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THE STRUCTURE, COMPOSITION AND HYDROLOGY OF WET MEADOW PLANT COMMUNITIES FRINGING SAGINAW BAY (LAKE HURON)

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THE STRUCTURE, COMPOSITION AND HYDROLOGY OF WET MEADOW PLANT COMMUNITIES FRINGING SAGINAW BAY (LAKE HURON)

By

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ABSTRACT

THE STRUCTURE, COMPOSITION AND HYDROLOGY OF WET MEADOW PLANT COMMUNITIES FRINGING SAGINAW BAY (LAKE HURON)

By

Kurt Edward Stanley

This 1996-1997 study determined the structure, composition, and above-ground productivity of Saginaw Bay coastal wet meadow vegetation, and the impact of hydrology, soils, anthropogenic disturbance, and Purple Loosestrife on this vegetation assemblage.

Groundwater, surface water, precipitation, and pan evaporation were monitored in a reference and disturbed wet meadow. Precipitation, seiche and storm surge inundation, and evapotranspiration controlled growing-season groundwater levels in un-flooded wet meadows. Mid-summer ET exceeded precipitation and storm surge inputs, lowering groundwater levels. Groundwater levels >60cm lower than Saginaw Bay were observed 20m from Saginaw Bay. Groundwater recharge occurred by vertical percolation, not horizontal groundwater inflow.

Fifteen of 93 species encountered contributed 84.0% of total vegetation importance value at 25 study sites. *Calamagrostis canadensis*, *Carex aquatilis*, *Carex sartwellii*, and *Carex stricta* contributed 60.1% of total IV. Twenty-seven species occurred in only one of 300 plots. The vegetation canopy was 1.2-1.5m tall, with half the leaves occurring 43-84cm above ground. There were three canopy layers, and vine-like species climbing among the three canopy layers.

Stem densities were greatest where mean mid-summer water levels ranged between +10cm and -10cm depth. Plot biomass and species richness peaked at greatest standing water levels due to the encroachment of marsh species. Anthropogenic disturbance altered these patterns. The vegetation exhibited identifiable lower and upper wet meadow sub-types. Thin peat and litter mats, short hummocks, and small-stature species occurred more often in upper wet meadows, whereas thick peat and litter mats, tall hummocks, and physically larger wet meadow emergent species occurred more often in lower wet meadows.

Fluctuating surface- and groundwater levels had the greatest impact of any abiotic factor on the vegetation. Hydroperiod directly impacted vegetation composition, and strongly influenced the pattern of occurrence of other abiotic factors.

Mean peak wet meadow standing crop was $669g/m^2$. Growing-season litter production was $152g/m^2$, and in-place litter decomposition was $186g/m^2$. Net above-ground primary productivity was $1007g/m^2/yr$.

There were few significant differences in the vegetation of either reference and disturbed, or Loosestrife and Loosestrife-free sites. The vegetation resisted anthropogenic disturbance impacts and Purple Loosestrife introduction, and exhibited resilience once disturbance ended. Soil disturbances (dredging, filling, excavation, and cultivation) were the most disruptive disturbance types. Wet meadow vegetation exhibited greater resilience following soil disturbance when hydrology was not disturbed.

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TABLE OF CONTENTS

CHAPTER 5
THE IMPACT OF ANTHROPOGENIC DISTURBANCE AND PURPLE LOOSESTRIFE ON SAGINAW BAY COASTAL WET MEADOW VEGETATION

APPENDICES

LIST OF TABLES

LIST OF FIGURES

Chapter 1 - General Introduction

The wetlands fringing Saginaw Bay are the largest remaining tract of freshwater coastal wetlands in the 48 contiguous United States (US Geological Survey, 1996). Wet meadows, the grass- or sedge-dominated herbaceous wetlands found between emergent marsh and upland margin, are an important part of this coastal wetland complex. Little is known about the ecology of these coastal wet meadows, because previous studies of the region's wetlands have focused on emergent marshes. There are two reasons for this. Historically, there has been more interest in marshes because they produce commercially-valuable fish, waterfowl, and fur-bearing animals. Also, agricultural conversion turned easily drained, "unproductive" wet meadows into very fertile and profitable farm acreage. Most Saginaw Bay coastal wet meadows were converted to agricultural uses in the late 19th and early 20th centuries (Albert et al., 1988).

Saginaw Bay coastal wet meadows perform various ecological functions. Yet, we lack a clear picture of their role in the overall ecological functioning of these freshwater coastal wetlands. Detailed studies of coastal wet meadow ecology are needed to increase our understanding of the functions performed by these wetlands.

Saginaw Bay coastal wet meadows shelter a number of threatened and endangered plant species (Albert et al., 1988; Nature Conservancy, 1994) Preserving and protecting threatened and endangered species requires a thorough understanding of the habitat in which they live. Yet, no comprehensive study of the plant ecology of Great Lakes coastal wet meadow habitat has ever been undertaken.

Previously drained Saginaw Bay coastal wet meadows present prime opportunities for successful wetland restoration. A key factor in successful wetland restoration is a clear understanding of pre-disturbance site characteristics (Prince and Burton, 1995). However, very little base-line data has been collected for any Great Lakes coastal wet meadow. This study was undertaken to help fill these gaps in our knowledge of this important wetland type.

