooding often causes physical damage to trees, resulting in open conditions. Floodwaters also disrupt the litter layer and deposit new soil, leaving areas of exposed mineral soil when floodwaters recede. The common occurrence of bare mineral soil in combination with the relatively open conditions probably facilitates the establishment of non-native species. Also, with high physiographic heterogeneity relative to that of coastal swamps, the wide variety of microsites characteristic of floodplain forests results in a greater likelihood of non-native species becoming established. In contrast, the coastal swamps, with their typical location adjacent to excessively drained ridges and the lack of microtopography where intermediate drainage conditions are represented, there is a strong barrier to the dispersal of many non-native species. Although non-native species may become abundant on the dry ridges, it is unlikely that the same species can also tolerate the inundated conditions of the swamp, and colonization of the swamp from the ridges is probably rare. Likewise, non-native species that establish in the nearby coastal marshes are unlikely to be tolerant of the shaded conditions in the swamp forests, and the colonization of the swamp forests by non-native species that are present in the marshes is probably rare unless there are large windthrow events that result in open conditions in the swamp.

Coastal Swamps and Ice-Block Depressions of Ice-Contact Terrain and Outwash Plains

Despite similarities in the composition and structure of the overstory and understory vegetation between the coastal swamp forests of Saginaw Bay and the first bottom of southern Michigan floodplain forests, depressional swamp forests in the southern part of the state (Kost 2001b) were markedly different from the coastal swamps. The hydrology and soil of coastal swamp forests of was different from that of swamp forests of depressions in ice-contact terrain and outwash plains in the interior part of the southern Michigan. While the soil surface of coastal swamps along Saginaw Bay was inundated in the early part of the growing season, the soil surface of inland depressional swamps was typically saturated but not inundated. Saturation of the soil surface in the interior depressional swamps typically leads to the accumulation of muck or peat, and organic deposits 10-15 ft deep have been reported in depressional wetlands of the Jackson Interlobate (Albert 1995). In contrast, periods of soil aeration following the draw down of water at the coastal swamps promotes rapid decomposition, which prevents the accumulation of muck. Although hardwood-dominated forests are the only remaining swamp forests along Saginaw Bay, both hardwood- and conifer-dominated swamps occur in depressional wetlands in the interior of the state.

Despite similarities in forest structure between the coastal swamps and the hardwood-dominated depressional swamps, they were markedly different from each other in species composition. The tree density (including overstory trees and understory saplings) in the coastal swamps of Saginaw Bay, 632-2,123 stems/ha, was within the range of tree densities found in interior hardwood-dominated depressional swamps, 319-3,992 stems/ha (Kost 2001b). Likewise, the basal area of the coastal swamps, 21.3-51.1 m^2/ha, was similar to that of the depressional hardwood swamps, 14.2-45.3 m^2/ha. However, the major overstory dominants of the coastal swamps were red ash, silver maple, American elm, and eastern cottonwood, but the major dominants of the depressional wetlands were red maple, black ash, American elm, and yellow birch (Kost 2001b, Barnes 1976).

Shrubs were a minor component of both types of hardwood-dominated swamp. The total number of shrub species per site in the coastal swamps, 1-8, was similar to that of the depressional swamps, 1-6 (Kost 2001b). Shrub species including Michigan holly, nannyberry, and common elder were present in both types of swamps. However, the shrub coverage of the depressional hardwood swamps, 1.0-21.3%, was greater than that of the coastal swamps, where the shrub coverage was only 0.1-2.5%.

With a total of 11-44 species per site in the coastal swamps and 2-38 species per site in the depressional hardwood swamps, the two types of swamps were similar to each other in species richness. Species such as false nettle, jewelweed, and fowl manna grass were among the most abundant species at both types of hardwood swamp. However, species such as cinnamon fern (*Osmunda cinnamomea*) and skunk cabbage (*Symplocarpus foetidus*), which were abundant in the depressional swamps (Kost 2001b) were absent from the coastal swamps. The abundance of such species in the depressional swamps leads to a much greater total coverage of the ground-cover layer. In addition, Canada mayflower and highbush blueberry (*Vaccinium corymbosum*) were often present in the depressional swamps, but absent from the coastal swamps. These two species grow on the acid tree bases in the depressional swamps, but their absence from the coastal swamps was primarily due to the transport of calcareous material to the soil surface during periods of inundation in the coastal swamps.

The conifer-dominated depressional swamps were markedly different from the coastal swamps in both composition and structure. Tamarack was the dominant overstory tree of all depressional swamps, and the dominant trees of the hardwood-dominated depressional swamps (red maple, black ash, American elm, and yellow birch) were usually present (Kost 2001b). The total basal area of the conifer-dominated swamps, 9.2-21.0 m^2/ha, was much lower than that of the coastal swamps, 21.3-51.1 m^2/ha. With such a low basal area in the conifer-dominated swamps, canopy coverage was much lower than that of the coastal swamps.

The low canopy coverage favored the development of a dense shrub layer characterized by a high diversity of species. While shrub coverage ranged from 0.1 to 2.5% in the coastal swamps, shrub coverage in the conifer-dominated depressional swamps ranged from 76 to 133%. Poison sumac (*Toxicodendron vernix*), which is very intolerant of shade (Barnes and Wagner 1981), was one of the most abundant species of all conifer-dominated depressional sites, but it was not present at any of the coastal swamps. With greater basal area and higher canopy coverage in the coastal swamps than the depressional hardwood swamps, light levels were probably too low for poison sumac.

With 35-63 total species per site (Kost 2001b), the ground-cover species diversity of the conifer-dominated depressional swamps was much greater than that of the coastal swamps, where there were only 11-44 species per site. Spring ephemerals were absent from the coastal swamps, where the soil surface was inundated in the spring, but ephemerals such as skunk cabbage and bitter cress (*Cardamine spp.*), were abundant in the conifer-dominated swamps. Ferns, including cinnamon fern, sensitive fern, marsh fern, spinulose wood fern (*Dryopteris spinulosa*), and royal fern (*Osmunda regalis*) were much more abundant in the conifer-dominated swamps than the coastal swamps. Although plants characteristic of acid soil, including highbush blueberry, Canada mayflower, and royal fern, were absent from the coastal swamps, they were typically present in the conifer-dominated swamps, where they were frequently found on tree base mounds above the influence of ground water.

Although non-native species were virtually absent from all coastal swamp forests, non-native species such as glossy buckthorn (*Rhamnus frangula*) and purple loosestrife (*Lythrum salicaria*) were often abundant in inland depressional swamps, especially under the relatively open canopy of conifer-dominated swamps.

Coastal Swamps and Swamps of Depressions in Fine- and Medium-Textured Moraines

Despite differences in physiography, soil, and vegetation between Saginaw Bay coastal swamps and swamp forests of ice-block depressions in ice-contact terrain and outwash plain landforms, there are probably greater similarities between the Saginaw Bay coastal swamps and swamp forests located in depressions within fine- and medium-textured morainal landforms. With soil textures frequently ranging from loam to clay loam (occasionally clay), drainage is slow in closed, depressional wetlands of fine- and medium-textured moraines. The soil surface of such depressions is typically inundated from early spring through mid-summer, and water levels fall below the surface later in the growing season. As in the coastal swamps, soil aeration following the draw down of water promotes rapid decomposition and prevents the accumulation of muck.

Because a large portion of the upland and wetland forests on fine- and medium-textured moraines in southern Michigan have been cleared to enable agricultural land use, interpretation of the historical vegetation of morainal depressional swamps is difficult. An A-ranked southern swamp forest element occurrence, located on a medium-textured ground moraine in Oakland County, near the border of Macomb County (T5N R11E S.13), may be one of the best remaining examples of a morainal depressional swamp in southern Michigan. The swamp was determined to be old growth based on the large trees (60-76 cm dbh), the closed canopy, and the lack of multiple-stemmed trees. Although the site was not located close to a stream or river, the soil surface was inundated during the early part of the growing season.

The southern swamp forest element occurrence located in a morainal depression was similar to the coastal swamps in the overstory species composition, the low abundance of shrubs, the presence of woody vines, the relatively low species diversity, and the occurrence of numerous areas were ground-cover vegetation was absent due to inundation of the soil surface. Dominant overstory trees were silver maple, red ash, American elm, slippery elm (*Ulmus rubra*), and eastern cottonwood. With the exception of slippery elm, the overstory dominants were the same as those of the coastal swamps. The only shrubs mentioned at the site were spicebush, Michigan holly, bladdernut (*Staphylea trifolia*), and mapleleaf viburnum (*Viburnum acerifolium*). Vines including poison ivy and Virginia creeper were present. Abundant ground-cover species included sensitive fern, wood nettle, clearweed (*Pilea pumila*), poison ivy, and spinulose wood fern, and there were numerous areas where ground-cover vegetation was absent due to inundation of the soil surface.

Although GLO survey records indicate that many of the morainal depressional swamps were dominated by conifers in the early 1800s (Comer et al. 1995), especially within the Lansing Till Plain, some of the morainal depressions were undoubtedly dominated by hardwoods. Many of the hardwood-dominated swamps might not have been described by the surveyors because they were either too small, they were not located along a section line, or if they were not inundated at the time of the surveys they might not have been recognized as swamps. The A-ranked southern swamp forest element occurrence may be one of the least disturbed hardwood-dominated swamps in a morainal depression in southern Michigan. It was similar to the Saginaw Bay swamp forests in hydrology and vegetation composition and structure. Numerous second-growth swamp forests with similar hydrology and a similar vegetative composition have been observed in depressions of the Fort Wayne and Defiance moraines of southeastern Michigan. The occurrence of similar swamp forests along the coast of Saginaw Bay and within depressions of fine- and medium-textured moraines illustrates that it is currently (if not also historically) a regionally important swamp forest type.

Potential for the Development of Indicators of Biological Integrity

Due to the complexity of ecological systems and the diverse impacts of a variety of human-induced disturbances on the biological component of such systems, it is often useful to develop indices that reflect the degree of impact of human-induced disturbances. Development of such indices, often referred to as Indices of Biotic Integrity, or IBIs, requires the documentation of clear relationships between biological attributes, such as vegetation composition or structure, and human-induced disturbances. To document such relationships, sample sites must encompass a broad portion of the gradient in human-induced disturbances, from highly degraded to nearly undisturbed. In addition, physical site characteristics must also be held constant to the greatest extent possible because physical site factors have a substantial influence on community composition and structure regardless of disturbance history, and to a large extent physical site factors regulate severity of the impact of human-induced disturbances on vegetation composition and structure.

Development of IBIs for the coastal swamp forests of the Lake Huron shoreline was confounded by both the low number of remaining coastal swamp forests and the variability in physical site characteristics among them. Because all swamp forests of the Saginaw Bay shoreline have been logged within the last century, and high levels of agricultural land cover and numerous drainage ditches characterize the Bay, it was not possible to establish baseline data representing minimal effects of human-induced disturbance. Because the harsh physical characteristics (inundated soil surface during the growing season and relatively high canopy coverage) preclude many plant species from becoming established in the Saginaw Bay coastal swamp forests, many variables relating to species composition that have been applied to inland swamp forests do not apply to these swamps. For example, variables such as plant species richness, coverage and species richness of the shrub layer, and a relatively even distribution of the ground-cover vegetation have been suggested as indicators of biological integrity in depressional swamp forests of ice-contact terrain and outwash plains in southern Michigan (Kost 2001b). The species richness and coverage of non-native species was also found to reflect the degree of impact of human-induced disturbances at most ice-contact sites. However, the relatively low overall species diversity, the low diversity and coverage of shrubs, and the low abundance of non-native species in the coastal swamp forests of Saginaw Bay were not found to demonstrate strong relationships with swamp size or disturbance level. The lack of such relationships is most likely related to the combined influences of inundation of the soil surface during the growing season and relatively high canopy coverage, which prohibit the establishment of non-native species regardless of swamp size or disturbance level. Therefore, in the swamp forests of Saginaw Bay we did not find variables in the overstory, understory, or ground-cover vegetation that could be used as effective indicators of biological integrity.

Due to the lack of a wide range of human-induced disturbances on the conifer-dominated coastal swamp forests studied in Alpena County and the Les Cheneaux Islands, it is not possible to develop useful IBIs from the present data set. All sites were logged in the late 19th or early 20th Century, and successful tree regeneration following logging probably resulted in the development of forests with a similar species composition to the previous forest. Other than the effects of selective browsing by deer as a result of dramatic increases in deer populations over the last century, there has been little, if any, direct disturbance to the conifer-dominated swamps since logging. Because the effects of deer browsing are most likely similar across all sites, it is not possible to examine the vegetation composition and structure in relation to a gradient of deer browsing intensities. In addition to the lack of direct disturbances, the lack of indirect disturbances, as interpreted from the surrounding land cover, makes it impossible to develop reliable IBIs from the present data set. The natural land-cover classes of deciduous forest, coniferous forest, forested wetland, and non-forested wetland, were the predominant land-cover classes surrounding each conifer-dominated swamp. Together these land-cover classes accounted for 93-99% of the land cover within 1 km of the study sites. In order to develop IBIs for the coastal conifer-dominated swamps of the Northern Lower Peninsula and Eastern Upper Peninsula, study sites would have to be selected closer to areas of either agricultural or urban land cover, or direct human-induced disturbances to the sites since the time of logging would have to be evident. For such a study to be effective, permission to sample high degraded swamps on private land is needed.

The inability to hold physical site characteristics constant confounds the interpretation of disturbance-related effects on vegetation composition and structure in the Lake Huron coastal wetlands. Because such a low number of coastal swamp forests remain along the Lake Huron shoreline, it is not possible to sample a large number of sites with a low range of variability in site characteristics among the sites, especially in Saginaw Bay, where virtually all of the conifer-dominated swamps have been eliminated and many of the present hardwood-dominated swamps occur on sites that were historically either conifer-dominated swamps or non-forested wetlands. In addition, climate-driven floristic differences among the coastal swamp forests of Saginaw Bay, Alpena County, and the Les Cheneaux Islands do not allow for meaningful comparisons of the effects of human-induced disturbance on forest composition and structure among the three major study areas.

Potential for Restoration and Biodiversity Management

Saginaw Bay

In the highly fragmented landscape of Saginaw Bay, where the majority of the natural vegetation has been degraded to enable agricultural land use, the few remaining swamp forests provide a refuge for both plant and animal species that depend on forested conditions. During field sampling an active goshawk nest was found in an oak tree on an upland ridge that marked the southeast boundary of the Tobico Marsh sample site and several active bald eagle nests were found along the northern end of Heisterman Island, close to the swales where sampling was conducted. A variety of other animal species are likely to depend on the swamp forests for at least part of their life cycle. Thus, the few existing swamp forests should be protected, and degraded sites that were historically forested should be restored wherever possible. Because the Saginaw Bay swamps were characterized by fast-growing tree species, and few non-native species were able to grow due to the combination of inundation of the soil surface and relatively high canopy coverage, it may be possible to attain a high degree of success in the restoration of such forests at a reasonable effort.

Although GLO survey records indicate that several of the Saginaw Bay coastal swamps might not have historically been forested, the existing swamp forests are among the largest remaining contiguous blocks of forest in a landscape where the majority of the forests have been cleared, and they should be protected. The restoration of wet prairies, which were also historically abundant along that bay but are now virtually absent, should proceed at sites where wet prairie vegetation already exists rather than attempting to convert existing swamps to wet prairies. For example, the King Road site was mapped as wet prairie, shrub swamp/emergent marsh, and sand dune in the *circa* 1800 vegetation map of Comer et al. (1995), but it is now dominated by second growth trees of a similar size and age to those of the other swamps of Saginaw Bay and no characteristic prairie species were present. The mention of a “wet ash swamp” by GLO surveyors within 1 km of the King Road sample site (not included in the map of Comer et al. 1995) illustrates that parts of the landscape near the King Road site, possibly including the sample site, were historically forested. Despite the lack of wet prairie species in the swamp forest, several characteristic wet prairie species, such as marsh blazing star (*Liatris spicata*) and prairie cordgrass (*Spartina pectinata*) were present in drainage ditches and on an area of broad, flat, poorly drained land near the swamp. Red ash trees had colonized the poorly drained flat land, and they have been cut recently, presumably as part of a wet prairie restoration project. The cut ash trees have sprouted vigorously, and repeated cutting will likely be needed to maintain the open conditions at this particular site where wet prairie vegetation already exists.

Due to the lack of conifer-dominated swamps in Saginaw Bay despite their historical abundance, restoration of conifer-dominated swamps is important. However, because the majority of the conifer-dominated swamps were converted to agricultural land use through cutting, drainage, and the burning of the muck soil (Deeter and Matthews 1926), restoration of conifer-dominated swamps will be more difficult and take a much longer time than the restoration of hardwood-dominated swamps. If future studies result in the discovery of sites where the muck has not been burned, the restoration of conifer-dominated swamps on such sites would be a high priority.

Alpena County and the Les Cheneaux Islands

Rare plant and rare animal species were observed during field sampling in the swamps of Alpena County and the Les Cheneaux Islands. Dwarf lake iris (*Iris lacustris*) was found at Misery Bay, El Cajon Bay, and on the upland portions of Marquette Island, between Duck Bay and Voight Bay. A red shouldered hawk was found near the Ossineke site. The occurrence of such species illustrates the importance of these swamps in the maintenance of regional biodiversity.

Although the present composition of the conifer-dominated swamps of Alpena County and the Les Cheneaux Islands is most likely similar to the historical vegetation at these sites, the virtual absence of northern white-cedar seedlings from all conifer-dominated sites is likely to pose problems to the long-term stability of the forests. Northern white-cedar seedlings were not present at any of the sites except Voight Bay and El Cajon Bay, where there were 60 seedlings/ha and 10 seedlings/ha, respectively (Figure 10, Appendix F). The majority of the seedlings at all sites were balsam fir, balsam poplar, or trembling aspen. The absence of northern white-cedar seedlings is undoubtedly related to browsing by deer, which have had a severe impact on northern white-cedar regeneration throughout the Upper Great Lakes region (Van Deelen et al. 1996, Zasada 1952). The establishment of deer exclosures in several of the cedar-dominated coastal swamps would be useful in illustrating the impacts of deer on northern white-cedar regeneration. The current study provides baseline data, which could be used to determine the effectiveness of deer exclosures in promoting northern white-cedar regeneration.