Wet meadows defined

Curtis (1959), describing Wisconsin sedge meadows, provided a concise general definition of wet meadow vegetation. He described it as an open community growing on wet soils, with greater than half the vegetation dominance contributed by sedges. These communities occupy a very low position in the soil catena, with the permanent water table lying just below the ground surface. Curtis indicated that sedge meadows graded into cattail or reed marshes as conditions become too wet for the meadow species. Water was always plentiful and never limiting, but excess water often resulted in stressful conditions for the plants living there. Curtis pointed out that sedge meadows and wet prairies are very similar wet soil community types, with wet prairies being dominated by grasses rather than sedges (Curtis, 1959).

Keddy and Reznicek (1986) described Great Lakes coastal wet meadows as being the grass- and sedge-dominated vegetation found in Great Lakes wetlands between the yearly mean and yearly maximum Great Lakes high water levels. They placed wet meadows just above the marsh on the wetland elevation continuum. Keddy and Reznicek noted that this continuum often extended up-slope and inland to include shrub- or forest-dominated wetlands located between the wet meadow zone and the upland boundary. They concluded that the lower limit of successful shrub or tree invasion of coastal wet meadows was determined by maximum annual Great Lakes high water levels, and that the lower limit of successful wet meadow establishment was determined by mean annual Great Lakes high water levels. They believed that the size and species composition of any particular coastal wet meadow depended on the impact of abiotic factors such as shoreline slope, substrate composition, wave exposure, water chemistry, and fire frequency (Keddy and Reznicek, 1986).

Curtis also indicated that fire was important to wet meadow maintenance. He observed that shrub-carr or Alder thickets commonly replaced wet meadow vegetation within 10-20 years after fire suppression began, except in only the wettest wet meadows. A study of Wisconsin sedge meadows described fire as a natural environmental element in wet meadows that suppressed shrub and tree encroachment (Frolik, 1941).

Great Lakes wetlands occur in a many geomorphic settings (Minc and Albert, 1998; Chow-Fraser and Albert, 1998; Keough et al., 1999). The Michigan Natural Features Inventory developed a hierarchical system which defined the various geomorphic settings found along Michigan's Great Lakes coastline (Minc and Albert, 1998). MNFI determined that Saginaw Bay wetlands were open coast wetlands (*sensu* Keough et al., 1999) consisting of open embayments, sand-spit and protected embayments, and one tributary embayment. Open embayments are fully exposed to wave energy, lateral currents, and ice scour, and so often develop only a narrow fringe of wetland. However, the broad, shallow, gently sloping Saginaw Bay lake bottom attenuates these energies, making the extensive, fine-textured Saginaw Bay clay lake-plains an ideal setting for emergent marsh and wet meadow development (Ibid., 1998). Sand-spit embayments, protected embayments, and tributary embayments are sheltered from most wave and current energy. These lower-energy environments permit organic sediment accumulation (Tilton et al., 1978) and extensive wetland development.

The vegetation association found in wet meadows has been variously labeled wet meadows (Rumberg and Sawyer, 1985; Kelley et al., 1985; Keddy and Reznicek, 1986; Kantrud et al., 1989; Keddy, 1990), sedge meadows (Curtis, 1959; Auclair et al., 1973; Wilcox et al., 1985), fresh meadows (Shaw and Fredine, 1956), fen meadows (Jaworski and Raphael, 1979), tussock meadow (Costello, 1936), wet prairie (Curtis, 1959; Hayes, 1964; Gunderson, 1994), wet grassland (Fliervoet and Werger, 1984; Vermeer, 1986), water meadows (Sjoberg and Danell, 1983), marsh meadow (Stout, 1914; Jeglum et al., 1974), and graminoid fen (Jeglum et al., 1974). The different terms arose from regional preferences (e.g., wet grassland is a European term) and from slight variations in the biotic and abiotic conditions found within this vegetation type. Variations among types generally involved differences in the identity of dominant species (e.g., sedges versus grasses), or minor differences in hydroperiod, substrate composition, water chemistry, or landscape position.

Important attributes of the wet meadow vegetation association are:

- Wet meadows are grass- or sedge-dominated herbaceous wetlands.
- They occur in low landscape positions, or as fringing wetlands at the margin of rivers, streams and lakes. When fringing wetlands, they occur on the landscape

between emergent shallow marshes and either shrub or forested wetlands, or the upland boundary.

- The soils are commonly saturated to within a few centimeters of the ground surface, but they are not normally inundated for long periods during the growing season.
- Plants must be adapted to occasional flooding, but generally need not tolerate long periods of inundation during the growing season.
- Fire and/or a sufficient duration of soil saturation are required to suppress woody plant invasion.
- Wet meadows accumulate peat.

These attributes describe the coastal wetland plant community located adjacent to Saginaw Bay between the cattail or bulrush marsh and the upland shrub or tree line. This wet meadow vegetation association was the subject of the study.

Purpose of the study

This study had three main goals. The first goal was to determine the above-ground vegetation structure, composition, and productivity of Saginaw Bay coastal wet meadows. The current literature lacks such information. Once developed, this information could be used to compare Saginaw Bay coastal wet meadows to other ecosystems, and as baseline data for future Great Lakes coastal wet meadow restoration efforts.

The second goal was to determine how hydrology influenced the above-ground vegetation structure, composition, and productivity of Saginaw Bay coastal wet meadows.