SUMMARY AND CONCLUSIONS

GLO survey records indicate that swamp forests once lined much of the Lake Huron shoreline from Saginaw Bay to the eastern Upper Peninsula, but as a result of intensive logging, agricultural development, mining, road construction, and urban development over the last 150 years, many of the coastal swamps have been lost through drainage or conversion to other wetland types. The loss of coastal swamps is most apparent in Saginaw Bay, where agriculture is the predominant land cover, and least apparent in the eastern Upper Peninsula, where the majority of the shoreline is forested. Although numerous studies have been conducted in swamp forests of Michigan, data specific to the coastal swamp forests is lacking. In order to characterize composition and structure of the vegetation in swamp forests along the southern, central, and northern parts of the Lake Huron shoreline, overstory, understory, and ground-cover vegetation was sampled in a total of 235 plots in 15 sites located in Saginaw Bay, Alpena County, and the Les Cheneaux Islands. Hydrological and soil characteristics were also sampled at each site.

The substrate of all swamp forests along Saginaw Bay was mineral soil. The soil surface was inundated in the early part of the growing season and water levels fell below the surface later in the growing season at all sites except one site on the Islands of Wildfowl Bay, where there was less than 100 cm of mineral soil over bedrock, and the soil surface was not inundated. Major overstory dominants of the Saginaw Bay swamps were red ash, silver maple, and eastern cottonwood. Together red ash and silver maple accounted for 77-98% of the overstory stems and 66-95% of the basal area at all sites. American elm trees were common in the subdominant overstory of all sites, but most of the elm trees were killed by Dutch Elm disease before becoming dominant trees. At all sites the composition of the understory was similar to that of the overstory, with the exception of eastern cottonwood, which was never present in the understory. Similarities between the overstory and understory vegetation suggests that in the absence of disturbance the forest composition is likely to remain largely unchanged. Shrubs were a minor component of all Saginaw Bay swamps, and the total shrub coverage was 2.5% or less at all sites. However, woody vines were present at all sites, and they were locally abundant. Characteristic ground-cover species include false nettle, fowl manna grass, jewelweed, goldenrod, northern bugle weed, common lake sedge, Virginia wild rye, and water-hemlock. At the Wildfowl Bay Island site that was not inundated, blue-joint grass, tussock sedge, and common lake sedge were the most abundant species.

The substrate of all sites in Alpena County and the Les Cheneaux Islands was sapric muck. The soil surface was saturated rather than inundated at all sites except Ossineke, in Alpena County. All sites except Ossineke were dominated by conifers. Northern white-cedar accounted for 76-91% of the overstory stems and 77-91% of the basal area at all sites except Ossineke, which was dominated by red ash. Additional overstory species of the conifer-dominated swamps include balsam fir, paper birch, white spruce, black spruce, balsam poplar, and trembling aspen. At all sites the understory composition was similar to that of the overstory, with two major exceptions: (i) balsam fir seedlings and saplings were much more abundant than overstory balsam fir trees, and (ii) northern white-cedar seedlings (taller than 50 cm) were absent from all sites except Voight Bay and El Cajon Bay, where the density of northern white seedlings was 60/ha and 10/ha, respectively. The low abundance of northern white-cedar seedlings is undoubtedly the result of intensive deer browsing, and such a low abundance of northern white-cedar regeneration poses a threat to the long-term stability of these forests. With a total coverage of less than 1%, shrubs were a minor component of all conifer-dominated sites. At the hardwood-dominated swamp at Ossineke, shrub coverage was 22%, and speckled alder, bog birch, and meadowsweet were the most abundant shrubs. Characteristic ground-cover species were colt's foot, large-leaved aster, Canada mayflower, dwarf raspberry, twinflower, dwarf bishop's cap, gay-wings, and small bedstraw. In contrast to the Saginaw Bay swamps, woody vines were absent from the Alpena County and Les Cheneaux swamps. Although ferns were not abundant in the Saginaw Bay swamps, horsetail and ferns such as rattlesnake fern, oak fern, and bulblet fern were abundant in the northern sites.

With the exception of the sites on the Islands of Wildfowl Bay, non-natural land-cover classes, primarily agriculture, accounted for 26-79% of the land cover within 1 km of the Saginaw Bay sites. Despite the highly intensive land use surrounding the swamps, the direct effects of disturbance were not obvious. Non-native species were not abundant in any of the swamps. The lack of non-native species may be a result of the dense shade and the relatively small seed pool for non-native species in the northern sites. In the Saginaw Bay sites, the low abundance of non-native species may be related to inundation of the soil surface during the growing season and the relatively high canopy coverage. Although the present vegetation of many of the Saginaw Bay swamps is different from the historical vegetation, as interpreted from GLO survey records, site-specific information for the relatively small swamp forests is lacking, making interpretation of changes from historical conditions difficult.

In contrast to the Saginaw Bay swamps, where agricultural land cover dominated the landscape, non-natural land-cover classes accounted for only 2-7% of the land cover within 1 km of the Alpena County and Les Cheneaux Islands sites. In all northern sites except Ossineke, the present vegetation was similar to the historical vegetation. The historical vegetation at Ossineke was most likely shrub swamp or open meadow.

There were several similarities and important differences in physical site conditions and vegetation composition and structure between the Saginaw Bay coastal swamps and interior forested wetlands of southern Michigan. Like the coastal swamps, floodplain forests are characterized by inundation of the soil surface followed by a draw down of water later in the growing season. The major overstory dominants of the coastal swamps, red ash, silver maple, American elm, and eastern cottonwood, were also the major dominants of floodplain forests. However, the cycles of erosion and deposition associated with over-the-bank flooding in floodplain forests leads to the development of a variety of microsites. The heterogeneity of floodplain forests relative to coastal swamps leads to a greater species diversity, but also a greater abundance of non-native species. Depressional swamps of ice-contact terrain and outwash plain landforms were characterized by saturation of the soil surface rather than inundation, muck soil rather than mineral soil, and the overstory dominants were red maple, black ash, American elm, yellow birch, and tamarack. In contrast to the coastal swamps, shrubs were abundant in the depressional swamps, especially conifer-dominated swamps. In the depressional swamps there was generally a greater diversity of ground-cover species and a higher coverage of the ground-cover layer. Although there is little data on depressional swamps within fine- and medium-textured morainal landforms, they may be similar to the coastal swamps in hydrology, and vegetation composition and structure.

One rare plant species, dwarf lake iris, and three rare animal species, goshawk, bald eagle, and red shouldered hawk were found within or adjacent to the swamp forests of the Lake Huron shoreline, and many other plant and animal species are likely to depend on these forests for at least part of their life cycle. Because the Saginaw Bay swamps were dominated by hardwoods and non-native species are not currently a major threat to any of the swamps, restoration of hardwood-dominated swamps in Saginaw Bay may be feasible with a reasonable amount of effort. However, due to the burning of organic matter to allow for agricultural use of swamps that were formerly dominated by conifers, restoration of conifer-dominated swamps is likely to be more difficult, and it should be focused on sites where the organic soil has not been destroyed. Although the swamp forests of Alpena County and the Les Cheneaux Island are probably similar to the historical forests of these sites, the lack of northern white-cedar regeneration due to intensive deer browsing is likely to pose a problem to the long-term stability of the forests. The establishment of deer exclosures could be used to examine the regeneration of northern white-cedar in the absence of deer, which could be used to guide further management decisions for the long-term protection of the swamp forests of the northern part of the Lake Huron shoreline.

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Appendix A. Comparison of the overstory species composition of seven coastal swamp forests along Saginaw Bay.

Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Acer saccharinum							
Stems/ha	250	593	307	185	487	225	33
BA (m^2/ha)	10.03	19.02	16.69	6.36	13.10	21.48	1.51
Avg DBH (cm)	20.2	20.9	22.9	20.9	17.1	30.6	22.6
Rel. Den. (%)	22.9	64.9	43.8	20.3	54.0	51.0	4.0
Rel. Dom. (%)	18.7	51.9	44.2	16.0	47.4	53.4	6.8
Fraxinus pensylvanica							
Stems/ha	537	215	300	405	267	381	746
BA (m^2/ha)	22.02	13.91	13.13	12.36	11.06	10.45	19.97
Avg DBH (cm)	20.9	29.5	23.9	18.8	21.2	17.6	17.2
Rel. Den. (%)	48.6	25.0	40.8	57.0	32.0	46.5	92.0
Rel. Dom. (%)	46.8	38.1	40.7	49.8	36.1	41.2	89.6
Ulmus americana							
Stems/ha	237	53	60	108	7	6	13
BA (m^2/ha)	2.94	0.81	1.24	2.39	0.15	0.12	0.50
Avg DBH (cm)	12.1	13.0	17.5	15.2	15.4	16.7	22.8
Rel. Den. (%)	20.2	7.9	6.8	18.3	1.0	1.4	1.9
Rel. Dom. (%)	6.4	2.2	3.7	13.8	0.6	0.4	2.1
Populus deltoides							
Stems/ha	83	---	10	25	43	---	---
BA (m^2/ha)	15.42	---	2.88	9.71	2.57	---	---
Avg DBH (cm)	49.6	---	60.4	65.4	24.5	---	---
Rel. Den. (%)	7.7	---	1.3	4.1	5.3	---	---
Rel. Dom. (%)	26.2	---	6.5	19.6	9.2	---	---
Quercus bicolor							
Stems/ha	7	3	37	---	43	---	---
BA (m^2/ha)	0.71	0.09	1.27	---	1.42	---	---
Avg DBH (cm)	34.4	22.3	20.2	---	18.6	---	---
Rel. Den. (%)	0.6	0.2	5.1	---	6.9	---	---
Rel. Dom. (%)	1.9	0.3	3.9	---	5.9	---	---
Fraxinus nigra							
Stems/ha	---	8	7	---	---	---	4
BA (m^2/ha)	---	0.16	0.19	---	---	---	0.04
Avg DBH (cm)	---	15.1	19.2	---	---	---	9.5
Rel. Den. (%)	---	0.6	0.7	---	---	---	0.6
Rel. Dom. (%)	---	0.4	0.4	---	---	---	0.2

Appendix A. (continued)

Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Quercus macrocarpa							
Stems/ha	---	8	---	---	---	---	13
BA (m^2/ha)	---	2.49	---	---	---	---	0.27
Avg DBH (cm)	---	68.0	---	---	---	---	14.8
Rel. Den. (%)	---	1.5	---	---	---	---	1.4
Rel. Dom. (%)	---	7.2	---	---	---	---	1.3
Salix spp.							
Stems/ha	---	---	---	---	7	3	---
BA (m^2/ha)	---	---	---	---	0.31	1.86	---
Avg DBH (cm)	---	---	---	---	23.6	61.2	---
Rel. Den. (%)	---	---	---	---	0.7	1.0	---
Rel. Dom. (%)	---	---	---	---	0.8	4.9	---
Tilia americana							
Stems/ha	---	---	3	---	---	---	---
BA (m^2/ha)	---	---	0.06	---	---	---	---
Avg DBH (cm)	---	---	13.4	---	---	---	---
Rel. Den. (%)	---	---	0.8	---	---	---	---
Rel. Dom. (%)	---	---	0.3	---	---	---	---
Betula papyrifera							
Stems/ha	---	---	3	---	---	---	---
BA (m^2/ha)	---	---	0.06	---	---	---	---
Avg DBH (cm)	---	---	14.9	---	---	---	---
Rel. Den. (%)	---	---	0.7	---	---	---	---
Rel. Dom. (%)	---	---	0.2	---	---	---	---
Populus tremuloides							
Stems/ha	---	---	---	3	---	---	---
BA (m^2/ha)	---	---	---	0.14	---	---	---
Avg DBH (cm)	---	---	---	26.7	---	---	---
Rel. Den. (%)	---	---	---	0.3	---	---	---
Rel. Dom. (%)	---	---	---	0.8	---	---	---

Appendix B. Comparison of tree species composition in the sapling (1.5-9.0 cm dbh) and seedling (taller than 50 cm and less than 1.5 cm dbh) layers of the understory of seven swamp forests along Saginaw Bay.

Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Acer saccharinum							
Saplings/ha	103	143	213	43	103	75	8
Seedlings/ha	10	---	3	15	3	---	---
Fraxinus pensylvanica							
Saplings/ha	227	30	173	180	160	138	443
Seedlings/ha	340	10	127	265	120	13	93
Ulmus americana							
Saplings/ha	673	285	140	190	40	---	---
Seedlings/ha	47	5	27	5	---	---	8
Fraxinus nigra							
Saplings/ha	---	20	33	---	---	---	---
Seedlings/ha	---	---	67	---	---	---	---
Quercus bicolor							
Saplings/ha	7	5	7	---	13	---	---
Seedlings/ha	---	---	7	---	---	---	---
Carpinus caroliniana							
Saplings/ha	---	---	7	---	---	---	---
Seedlings/ha	---	---	7	---	---	---	---
Thuja occidentalis							
Saplings/ha	---	10	---	---	---	---	---
Seedlings/ha	---	---	---	---	---	---	---

Appendix C. Comparison of shrub species composition in the understory of seven swamp forests along Saginaw Bay.

Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Cornus amomum							
Stems/ha	83	67	72	581	1,444	---	125
Mean Coverage (%)	0.20	0.05	0.20	0.75	1.40	---	0.17
Viburnum lentago							
Stems/ha	---	22	314	22	77	---	---
Mean Coverage (%)	---	0.05	0.80	0.05	0.07	---	---
Ilex verticillata							
Stems/ha	---	482	206	1,431	---	---	---
Mean Coverage (%)	---	0.65	0.20	1.10	---	---	---
Sambucus canadensis							
Stems/ha	---	22	26	---	90	---	---
Mean Coverage (%)	---	0.05	0.13	---	0.13	---	---
Rubus occidentalis							
Stems/ha	---	22	---	---	77	---	25
Mean Coverage (%)	---	0.05	---	---	0.07	---	0.17
Rubus strigosus							
Stems/ha	---	22	---	---	191	---	8
Mean Coverage (%)	---	0.05	---	---	0.20	---	0.08
Cephalanthus occidentalis							
Stems/ha	568	---	52	---	---	13	---
Mean Coverage (%)	0.67	---	0.07	---	---	0.13	---
Ribes americanum							
Stems/ha	---	22	---	---	52	---	---
Mean Coverage (%)	---	0.05	---	---	0.07	---	---
Rosa palustris							
Stems/ha	103	---	---	22	---	---	---
Mean Coverage (%)	0.07	---	---	0.05	---	---	---
Prunus virginiana							
Stems/ha	---	---	26	---	26	---	---
Mean Coverage (%)	---	---	0.03	---	0.07	---	---
Lindera benzoin							
Stems/ha	---	---	106	---	---	---	---
Mean Coverage (%)	---	---	0.13	---	---	---	---

Appendix C. (continued)

Species	King Road (n=15)	Wigwam Bay (n=20)	Pigeon Road (n=15)	Tobico Marsh (n=20)	Pin-conning (n=15)	Wildfowl Swale (n=8)	Wildfowl Glade (n=12)
Crataegus spp.							
Stems/ha	---	---	90	---	---	---	---
Mean Coverage (%)	---	---	0.13	---	---	---	---
Cornus foemina							
Stems/ha	---	---	---	81	---	---	---
Mean Coverage (%)	---	---	---	0.40	---	---	---
Lonicera tatarica							
Stems/ha	---	---	---	224	---	---	---
Mean Coverage (%)	---	---	---	0.15	---	---	---
Spiraea alba							
Stems/ha	52	---	---	---	---	---	---
Mean Coverage (%)	0.07	---	---	---	---	---	---
Zanthoxylum americanum							
Stems/ha	---	---	232	---	---	---	---
Mean Coverage (%)	---	---	0.40	---	---	---	---

Appendix D. Summary of groundcover vegetation of seven coastal swamp forests along Saginaw Bay (values are frequency %, average coverage is in parentheses).

Species	King Road	Wigwam Bay	Pigeon Road	Tobico Marsh	Pin-conning	Wildfowl Swale	Wildfowl Glade
TREES							
Native Species							
Acer saccharinum	20 (0.8)	55 (0.6)	13 (0.3)	25 (0.9)	67 (0.9)	25 (0.4)	8 (0.1)
Fraxinus pennsylvanica	53 (3.0)	20 (0.8)	20 (0.2)	30 (1.1)	27 (0.6)	50 (5.5)	50 (0.6)
Quercus bicolor	13 (0.1)	5 (0.1)	---	---	13 (0.3)	---	---
Ulmus americana	13 (0.1)	10 (0.4)	---	---	7 (0.1)	13 (0.1)	---
TALL SHRUBS							
Native Species							
Cornus amomum	---	5 (0.1)	7 (0.7)	5 (0.8)	---	---	17 (0.9)
Lindera benzoin	---	---	13 (1.3)	---	---	---	---
Non-native Species							
Lonicera tatarica	---	---	---	10 (1.1)	---	---	---
SHORT SHRUBS							
Native Species							
Euonymus obovatus	---	---	7 (0.1)	---	---	---	---
Lonicera dioica	---	---	7 (0.1)	---	---	---	---
Ribes americanum	---	5 (0.2)	7 (0.1)	10 (0.1)	---	---	---
Ribes cynosbati	---	---	7 (0.3)	---	---	---	---
Rosa palustris	---	---	---	5 (0.3)	---	---	---
Rubus strigosus	---	---	---	---	---	13 (0.4)	8 (0.1)
WOODY VINES							
Native Species							
Menispermum canadense	---	---	13 (0.1)	---	---	---	---
Parthenocissus quinquefolia	7 (0.1)	---	27 (0.7)	5 (0.1)	---	---	8 (0.6)
Smilax tamnoides	---	---	---	---	7 (0.2)	---	---
Toxicodendron radicans	---	---	7 (0.1)	5 (0.2)	---	---	---
Vitis riparia	33 (0.4)	---	---	5 (0.1)	---	13 (0.1)	8 (0.1)
Non-native species							
Solanum dulcamara	---	15 (0.3)	---	20 (2.7)	13 (0.3)	---	---
FORBS							
Native Species							
Alisma plantago-aquatica	---	---	---	5 (0.2)	---	---	---
Amphicarpaea bracteata	---	---	7 (0.1)	---	---	---	---
Arisaema triphyllum	---	---	---	5 (0.1)	---	13 (0.1)	---
Aster nova-angliae	---	---	---	---	---	---	8 (0.1)
Bidens cernuus	---	---	---	5 (0.1)	---	---	---
Boehmeria cylindrica	---	20 (1.5)	---	10 (0.5)	27 (0.5)	50 (2.1)	8 (0.7)
Cicuta maculata	---	5 (0.2)	20 (1.1)	50 (2.7)	---	---	---
Circaea lutetiana	---	10 (0.2)	---	5 (0.2)	7 (0.3)	---	---
Erechtites hieraciifolia	7 (0.1)	---	---	---	---	---	---
Erigeron philadelphicus	---	---	---	---	---	13 (0.1)	---
Fragaria virginiana	---	---	---	---	---	---	---