Such information is key to understanding the plant ecology of coastal wet meadows, and to the proper design, implementation, and completion of successful Great Lakes coastal wet meadow restoration projects.

The third goal was to determine how above-ground vegetation structure, composition, and productivity differed between human-impacted and relatively undisturbed reference wet meadows. Cultivation, diking, and ditching are the most common and most damaging human impacts in these wetlands. Such disturbances degrade native flora and facilitate establishment of invasive exotic and native non-wetland plants. Differences between disturbed and reference wet meadow vegetation should provide important clues about how biotic and abiotic factors impact the plant ecology of these wetlands. The distribution of native and exotic plants within disturbed coastal wet meadows may provide insights into the re-vegetation trajectories to be expected in future coastal wet meadow restorations.

Study Region

The study took place in the coastal zone of Saginaw Bay, the southwestern lobe of Lake Huron, one of the five Laurentian Great Lakes of north-central North America (Figure 1-1). Formed by Pleistocene glaciation, the Saginaw Bay basin has been reshaped many times by glacial advances and retreats (Dorr and Eschman, 1970). Since the most recent glaciation ended approximately 12000 BP, post-glacial isostatic rebound and changes in Great Lakes water levels have further altered shore line location and elevation

(Ibid., 1970). Saginaw Bay has maintained its current shoreline configuration for about the last 2500 years (Ibid., 1970).

The Saginaw Bay watershed, contained entirely within the state of Michigan, drains 22533km^2, an amount equaling 15% of Michigan's land area (SBNWI, 1998). Saginaw Bay itself covers 2960km^2, and has a shore line length of 622km^2 (Ibid., 1998). Saginaw Bay is a shallow embayment with a gently sloping bottom formed by the inter-layering of glacial till, glacial outwash, and lacustrine silts and clays deposited since glaciation ended. The average depth of the inner bay is 4.6m. The outer bay averages 14.6m deep. This favorable combination of basin morphology, substrate composition, and hydrologic regime enhances wetland development in the Saginaw Bay coastal zone (Jaworski et al., 1979; Geis, 1985).

Historically, wet meadow vegetation extended up to 5km inland along the eastern Saginaw Bay shore line (Davis, 1900; Jaworski and Raphael, 1978; Albert et al., 1988). Agricultural development has limited the present wet meadow zone to a narrow strip along the coast. Saginaw Bay coastal wetlands may have covered more than 28350ha prior to European settlement (Prince and Burton, 1995). Current estimates of extant Saginaw Bay coastal wetland range between 6075-7300ha (USGS, 1996; SBNWI, 1998).

Land use history

Prior to Europeans settlement, the region was home to various American Indian tribes. About 4000 BP, the "Old Copper" people inhabited sites near what is now Bay City (Weesies, 1980). The "Hopewell" Indians occupied the region from about 500 BC to

700 AD, leaving burial mounds as evidence of their presence (Ibid., 1980). The Sauk, the tribe from which the name for Saginaw Bay is derived, occupied the region until the 18th century, when they were displaced by the Fox, Potawatomi, Ojibway, and Chippewa Indian tribes (Clifton, 1997). These tribes were primarily hunter-gatherers who practiced limited row crop cultivation to supplement their diet (Mettert, 1986; Clifton, 1997). However, by culture and custom the American Indian trod lightly on the land, so human impacts were minimal prior to European settlement (Dodge, 1920).

European settlement began in the 1830s, with early economic activity centered around lumbering the forest-rich land. Agricultural activity increased in the 1850s on the recently cleared landscape, but tree stumps and wet, swampy land were impediments to farming (Linsemier, 1980). Major forest fires occurred along Saginaw Bay's eastern shore in 1871 and 1881, and several times between 1900 and 1920 along the western shore, destroying the remaining forests, and clearing additional land for agricultural production (Dodge, 1920; Mettert, 1986).

Efforts to drain coastal wetlands were well under way at the end of the 19th century (Davis, 1908; Prince and Burton, 1995). By 1917, agricultural drains totaling 1016km had been constructed in the counties bordering southern Saginaw Bay (Miller and Simmons, 1919). Nearly 70% of the inland wetlands of these counties have since been converted to cropland, and less than 1% of the region's original wet meadows still exist today (Prince and Burton, 1995).

The 22-county Saginaw Bay watershed is home to 1.4 million people (SBNWI, 1998). Watershed land use patterns remain mostly rural, and can be divided into agricultural use (46%), forested land (29%), open land (11%), urban land (8%), wetlands

(4%), and open water (2%). The major agricultural crops are sugar beets, dry beans, potatoes, corn, wheat, and barley (SBNWI, 1998). Sport fishing, pleasure boating, swimming, and bird watching make important contributions to the local economy. The population of the region is expected to increase, placing additional strains on the natural resources of the Saginaw Bay watershed.

Climate

Saginaw Bay is located in the northern temperate zone, but regional climate is not typical for its position on the North American continent. Michigan's climate has been described as "semi-marine" (Eichenlaub et al., 1990) due to the influence of the nearby Great Lakes. The Great Lakes moderate climatic extremes, yielding cooler, wetter summers and warmer, snowier winters than would normally be found in a mid-continent climatic zone (Keen, 1993).

The regional mean annual temperature is 8°C, ranging between -32°C and +38°C. Mean annual precipitation is 737mm, with approximately 60% of the annual total falling between April and September (Michigan Department of Agriculture, 1989). Mean annual snowfall is 1054mm (Ibid., 1989). Evaporation exceeds mean May-October precipitation by 32%, highlighting the importance of fall and winter precipitation in annual soil moisture replenishment (Ibid., 1989). The growing season ranges from 126 days at Standish to 168 days at Bay City (Appendix A1).

Michigan is located in the ecological transition zone linking North American boreal coniferous and temperate deciduous forests. This so-called "tension zone" passes across

Michigan's lower peninsula from Muskegon to Saginaw. It also divides Michigan's Thumb region on a line commencing just south of Sand Point on Saginaw Bay's eastern shore and proceeding south to Caro, and then southeast from there to Lexington on Lake Huron's western shore (Dodge, 1995). The existence of the tension zone has been attributed to climatic factors (Potzger, 1948) and plant range limitations (Kapp, 1978; McCann, 1979). However, the changes in vegetation composition associated with Michigan's tension zone are more strongly correlated with soil factors than with climate, and edaphic factors probably account for the observed vegetation changes (Livingston, 1903, 1905; Elliott, 1953; Veach, 1953; Medley and Harmon, 1987). The mixture of biomes occurring within the state contributes to the diversity of Michigan's flora, estimated at over 2500 vascular species (Voss, 1996).

Soils

Regional soils were derived from shale, limestone and dolomitic bedrock located in Michigan's northern lower peninsula (Dorr and Eschman, 1970). The parent rock was crushed and transported south by Pleistocene glaciation to be deposited as glacial till, glacial outwash, or lacustrine sediments, or by wind as alluvium (Dorr and Eschman, 1970; Mettert, 1986).

Pedogenesis is well advanced in the region. Organic matter has accumulated in the soil since the most recent glaciation event and the soils for the most part exhibit well developed horizons (Mettert, 1986). The state of soil development provides few, if any, limitations to plant growth.

The soils bordering Saginaw Bay are mostly poorly to very poorly drained sandy and loamy soils in the south and clay and clay loam soils in the north (Linsemier, 1980; Mettert, 1986). These loamy and clayey soils tend to be calcareous, and when properly drained can be highly productive agricultural land (Mettert, 1986). Excessively drained sandy soils, deposited by earlier, higher glacial lake stages, are often found on coastal beach ridges and along the northeastern shore of Saginaw Bay. These beach ridges, sometimes called "islands" (Davis, 1908; Dodge, 1920), are often used as sites for residences and other purposes (Mettert, 1986).

Mucks and aquents are common in the low-lying, frequently inundated coastal areas. Despite high organic matter content, these soils are generally unsuitable for most human uses because proximity to Saginaw Bay make drainage difficult and expensive (Mettert, 1986).

The USDA-NRCS has only begun describing and mapping wetland soils in the last 25 years (Tilton et al., 1978). Recent soil surveys for St. Clair and Monroe counties (Michigan) included soil profiles for wetlands bordering Lake St. Clair and Lake Erie (see Tilton et al., 1978). These profiles provide clues at to the probable stratigraphy of Saginaw Bay wetland soils. However, no wetland soil profile descriptions are available for the soils bordering Saginaw Bay.

Study sites

Using maps and aerial photographs, 31 potential coastal wet meadow study sites were identified on the Saginaw Bay coast between Port Austin, MI and Au Gres, MI

(Figure 1-2). Aerial photographs were used to identify and eliminate forested or cultivated sites, and coast line occupied by artificial structures. Visits to remaining sites pinpointed the location of coastal wet meadows. Six sites were unsuitable for this study, being either too small or having wet meadow vegetation that was being rapidly displaced by cattail marsh. In the end, 25 coastal wet meadows were included in the study (Appendix A2).

Sites 1 and 2 were used in the study of coastal wet meadow hydrology. Detailed hydrologic and vegetation data were collected at these two sites. Vegetation surveys were performed at the remaining 23 wet meadow sites, and soil samples were collected at all 25 wet meadow sites.

Previous research

General information concerning the botany and ecology of Great Lakes coastal wet meadow vegetation can be found in studies of wetlands bordering Lake Michigan (Ward, 1896; Harris et al., 1981; Kelley et al., 1985; Wilcox et al., 1985), the St. Marys River (Duffy et al., 1987), Lake St. Clair (Pieters, 1894; Reighard, 1894; Hayes, 1964; Herdendorf et al., 1986), the Detroit River (Campbell, 1896; Manny et al., 1988), Lake Erie (Pieters, 1901; Herdendorf, 1987; Sherman et al., 1996), and the St. Lawrence River (Auclair et al., 1973). Keddy and others (Keddy, 1983; Wilson and Keddy, 1986a, 1986b; Shipley et al., 1991; Weiher and Keddy, 1995; Twolan-Strutt and Keddy, 1996, as examples) have experimentally studied the influence of environmental gradients on plant competition, including plants of Great Lakes coastal wet meadows. Regional wetland surveys (Tilton et al., 1978; Jaworski and Rapahel, 1979; Herdendorf et al., 1981) provide data about Great Lakes coastal wetlands, and the Michigan Natural Features Inventory compiled reports on Michigan's coastal wetland systems (Albert et al., 1988, 1989; Comer, et al., 1993; Minc, 1996; Minc, 1997a, 1997b). Nonetheless, the extent of botanical research conducted in Great Lakes coastal wetlands was recently characterized as "cursory" (Klarer and Millie, 1992).