Appendix D. (continued)

Species	King Road	Wigwam Bay	Pigeon Road	Tobico Marsh	Pin-conning	Wildfowl Swale	Wildfowl Glade
FORBS							
Native Species (continued)							
Galium aparine	---	---	7 (0.1)	---	---	13 (0.1)	25 (0.4)
Galium triflorum	---	10 (0.1)	---	10 (1.1)	13 (1.0)	---	75 (1.8)
Geum canadense	---	5 (0.4)	7 (0.2)	10 (0.4)	13 (1.1)	---	---
Impatiens capensis	---	35 (3.1)	7 (0.1)	15 (0.6)	47 (4.3)	13 (0.1)	8 (0.4)
Laportea canadensis	---	5 (0.1)	---	---	---	---	---
Lathyrus palustris	---	---	---	---	---	---	42 (0.8)
Lemna minor	---	---	---	25 (0.3)	7 (0.1)	---	---
Lemna trisulca	---	---	---	35 (0.4)	---	---	---
Lilium michiganense	---	---	7 (0.1)	---	---	---	---
Linnaea borealis	---	---	---	---	---	---	---
Lycopus americanus	---	5 (0.1)	---	---	---	---	---
Lycopus uniflorus	13 (0.5)	---	---	5 (0.1)	---	38 (0.4)	8 (0.1)
Lysimachia ciliata	---	---	7 (0.1)	---	---	---	---
Lysimachia thyrsiflora	---	---	---	5 (0.1)	---	---	17 (0.8)
Maianthemum canadense	---	---	---	---	---	13 (0.3)	---
Mentha arvensis	---	---	---	5 (0.1)	---	---	---
Phryma leptostachya	---	---	---	5 (0.3)	---	---	---
Pilea pumila	---	15 (0.3)	---	---	---	---	---
Polygonum sp.	---	---	---	---	---	---	17 (0.3)
Ranunculus flabellaris	---	---	---	5 (0.1)	---	---	---
Rubus pubescens	---	---	---	---	7 (0.3)	---	---
Sanicula gregaria	---	5 (0.4)	---	5 (1.0)	---	---	---
Scutellaria galericulata	7 (0.1)	---	---	---	---	---	50 (1.8)
Scutellaria lateriflora	7 (0.8)	---	---	5 (0.1)	---	---	---
Sium suave	---	---	---	40 (0.9)	---	---	---
Smilacina stellata	---	5 (0.2)	7 (0.1)	---	---	---	---
Solidago gigantea	---	---	---	---	7 (0.5)	---	---
Solidago spp.	---	25 (2.4)	27 (2.1)	20 (1.2)	20 (1.6)	13 (0.1)	---
Thalictrum dasycarpum	---	---	7 (0.1)	---	7 (0.4)	---	---
Urtica dioica	---	---	---	---	---	---	17 (0.3)
Viola pubescens	---	10 (0.4)	---	---	---	---	---
Viola sorroria	---	---	---	5 (0.9)	---	13 (0.3)	---
Viola sp.	---	5 (0.1)	---	10 (0.4)	7 (0.2)	---	---
Zizia aurea	---	---	---	5 (0.1)	---	---	---
Unknown aquatic plant # 1	---	---	---	5 (0.1)	---	---	---
Unknown aquatic plant # 2	---	5 (0.1)	---	5 (0.1)	---	---	---
Non-native species							
Cirsium arvense	---	---	---	---	---	---	17 (0.6)
Lysimachia nummularia	---	5 (0.1)	---	---	---	---	---

Appendix D. (continued)

Species	King Road	Wigwam Bay	Pigeon Road	Tobico Marsh	Pin-conning	Wildfowl Swale	Wildfowl Glade
GRAMINOIDS							
Native Species							
Calamagrostis canadensis	---	---	---	5 (0.3)	---	---	83 (24.5)
Carex amphibola	---	5 (0.3)	---	---	---	---	---
Carex blanda	---	---	7 (0.1)	---	---	---	---
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 (0.1)	---	---	---
Carex oligosperma	---	10 (0.4)	---	---	---	---	---
Carex stipata	---	10 (0.6)	---	15 (0.4)	---	---	---
Carex stricta	---	---	---	---	---	---	75 (8.2)
Carex sp. # 1	---	5 (0.3)	---	5 (0.1)	---	---	---
Carex sp. # 2	---	---	---	5 (0.5)	20 (2.5)	---	8 (6.3)
Elymus virginicus	---	20 (0.4)	20 (0.6)	10 (4.0)	---	---	---
Glyceria striata	---	55 (11.1)	13 (0.9)	20 (6.1)	33 (5.7)	13 (5.0)	8 (0.6)
Juncus balticus	---	---	---	---	13 (1.4)	---	---
Non-native species							
Phalaris arundinacea	---	---	---	---	---	---	8 (1.3)
FERNS							
Native Species							
Athyrium filix-femina	---	---	---	---	---	13 (0.3)	---
Dryopteris cristata	20 (1.3)	---	---	---	---	---	---
Equisetum fluviatile	---	---	---	5 (0.1)	---	---	---
Onoclea sensibilis	---	15 (1.8)	---	---	---	---	8 (2.8)
Osmunda regalis	---	---	---	---	7 (0.1)	---	---
Pteridium aquilinum	---	---	---	---	---	---	---
Thelypteris palustris	---	5 (0.1)	---	---	7 (0.1)	---	8 (0.2)
NON-PLANT COVERAGE							
Water coverage	---	20 (1.0)	73 (73.3)	95 (93.0)	40 (21.0)	50 (47.5)	---
Water depth (cm)	---	20 (0.3)	73 (9.7)	95 (14.9)	40 (2.3)	50 (13.8)	---
High water mark (cm)	100 (28.5)	80 (15.1)	80 (24.9)	---	40 (8.9)	---	---
Depth to Rock (cm)	---	---	---	---	---	63 (36.5)	8 (3.8)
Depth to Water table (cm)	---	---	---	5 (0.7)	---	---	---
Woody Debris	20 (1.8)	40 (8.5)	13 (0.4)	20 (1.0)	7 (1.2)	25 (5.4)	8 (0.4)

Appendix E. Comparison of the overstory species composition of three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands.

	Alpena			Les Cheneaux Islands				
Species	Misery Bay (n=20)	El Cajon Bay (n=20)	Ossi-nike (n=20)	St. Martin (n=20)	Duck Bay (n=10)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)
Thuja occidentalis								
Stems/ha	1,520	1,405	8	1,863	1,335	2,155	2,015	2,485
BA (m^2/ha)	48.75	49.08	0.26	65.03	51.51	52.93	43.48	49.47
Avg DBH (cm)	20.8	21.1	19.1	19.0	21.6	16.6	16.3	15.5
Rel. Den. (%)	80.0	75.5	0.7	84.7	83.5	89.2	86.6	91.3
Rel. Dom. (%)	78.5	78.3	1.6	82.8	77.3	88.5	78.2	91.0
Betula papyrifera								
Stems/ha	58	45	20	75	30	93	15	70
BA (m^2/ha)	1.39	1.11	0.74	2.30	1.95	2.55	0.51	1.63
Avg DBH (cm)	16.4	17.6	20.6	19.4	24.6	17.1	20.1	17.7
Rel. Den. (%)	3.3	2.6	2.8	3.8	2.4	3.8	0.8	2.9
Rel. Dom. (%)	2.2	1.7	3.1	3.4	2.8	3.8	1.2	2.8
Abies balsamea								
Stems/ha	85	103	25	58	45	90	40	---
BA (m^2/ha)	1.39	1.58	0.26	3.95	0.60	1.72	0.46	---
Avg DBH (cm)	13.8	13.8	11.5	19.4	12.6	15.1	11.9	---
Rel. Den. (%)	5.6	8.3	3.8	2.8	2.7	4.3	2.3	---
Rel. Dom. (%)	2.3	4.4	1.0	3.7	1.2	3.3	0.9	---
Picea glauca								
Stems/ha	---	5	---	95	55	45	15	---
BA (m^2/ha)	---	0.30	---	4.16	4.46	1.83	0.42	---
Avg DBH (cm)	---	27.9	---	23.5	29.8	22.6	19.6	---
Rel. Den. (%)	---	0.2	---	5.1	3.6	2.0	0.6	---
Rel. Dom. (%)	---	0.4	---	6.7	6.4	3.1	0.7	---
Picea mariana								
Stems/ha	48	43	8	25	---	5	50	30
BA (m^2/ha)	2.93	1.86	0.09	0.88	---	0.21	0.93	1.11
Avg DBH (cm)	26.2	22.6	12.7	20.3	---	21.6	14.3	21.1
Rel. Den. (%)	2.6	2.2	1.2	1.3	---	0.2	2.0	1.1
Rel. Dom. (%)	4.9	2.8	0.4	1.5	---	0.4	1.6	2.0
Populus balsamifera								
Stems/ha	5	23	---	15	90	5	120	40
BA (m^2/ha)	0.35	0.63	---	0.63	6.97	0.26	5.02	0.98
Avg DBH (cm)	29.9	21.2	---	22.1	35.3	25.6	22.4	17.9
Rel. Den. (%)	0.3	1.2	---	0.7	6.7	0.2	5.9	1.7
Rel. Dom. (%)	0.6	1.0	---	1.0	11.5	0.5	9.4	1.8