The Saginaw Bay coastal wetland flora has been fairly well described (Davis, 1900, 1908; Michigan Geological and Biological Survey, 1911; Dodge, 1920; Herdendorf et al., 1981; Albert et al., 1988, 1989; Prince and Burton, 1995). Early vegetation surveys established an historical record of the coastal wetland flora of Huron County (Davis, 1900), Tuscola County (Davis, 1908), and Bay and Arenac counties, MI (Dodge, 1920). Perhaps most remarkable was the 1908 biological survey of the eastern shore of Saginaw Bay performed under the direction of Alexander Ruthven (Michigan Geological and Biological Survey, 1911). Ruthven selected this region to study because "the area is almost wholly uncultivated and in a primitive condition, and would consequently be expected to harbor the primitive fauna and flora" (Michigan Geological and Biological Survey, 1911, p. 13). From a base camp at Sand Point, Ruthven and a team of seven biologists produced detailed descriptions of the identity, ecology, and distribution of the region's plants, mammals, birds, amphibians and reptiles, insects, and fish. C.H. Coons' descriptions of "sedge and grass swamps" and "reed swamp formation - Phragmites association" provide valuable insights into the structure, species composition and ecology of the region's pristine coastal wet meadows (Coons, 1911). C. K. Dodge documented 886 terrestrial and wetland plant species that summer, many of which can still be found in the region today. Most remarkably, Ruthven photographed several coastal wetlands, leaving a visual record of how they appeared in 1908. These sites still look very much as they did 90 years ago.

Recent work by the Michigan Natural Features Inventory supports these earlier observations (Comer, et al., 1995; Comer, 1996). More recent vegetation surveys describe the current species composition (Herdendorf et al., 1981; Albert et al., 1988, 1989; Prince and Burton, 1995), location, and extent (Jaworski and Raphael, 1979; Herdendorf et al., 1981; Albert et al., 1988, 1989; Comer, 1996) of Saginaw Bay coastal wetland vegetation. However, ecological descriptions of the vegetation are less common, and a detailed examination of the factors controlling the structure, productivity, and species composition of Saginaw Bay coastal wet meadow vegetation has never been completed.

Organization of the study

This study will be described in five chapters. Chapter 1 (this chapter) provides a general introduction to the study. Chapter 2 will discuss the hydrologic factors acting on Saginaw Bay coastal wet meadow vegetation. Chapter 3 will discuss the vegetation structure, plant species composition, and plant species relationships of Saginaw Bay coastal wet meadows. Chapter 4 will discuss the above-ground biomass and productivity of Saginaw Bay coastal wet meadow vegetation. Chapter 5 will discuss the impact of disturbance on the coastal wet meadow vegetation association.

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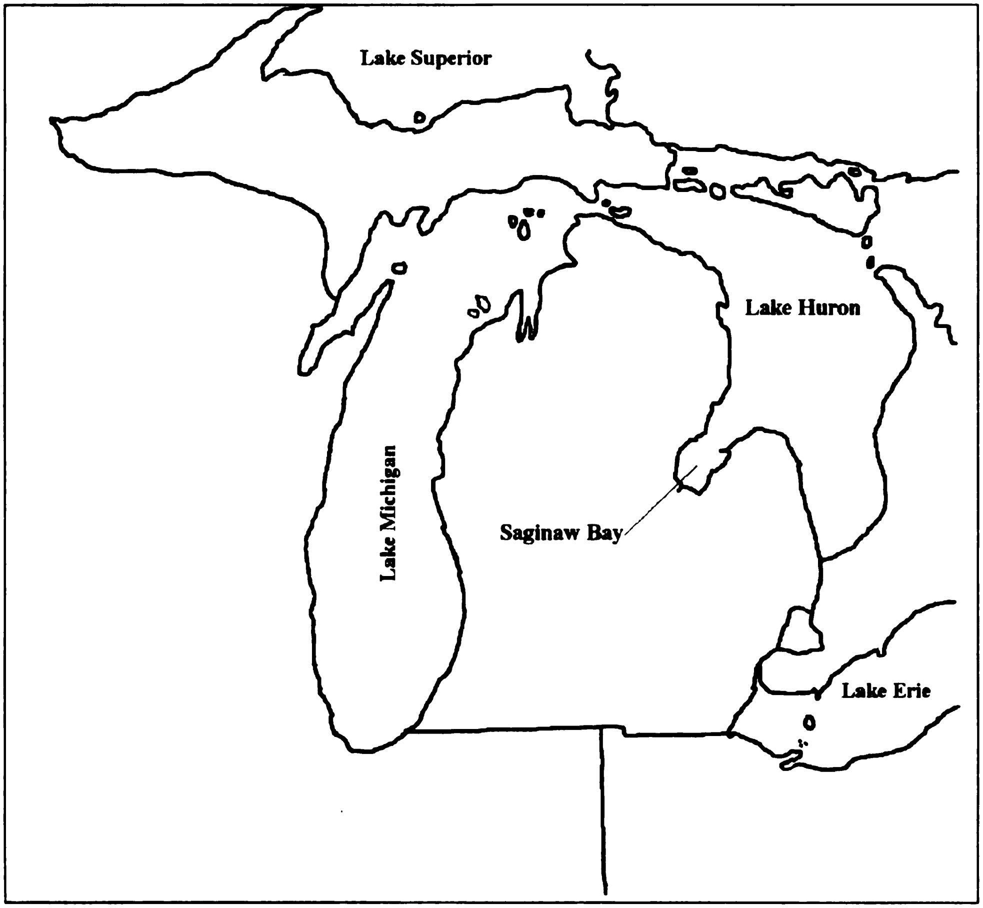

Figure 1-1. Western Great Lakes region, with Saginaw Bay indicated.

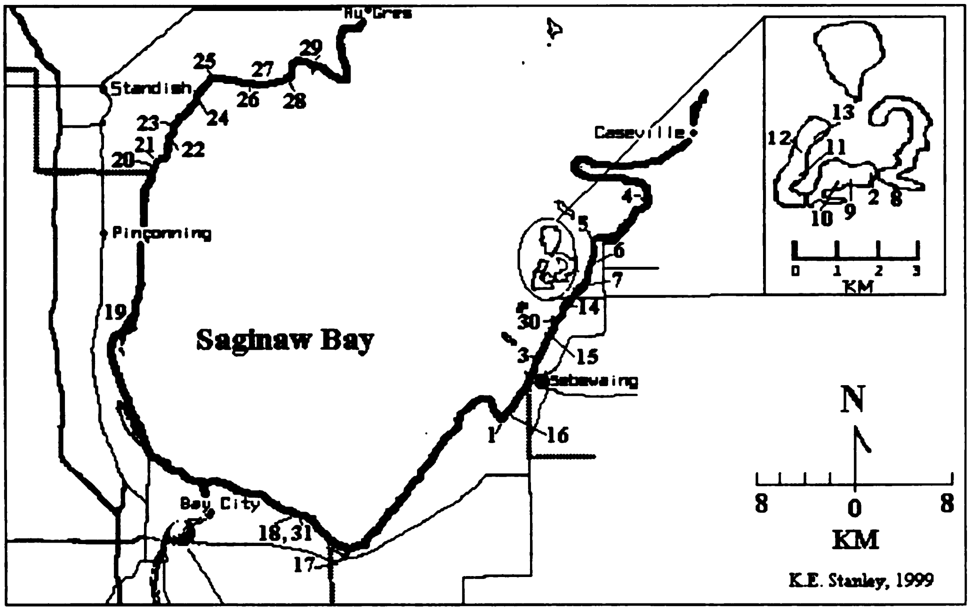

Figure 1-2. The location of coastal wet meadows in the Saginaw Bay coastal zone. Of 31 known wet meadow sites, Sites 7, 12, 16, 17, 23, and 29 were not included in the study. There were no coastal wet meadows between Caseville and Port Austin on Saginaw Bay's eastern shore. Map data from US Census Bureau TIGER database and Michigan Department of Natural Resources.

Chapter 2 - The hydrology of Saginaw Bay coastal wet meadows: Natural systems and disturbance impacts

Introduction

Hydrology is the driving force behind the development and maintenance of wetland ecosystems (Mitsch and Gosselink, 1993; National Academy of Sciences, 1995). Hydroperiod, the temporal pattern of water level fluctuation in a lake, stream, or wetland, is key to determining the structure, function, and species composition of wetland vegetation (Mitsch and Gosselink, 1993). Any examination of wetland vegetation must be rooted in an understanding of how hydrology influences the landscape on which the plant community is assembled.

Early investigators noted the link between water depth and vegetation zonation in Great Lakes coastal wetlands (Pieters, 1894; Pieters, 1901; Michigan Geological and Biological Survey, 1911). Others have reported that fluctuating water levels enhance wetland plant diversity in Great Lakes coastal wetlands (Stuckey, 1975; Burton, 1985, Keddy and Reznicek, 1986; Klarer and Millie, 1992; Wilcox, 1995). Water level fluctuations of variable frequency and amplitude are known to produce greater plant diversity than do regular hydroperiods (Wilcox and Meeker, 1991). Characteristics of water level fluctuation include magnitude, duration, timing, and frequency of occurrence (Wilcox, 1995) and variation in these characteristics can result in the development of different wetland types (Keddy, 1983; Keddy and Reznicek, 1986; Keddy, 1989; Wilcox, 1995). Understanding the fluctuations of Saginaw Bay, a portion of Lake Huron, is a key to understanding the vegetation structure and distribution of its coastal wet meadows.

Great Lakes hydroperiods can be divided into three distinct groupings: multiple-year, seasonal (within-year), and fluctuations that occur on the order of hours or days, such as seiches and storm surges (Keough, 1990). The most apparent of the multiple-year events are the 7-11 year cycles described by various investigators (Cohn and Robinson, 1976; Burton, 1985; Kelley et al., 1985, among others), though opinions differ as to the length, or even the existence, of these cycles (Keough, 1990). Between 1994 and 1997, the Great Lakes were in the increasing phase of their most recent 11-year hydroperiod (Figure 2-1), peaking in July 1997 at approximately 20cm below the highest Lake Huron levels recorded since 1918 (USACOE, 1998).