Appendix E. (continued)

Species	Alpena: Misery Bay (n=20)	Alpena: El Cajon Bay (n=20)	Alpena: Ossi-nike (n=20)	Les Cheneaux Islands: St. Martin (n=20)	Les Cheneaux Islands: Duck Bay (n=10)	Les Cheneaux Islands: Paquin Lake (n=20)	Les Cheneaux Islands: Voight Bay (n=10)	Les Cheneaux Islands: Brulee Point (n=10)
Populus tremuloides								
Stems/ha	103	45	3	---	5	3	10	---
BA (m^2/ha)	6.87	3.04	0.02	---	0.14	0.16	1.35	---
Avg DBH (cm)	28.3	28.2	9.1	---	18.2	28.8	41.4	---
Rel. Den. (%)	6.3	3.4	0.4	---	0.3	0.1	0.6	---
Rel. Dom. (%)	10.6	5.5	0.2	---	0.2	0.3	2.7	---
Fraxinus nigra								
Stems/ha	---	13	20	25	---	3	---	50
BA (m^2/ha)	---	0.37	0.51	0.39	---	0.10	---	0.56
Avg DBH (cm)	---	19.5	16.6	12.2	---	13.3	---	11.3
Rel. Den. (%)	---	1.3	2.6	1.3	---	0.1	---	2.5
Rel. Dom. (%)	---	1.9	2.1	0.7	---	0.0	---	1.4
Larix laricina								
Stems/ha	---	---	13	5	---	3	5	15
BA (m^2/ha)	---	---	0.39	0.12	---	0.02	0.14	0.42
Avg DBH (cm)	---	---	20.0	17.4	---	9.1	19.5	18.4
Rel. Den. (%)	---	---	1.6	0.2	---	0.1	0.2	0.6
Rel. Dom. (%)	---	---	2.6	0.2	---	0.1	0.2	1.0
Pinus strobus								
Stems/ha	3	3	5	---	---	---	25	---
BA (m^2/ha)	0.19	0.30	0.05	---	---	---	3.11	---
Avg DBH (cm)	31.5	39.8	9.4	---	---	---	38.9	---
Rel. Den. (%)	0.2	0.1	0.8	---	---	---	1.0	---
Rel. Dom. (%)	0.3	0.4	0.2	---	---	---	5.2	---
Fraxinus pensylvanica								
Stems/ha	10	43	760	---	---	---	---	---
BA (m^2/ha)	0.16	1.18	17.09	---	---	---	---	---
Avg DBH (cm)	13.9	18.1	18.4	---	---	---	---	---
Rel. Den. (%)	1.2	3.5	78.6	---	---	---	---	---
Rel. Dom. (%)	0.3	2.4	81.1	---	---	---	---	---
Acer rubrum								
Stems/ha	10	8	48	---	---	---	---	---
BA (m^2/ha)	0.21	0.09	1.65	---	---	---	---	---
Avg DBH (cm)	16.6	11.7	20.4	---	---	---	---	---
Rel. Den. (%)	0.5	0.4	6.9	---	---	---	---	---
Rel. Dom. (%)	0.3	0.2	7.2	---	---	---	---	---
Betula alleghaniensis								
Stems/ha	---	---	---	---	10	---	---	---
BA (m^2/ha)	---	---	---	---	0.37	---	---	---
Avg DBH (cm)	---	---	---	---	22.0	---	---	---
Rel. Den. (%)	---	---	---	---	0.6	---	---	---
Rel. Dom. (%)	---	---	---	---	0.5	---	---	---

Appendix E. (continued)

Species	Alpena: Misery Bay (n=20)	Alpena: El Cajon Bay (n=20)	Alpena: Ossi-nike (n=20)	Les Cheneaux Islands: St. Martin (n=20)	Les Cheneaux Islands: Duck Bay (n=10)	Les Cheneaux Islands: Paquin Lake (n=20)	Les Cheneaux Islands: Voight Bay (n=10)	Les Cheneaux Islands: Brulee Point (n=10)
Acer saccharinum								
Stems/ha	---	---	3	---	---	---	---	---
BA (m^2/ha)	---	---	0.16	---	---	---	---	---
Avg DBH (cm)	---	---	28.7	---	---	---	---	---
Rel. Den. (%)	---	---	0.3	---	---	---	---	---
Rel. Dom. (%)	---	---	0.4	---	---	---	---	---
Acer pensylvanicum								
Stems/ha	---	3	---	3	---	---	---	---
BA (m^2/ha)	---	0.02	---	0.05	---	---	---	---
Avg DBH (cm)	---	11.3	---	14.3	---	---	---	---
Rel. Den. (%)	---	0.3	---	0.1	---	---	---	---
Rel. Dom. (%)	---	0.1	---	0.1	---	---	---	---
Sorbus americana								
Stems/ha	---	---	---	---	5	---	---	---
BA (m^2/ha)	---	---	---	---	0.09	---	---	---
Avg DBH (cm)	---	---	---	---	16.2	---	---	---
Rel. Den. (%)	---	---	---	---	0.2	---	---	---
Rel. Dom. (%)	---	---	---	---	0.1	---	---	---
Fraxinus americana								
Stems/ha	---	3	---	---	---	---	---	---
BA (m^2/ha)	---	0.12	---	---	---	---	---	---
Avg DBH (cm)	---	23.5	---	---	---	---	---	---
Rel. Den. (%)	---	0.3	---	---	---	---	---	---
Rel. Dom. (%)	---	0.6	---	---	---	---	---	---
Quercus rubra								
Stems/ha	---	---	3	---	---	---	---	---
BA (m^2/ha)	---	---	0.02	---	---	---	---	---
Avg DBH (cm)	---	---	10.7	---	---	---	---	---
Rel. Den. (%)	---	---	0.4	---	---	---	---	---
Rel. Dom. (%)	---	---	0.2	---	---	---	---	---
Acer saccharum								
Stems/ha	---	10	---	---	---	---	---	---
BA (m^2/ha)	---	0.12	---	---	---	---	---	---
Avg DBH (cm)	---	12.9	---	---	---	---	---	---
Rel. Den. (%)	---	0.9	---	---	---	---	---	---
Rel. Dom. (%)	---	0.3	---	---	---	---	---	---

Appendix F. Comparison of species composition in the sapling (1.5-9.0 cm dbh) and seedling (taller than 50 cm and less than 1.5 cm dbh) layers in the understory of three swam forests in Alpena County and five swamp forests in the Les Cheneaux Islands.

	Alpena			Les Cheneaux Islands				
Species	Misery Bay (n=20)	El Cajon Bay (n=20)	Ossi-nike (n=20)	St. Martin (n=20)	Duck Bay (n=10)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)
Thuja occidentalis								
Saplings/ha	215	145	5	485	410	645	1,040	1,190
Seedlings/ha	---	10	5	---	---	---	60	---
Abies balsamea								
Saplings/ha	45	520	290	10	200	100	210	50
Seedlings/ha	75	785	140	5	80	---	410	---
Fraxinus nigra								
Saplings/ha	30	---	5	45	---	10	---	250
Seedlings/ha	---	---	---	---	---	---	---	---
Populus balsamifera								
Saplings/ha	---	---	---	---	---	---	---	---
Seedlings/ha	5	---	---	---	270	5	---	20
Populus tremuloides								
Saplings/ha	---	30	---	---	---	---	---	---
Seedlings/ha	35	95	---	---	40	---	---	---
Picea mariana								
Saplings/ha	---	---	25	---	---	---	20	---
Seedlings/ha	---	10	10	---	---	---	---	---
Picea glauca								
Saplings/ha	---	---	---	---	---	5	---	---
Seedlings/ha	---	---	---	---	20	---	---	---
Larix laricina								
Saplings/ha	---	10	5	---	---	5	---	---
Seedlings/ha	---	5	15	---	---	---	---	---
Betula papyrifera								
Saplings/ha	5	---	5	---	---	---	10	---
Seedlings/ha	---	---	---	---	---	---	---	---
Fraxinus pensylvanica								
Saplings/ha	---	5	320	---	---	---	---	---
Seedlings/ha	---	5	115	---	---	---	---	---
Acer rubrum								
Saplings/ha	5	---	10	---	---	---	---	---
Seedlings/ha	---	---	---	---	---	---	---	---

Appendix F. (continued)

Species	Alpena: Misery Bay (n=20)	Alpena: El Cajon Bay (n=20)	Alpena: Ossi-nike (n=20)	Les Cheneaux Islands: St. Martin (n=20)	Les Cheneaux Islands: Duck Bay (n=10)	Les Cheneaux Islands: Paquin Lake (n=20)	Les Cheneaux Islands: Voight Bay (n=10)	Les Cheneaux Islands: Brulee Point (n=10)
Pinus strobus								
Saplings/ha	---	---	10	---	---	---	---	---
Seedlings/ha	---	---	20	---	---	---	---	---
Acer saccharinum								
Saplings/ha	---	8	3	---	---	---	---	---
Seedlings/ha	---	---	---	---	---	---	---	---
Acer pensylvanicum								
Saplings/ha	---	---	---	---	---	---	---	---
Seedlings/ha	---	5	---	---	---	---	---	---

Appendix G. Comparison of shrub species composition in the understory of three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands.

	Alpena			Les Cheneaux Islands				
Species	Misery Bay (n=20)	El Cajon Bay (n=20)	Ossi-nike (n=20)	St. Martin (n=20)	Duck Bay (n=10)	Paquin Lake (n=20)	Voight Bay (n=10)	Brulee Point (n=10)
Alnus rugosa								
Stems/ha	---	---	5,045	---	---	10	---	470
Mean coverage (%)	---	---	13.3	---	---	0.1	---	0.7
Spiraea alba								
Stems/ha	---	---	5,165	---	---	---	10	---
Mean coverage (%)	---	---	7.1	---	---	---	0.1	---
Potentilla fruticosa								
Stems/ha	---	---	210	---	---	---	110	---
Mean coverage (%)	---	---	0.3	---	---	---	0.2	---
Rhamnus alnifolia								
Stems/ha	---	---	---	---	---	---	---	20
Mean coverage (%)	---	---	---	---	---	---	---	0.1
Cornus rugosa								
Stems/ha	---	15	---	---	---	---	---	---
Mean coverage (%)	---	0.1	---	---	---	---	---	---
Acer spicatum								
Stems/ha	---	5	---	---	---	---	---	---
Mean coverage (%)	---	0.2	---	---	---	---	---	---
Amelanchier spp.								
Stems/ha	---	5	---	---	---	---	---	---
Mean coverage (%)	---	0.1	---	---	---	---	---	---
Betula pumila								
Stems/ha	---	---	630	---	---	---	---	---
Mean coverage (%)	---	---	0.8	---	---	---	---	---
Rubus strigosus								
Stems/ha	---	---	80	---	---	---	---	---
Mean coverage (%)	---	---	0.3	---	---	---	---	---
Rosa palustris								
Stems/ha	---	---	40	---	---	---	---	---
Mean coverage (%)	---	---	0.3	---	---	---	---	---
Cornus amomum								
Stems/ha	---	---	20	---	---	---	---	---
Mean coverage (%)	---	---	0.2	---	---	---	---	---
Salix spp.								
Stems/ha	---	---	10	---	---	---	---	---
Mean coverage (%)	---	---	0.1	---	---	---	---	---
Ilex verticilata								
Stems/ha	---	---	5	---	---	---	---	---
Mean coverage (%)	---	---	0.1	---	---	---	---	---

Appendix H. Comparison of the ground-cover vegetation among three swamp forests of Alpena County and five swamp forests of the Les Cheneaux Islands (values are frequency %, average coverage is in parentheses).

	Alpena			Les Cheneaux Islands				
Species	Misery Bay	El Cajon Bay	Ossi-nike	St. Martin	Duck Bay	Paquin Lake	Voight Bay	Brulee Point
TREES								
Native Species								
Abies balsamea	25 (0.7)	55 (3.0)	---	40 (0.4)	10 (0.1)	35 (0.4)	80 (1.8)	20 (0.2)
Acer rubrum	---	---	25 (0.3)	---	---	---	---	---
Acer saccharinum	---	---	20 (0.2)	---	---	---	---	---
Betula papyrifera	10 (0.1)	25 (0.3)	5 (0.1)	15 (0.2)	10 (0.1)	5 (0.1)	10 (0.1)	---
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 (0.1)	---	---	---	---
Picea mariana	---	5 (0.1)	---	---	---	---	---	10 (0.1)
Populus balsamifera	5 (0.1)	---	---	15 (0.3)	20 (0.3)	---	---	---
Populus tremuloides	20 (0.6)	20 (0.6)	---	---	---	---	---	---
Quercus rubra	---	5 (0.1)	---	---	---	---	---	---
Thuja occidentalis	5 (0.1)	---	---	20 (0.2)	---	30 (0.4)	10 (0.1)	---
TALL SHRUBS								
Native Species								
Acer pensylvanicum	---	---	---	---	10 (0.1)	10 (0.4)	---	---
Acer spicatum	---	5 (0.1)	---	20 (0.2)	20 (0.2)	---	---	---
Alnus rugosa	---	---	15 (0.7)	---	---	5 (0.5)	---	10 (2.5)
Amelanchier spp.	5 (0.1)	10 (0.2)	---	---	---	---	---	20 (0.2)
Cornus amomum	---	---	15 (0.2)	---	---	---	---	10 (0.2)
Ilex verticillata	---	---	5 (0.1)	---	---	---	---	10 (0.1)
Sambucus canadensis	---	---	---	5 (0.1)	---	---	---	20 (0.2)
Sorbus americana	---	---	---	5 (0.1)	---	10 (0.2)	---	---
Viburnum trilobum	---	---	---	---	---	---	---	10 (0.1)
SHORT SHRUBS								
Native Species								
Arctostaphylos uva-ursi	---	---	---	---	---	---	10 (0.5)	---
Betula pumila	---	---	15 (0.4)	---	---	---	---	---
Ledum groenlandicum	---	---	---	---	---	5 (0.1)	---	---
Lonicera canadensis	5 (0.1)	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	---	---	55 (3.5)	---	---	---	10 (0.7)	---
Gaultheria hispidula	---	---	---	---	---	10 (0.1)	20 (0.6)	30 (1.1)

Appendix H. (continued)

Species	Alpena: Misery Bay	Alpena: El Cajon Bay	Alpena: Ossi-nike	Les Cheneaux Islands: St. Martin	Les Cheneaux Islands: Duck Bay	Les Cheneaux Islands: Paquin Lake	Les Cheneaux Islands: Voight Bay	Les Cheneaux Islands: Brulee Point
FORBS								
Native Species								
Actaea sp.	---	5 (0.2)	---	5 (0.2)	---	---	---	---
Allium sp.	---	---	---	---	---	---	20 (0.2)	---
Aralia nudicaulis	5 (0.8)	15 (1.5)	---	5 (0.4)	---	---	---	---
Aster ciliolatus	---	---	---	---	---	15 (0.4)	---	20 (0.2)
Aster macrophyllus	40 (0.4)	60 (2.0)	---	20 (0.2)	---	---	40 (0.4)	50 (1.0)
Aster puniceus	---	5 (0.1)	5 (0.1)	---	---	---	---	20 (0.2)
Aster sp. # 1	10 (0.3)	10 (0.1)	5 (0.1)	---	---	---	---	20 (0.2)
Aster sp. # 2	---	5 (0.3)	---	---	---	---	---	20 (0.3)
Caltha palustris	---	5 (0.3)	---	5 (0.4)	---	---	---	---
Campanula aparinoides	---	---	50 (0.5)	---	---	---	---	20 (0.2)
Cicuta bulbifera	---	---	5 (0.1)	---	---	---	---	---
Circaea alpina	---	---	---	5 (0.4)	10 (0.1)	---	---	---
Clematis virginiana	---	---	5 (0.1)	---	---	---	---	---
Clintonia borealis	---	---	---	15 (0.2)	10 (0.1)	---	---	---
Coptis trifolia	---	10 (0.1)	---	20 (0.3)	10 (0.1)	15 (0.2)	---	20 (0.6)
Cornus canadensis	---	10 (0.3)	---	10 (0.2)	---	---	---	40 (0.9)
Cypripedium sp.	---	---	---	5 (0.1)	---	---	10 (0.1)	---
Fragaria virginiana	---	---	5 (0.1)	10 (0.1)	---	---	10 (0.1)	20 (0.3)
Galium triflorum	---	15 (0.2)	25 (0.3)	20 (0.2)	30 (0.4)	---	10 (0.1)	40 (0.4)
Habenaria obtusata	---	---	---	---	---	5 (0.1)	---	---
Impatiens capensis	---	---	10 (0.1)	---	---	---	---	---
Iris lacustris	---	5 (0.5)	---	---	---	---	10 (6.5)	---
Iris versicolor	---	---	25 (1.1)	5 (0.1)	---	---	---	---
Lathyrus palustris	---	---	10 (0.4)	---	---	---	---	---
Lilium michiganense	---	---	---	---	---	---	10 (0.1)	---
Linnaea borealis	---	15 (0.4)	---	20 (0.4)	---	5 (0.1)	40 (0.8)	40 (2.0)
Lycopus americanus	---	---	5 (0.1)	---	---	---	---	---
Lycopus uniflorus	---	5 (0.1)	60 (1.7)	---	---	---	---	30 (0.3)
Lysimachia thyrsiflora	---	---	85 (1.2)	---	---	---	---	---
Maianthemum canadense	25 (0.3)	55 (1.3)	---	75 (1.1)	50 (1.1)	20 (0.2)	30 (0.3)	50 (0.9)
Mentha arvensis	---	---	25 (1.0)	5 (0.1)	---	---	---	---
Mitella nuda	---	10 (0.6)	10 (0.5)	40 (1.1)	40 (2.9)	15 (0.9)	50 (0.7)	70 (1.9)
Orchid sp.	5 (0.1)	5 (0.1)	---	10 (0.1)	---	---	---	---
Oxalis stricta	---	---	---	5 (0.1)	---	---	---	---
Parnassia glauca	---	---	---	---	---	5 (0.1)	---	---
Petasites frigidus	15 (0.5)	30 (0.9)	---	5 (0.1)	---	---	---	10 (0.7)
Pinguicula vulgaris	---	---	---	---	---	---	10 (0.5)	---
Polygala paucifolia	---	10 (0.1)	---	45 (0.9)	10 (0.6)	---	60 (1.4)	---
Polygonum sp.	---	---	25 (0.5)	---	---	---	---	---
Potentilla palustre	---	---	20 (0.5)	---	---	---	10 (0.1)	---
Potentilla simplex	---	---	---	---	---	---	10 (0.4)	---
Prenanthes alba	---	---	---	---	10 (0.2)	---	---	---
Prunella vulgaris	---	---	---	10 (0.3)	---	5 (0.1)	20 (0.2)	20 (0.9)
Pyrola asarifolia	---	---	---	---	---	---	---	10 (0.2)