Within-year cycles are annual lake-level fluctuations driven by spring rains and snow melt (Figure 2-2). Annual Great Lakes water-level fluctuations exhibit a certain periodicity; they are generally at their lowest in the winter and their highest in the summer. By contrast, the amplitude of year-to-year and within-year water-level fluctuations are more variable, and much less predictable.

Seiches are regular, recurrent water surface oscillations, or "free standing waves" (Mortimer and Fee, 1976), most commonly caused by winds or changes in barometric pressure (Herdendorf, 1987; Keough, 1990; Bedford, 1992; Keough et al., 1999). Seiches occur in all the Great Lakes, typically exhibiting a 2-14hr frequency and 20-30cm amplitude (Sager et al., 1985; Herdendorf, 1987; Keough, 1990; Batterson et al., 1991). Several seiche modes can operate independently and simultaneously in a lake; at least five modes have been identified for Lake Huron (Mortimer and Fee, 1976). Different seiche modes reinforce or cancel each other out, yielding a complex pattern of surface water oscillation. A lake's seiche frequency is determined by its basin geomorphology and so is predictable, whereas seiche amplitude is determined by meteorological conditions, and is therefore less predictable (Keough, 1990; Bedford, 1992).

Storm surges, the major driver of lake seiches, are unpredictable water level fluctuations associated with the passage of storm fronts (Keen, 1993). When a storm surge occurs, winds push water to one end of a lake, increasing lake levels on the downwind side of the lake. When the winds decrease, the water "sloshes" back across the lake surface, reinforcing seiche amplitude (Ibid., 1993). Storm surges of 0.5-3m occur in the Great Lakes, and the residual effects of large storm surges can last for days (Herdendorf, 1987; Keen, 1993).

Solar and lunar tides occur in the Great Lakes, but have negligible impact on Great Lakes water levels (Verber, 1960; Platzman, 1966; Mortimer and Fee, 1976). Theoretical studies suggest that tides up to 1.2cm occur in Lake Huron (Hamblin, 1976). In any case, the maximum observed Great Lakes tidal fluctuations, measured in Lake Erie, were only 3.3cm (Herdendorf, 1987).

The impact of Great Lakes surface water fluctuations on coastal vegetation has been described for Lake Michigan (Harris et al., 1981; Burton, 1985; Kelley et al., 1985; Keough, 1990), Lake Erie (Keddy and Reznicek, 1986), and Lake Huron coastal wetlands (Batterson et al., 1991). While focused on coastal marsh vegetation, these studies have provided some indication of how lake hydroperiods impact coastal wet meadow vegetation.

Less is known about how other hydrologic factors, such as groundwater, precipitation, and evapotranspiration, influence coastal wet meadow vegetation. Groundwater and precipitation inputs, and evapotranspiration losses, are probably of minor importance in the hydrologic budget of inundated coastal marshes. However, Great Lakes surface water levels may not always dominate coastal wet meadow hydrology. Great Lakes coastal wet meadows occur above the lake surface elevation (Keddy and Reznicek, 1986), so groundwater, precipitation, and evapotranspiration may play a significant role in coastal wet meadow hydrology.

Evidence collected from similar Great Lakes coastal wetlands supports this argument. Hydrologic studies of non-contiguous bogs, fens, and inter-dunal marshes and swales bordering Lake Michigan in Indiana (Wilcox et al., 1986; Doss, 1993; Shedlock et al., 1993; Souch et al., 1998), and dune ponds and wet pannes bordering Lake Michigan in Michigan (Barko et al., 1977; Hiebert et al., 1986) have illustrated the importance of groundwater, precipitation, and evapotranspiration in these coastal systems. However, conclusive studies of contiguous coastal wet meadow hydrology are lacking in the literature.

Objectives

The goal of this chapter was to describe the hydrology of Saginaw Bay coastal wet meadows. The specific objectives were:

1. to describe the groundwater, surface water, precipitation, and evapotranspiration hydrology of selected sites;
2. to describe how the soil moisture content of non-saturated wet meadows varies through the growing season, and;
3. to describe how groundwater, surface water, precipitation,

evapotranspiration, and soil moisture content act and interact to shape the hydrologic regime of Saginaw Bay coastal wet meadows.

Sites

Two sites were utilized in the study, one reference site, and a site which had undergone extensive anthropogenic (human-induced) hydrologic and vegetation disturbance. There are no truly undisturbed coastal wet meadows in the Saginaw Bay coastal zone, so the reference site was selected not because it was pristine or even undisturbed, but rather because it was representative of "natural or quasi-natural wetlands that either occur presently in the region or occurred there at one time" (Brinson, 1993, p.61).

Various methods have been used to disrupt the natural hydrology of Saginaw Bay coastal wet meadows. Dikes or levees were often constructed to prevent flooding of low-lying land, and then ditches, drains, tiles, or mechanical pumping were utilized to de-saturate the newly protected land. Ditches or tiles installed on the land-ward side of dikes collected water and conducted it away from the site, or to holding ponds near the dike. Natural drainage features, such as swales, were sometimes modified to enhance site drainage efficiency. The ditches and tiles discharged into agricultural drains, which conducted water to Saginaw Bay. Where the land surface was at or below the level of Saginaw Bay, pumps were used to lift water from ditches to drains over the dikes. Recovered land was commonly placed into agricultural production.