Appendix H. (continued)

Species	Alpena			Les Cheneaux Islands				
	Misery Bay	El Cajon Bay	Ossi-nike	St. Martin	Duck Bay	Paquin Lake	Voight Bay	Brulee Point
FORBS								
Native Species (continued)								
Pyrola sp.	5 (0.2)	---	---	5 (0.1)	---	---	30 (1.9)	---
Ranunculus flabellaris	---	---	---	---	---	---	---	---
Ranunculus sp.	---	---	15 (0.6)	---	---	---	---	---
Rubus pubescens	---	10 (0.6)	45 (3.4)	15 (1.9)	10 (0.2)	15 (0.2)	---	60 (4.1)
Scutellaria galericulata	---	---	25 (0.3)	5 (0.1)	---	---	---	10 (0.1)
Senecio aureus	---	5 (0.2)	---	5 (0.3)	---	---	---	10 (0.1)
Smilacina stellata	---	5 (0.1)	---	---	---	---	---	---
Solidago rugosa	5 (0.1)	10 (0.4)	5 (0.1)	10 (0.1)	---	---	---	40 (1.1)
Solidago spp.	10 (0.1)	5 (0.1)	---	---	---	5 (0.1)	---	---
Streptopus roseus	---	---	---	---	10 (0.1)	---	---	---
Trientalis borealis	10 (0.1)	15 (0.6)	---	65 (1.1)	40 (0.7)	70 (1.9)	---	50 (0.9)
Viola cucculata	20 (0.4)	---	---	---	---	---	---	---
Viola sp.	---	5 (0.1)	5 (0.1)	10 (0.1)	10 (0.2)	---	10 (0.1)	---
Unknown # 1	---	5 (0.1)	---	---	10 (0.1)	10 (0.2)	10 (0.1)	---
Unknown # 2	---	5 (0.1)	---	---	---	---	20 (0.2)	---
Unknown # 3	---	5 (0.1)	---	---	---	---	10 (0.4)	---
Non-native species								
Cirsium vulgare	5 (1.5)	---	---	---	---	---	---	---
Epipactis helleborine	---	25 (0.3)	---	---	10 (0.1)	---	---	---
Hieraceum aurantaiacum	---	---	---	---	---	5 (0.2)	---	---
Hieraceum sp.	---	---	---	---	10 (1.0)	---	10 (0.1)	---
Hypericum sp.	---	---	---	---	---	---	10 (0.1)	---
Taraxacum officionale	25 (0.5)	5 (0.1)	---	---	---	---	---	20 (0.3)
GRAMINOIDS								
Native Species								
Calamagrostis canadensis	---	---	85 (8.6)	---	---	---	---	10 (0.2)
Carex alpina	---	---	5 (0.4)	---	---	---	---	---
Carex amphibola	5 (0.5)	---	---	---	---	---	---	---
Carex deweyana	20 (0.8)	30 (7.0)	---	---	---	---	---	---
Carex disperma	---	---	---	10 (1.2)	30 (0.6)	45 (2.6)	---	80 (1.5)
Carex eburnea	20 (0.3)	25 (1.2)	---	30 (0.4)	---	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	---	---	30 (2.6)	---	---	---	---	10 (0.5)
Carex leptalea	---	---	5 (0.8)	---	---	---	---	---
Carex leptonervia	---	---	---	---	10 (0.4)	---	---	---
Carex pedunculata	---	---	---	70 (4.2)	10 (0.7)	5 (0.4)	---	---
Carex richardsonii	---	5 (0.1)	---	---	---	---	---	---
Carex rosea	---	---	---	---	---	---	20 (0.2)	---
Carex stricta	---	5 (4.3)	75 (15.7)	---	---	---	---	20 (0.8)
Carex trisperma	---	---	15 (1.2)	---	---	10 (1.3)	---	---

Appendix H. (continued)

Species	Alpena			Les Cheneaux Islands				
	Misery Bay	El Cajon Bay	Ossi-nike	St. Martin	Duck Bay	Paquin Lake	Voight Bay	Brulee Point
GRAMINOIDS								
Native Species (continued)								
Carex sp. # 1	10 (0.4)	10 (0.5)	5 (0.2)	10 (0.2)	---	5 (0.1)	---	---
Carex sp. # 2	5 (0.1)	---	5 (0.1)	5 (0.2)	---	---	---	---
Carex sp. # 3	5 (1.3)	---	---	---	---	---	---	---
Eleocharis acicularis	---	---	---	---	---	---	10 (4.0)	---
Glyceria striata	---	---	---	10 (0.1)	---	5 (0.1)	---	10 (0.2)
Panicum sp.	---	---	---	---	---	10 (0.2)	---	---
Unknown grass	---	5 (0.1)	---	---	---	---	10 (0.1)	---
Juncus sp.	---	---	---	---	---	---	10 (0.1)	---
FERNS AND HORSETAILS								
Native Species								
Athyrium filix-femina	---	---	---	---	40 (4.7)	---	---	---
Botrichyium virginianum	25 (0.5)	10 (0.1)	---	25 (0.3)	---	---	30 (0.3)	50 (0.9)
unknown fern	---	---	5 (0.1)	---	---	---	---	---
Cystopteris bulbifera	---	15 (9.2)	---	---	---	---	---	---
Dryopteris cristata	---	---	---	5 (0.1)	20 (0.3)	---	---	10 (0.1)
Equisetum fluviatile	5 (1.5)	10 (0.3)	15 (0.6)	25 (1.4)	10 (0.1)	10 (0.4)	---	80 (11.6)
Equisetum palustre	---	---	---	10 (0.1)	---	5 (0.1)	---	10 (0.1)
Equisetum scirpoides	5 (0.1)	---	---	---	---	5 (0.1)	---	---
Gymnocarpium dryopteris	---	5 (0.2)	---	5 (0.1)	10 (0.2)	---	---	---
Onoclea sensibilis	---	---	20 (2.4)	---	---	---	---	---
Osmunda regalis	5 (0.1)	---	---	---	---	---	---	---
Pteridium aquilinum	---	5 (1.0)	---	---	---	---	---	---
Thelypteris palustris	---	---	45 (2.9)	---	---	---	---	---
NON-PLANT COVERAGE								
Water coverage	20 (3.9)	5 (0.1)	75 (33.0)	15 (0.6)	---	10 (1.8)	10 (0.3)	10 (0.4)
Water depth (cm)	20 (0.6)	5 (0.1)	75 (6.1)	15 (0.4)	---	10 (0.3)	10 (0.2)	10 (0.3)
High water mark (cm)	---	---	35 (12.6)	---	---	---	---	---
Depth to Rock (cm)	---	---	20 (6.0)	---	---	---	---	---
Woody Debris	50 (5.5)	25 (2.3)	10 (2.5)	40 (4.8)	50 (8.3)	35 (5.2)	50 (14.8)	30 (3.2)