The reference site was located approximately 20m west of a boat channel bisecting Middle Ground Island, one of a small group of islands comprising the Wildfowl Bay State

Game Area. Wildfowl Bay SGA is located about 12km north of Sebewaing, MI and 2km off the coast in eastern Saginaw Bay (Figure 2-3, Site #2). Middle Ground Island is a low barrier island consisting of highly permeable sand deposits beneath loamy sand and organic surface soils. The reference site sloped from south to north, with its maximum elevation occurring on the south shore of the island, where it was approximately 50cm higher than Saginaw Bay. This low relief meant that the entire site was subject to inundation during storms and in high water years. The island was approximately 180m wide at the site.

The reference site was not pristine. Temporary hunting and fishing camps are occasionally established on Middle Ground Island, but none were established within 1km of the site during the study, and no permanent residences have ever been built there (T.J. Jahr, Jr, pers. comm.). Cattle were grazed on the island during the 1930's, but this land use pattern was discontinued by 1940 (T.J. Jahr, Jr, pers. comm.). No cultivation was reported by long-time local residents.

An aerial photo chronosequence of the site indicated that the boat channel was excavated prior to 1938, and that it was a stable feature on the landscape. The presence of the boat channel rendered the site a peninsula with a well-defined east-west oriented south shoreline and north-south oriented east shorelines. These fixed and stable shorelines provided a unique opportunity to study the hydrology of this wet meadow.

Despite these impacts, the Middle Ground Island site was suitable as a reference site because site hydrology was minimally-disturbed compared to most Saginaw Bay coastal wet meadows. The available evidence indicated that vegetation at the site was representative of the current state of Saginaw Bay wet meadows (Albert et al., 1988, 1989; and see Chapter 3), and in many respects reflected the pre-settlement vegetation of the region (Michigan Geological and Biological Survey,1911; Comer, 1996).

The disturbed site, located about 19km southwest of the reference site on Saginaw Bay's eastern shore (Figure 2-3, Site #1), had undergone extensive hydrologic and vegetation alteration. It bordered Saginaw Bay in an area in which coastal wetlands historically extended up to three miles inland (Davis, 1900; Jaworski and Raphael, 1979; Albert et al., 1988). An agricultural drain, diked on either side, had been constructed along the northern site boundary between 1940-1949. Immediately north of this drain and dike system was the cattail marsh. The dike on the south side of the drain, 3m tall and 3m wide at the base, prevented site inundation by Saginaw Bay. The drain carried excess surface water from nearby fields to Saginaw Bay. The site, whose soils consisted of approximately 45cm loamy sand over glacial till, had either been cultivated or used as a pasture for 80-100 years prior to its abandonment in the late-1980's (K. Wildner, pers. comm.). Drained and cultivated farm fields bordered the disturbed site on the east and west. Although drainage tiles were never installed at the site (D. Schafer, pers. comm.), a ditch had been constructed, and a natural swale had been modified, on the site between 1949-1955 to improve site drainage. The water level in these structures, isolated from Saginaw Bay behind the dike, was regulated until 1989 by pumping water from the on-site ditch over the dike into the drain (K. Streeter, pers. comm.).

The growing season in southern Saginaw Bay averages 168 days, generally running from early May to early October (Office of the Michigan State Climatologist, unpublished data). Regional mean annual precipitation (1961-1990) was 67.9cm. Monthly rainfall was greatest in late summer, with 16.7cm (24.6%) of the annual total occurring in August and September. Mean monthly totals ranged from 2.7cm in January to 9.0cm in September (see Appendix B1).

Methods

During 1996-1997, groundwater, surface water, precipitation, and pan evaporation data were collected at the two hydrologic study sites. Data for these four hydrologic variables were collected weekly from May through September. In other months, groundwater data only were collected approximately monthly. The soil moisture content of non-saturated wet meadow soils was determined at the two sites four times during the 1996 growing season.

Staff gauges were installed to monitor surface water levels (±0.1cm) at the sites. One was installed in Saginaw Bay at the reference site (Staff Gauge #3, Figure 2-4), and two staff gauges were installed at the disturbed site, one in the on-site drainage ditch (SG1, Figure 2-5), and the other in the drain on the north side of the dike, which discharged into Saginaw Bay (SG2). Data on the frequency and amplitude of Saginaw Bay seiches and storm surges were obtained from the National Oceanographic and Atmospheric Administration (NOAA, 2000).

Gardeners rain gauges were employed to measure precipitation. Accumulated rainfall was recorded and the rain gauges emptied each time groundwater data were collected. Readings were determined to the nearest 0.01in in the field, then converted to metric units for analysis.

Pan evaporation data were used to estimate actual wet meadow evapotranspiration

("ET"). Centimeter rulers were glued into 5.7L (33cm x 17cm x 12cm) translucent plastic containers. One of these open-top containers was placed in contact with the soil surface at each site after all vegetation within a 1m radius of each pan had been clipped at the substrate. Each container was filled to a pre-determined level with water, and evaporative water loss was measured (±0.1cm) at each subsequent visit, after which the containers were refilled to the pre-determined level. Vegetation was clipped as necessary to maintain the open space around the container. Evaporative losses for each time period were determined by subtraction, after correcting for precipitation inputs.

Potential evapotranspiration (PET) was estimated from measured pan evaporation using the formula

$$PET = C_e E_p \qquad \text{(Equation 2-1)}$$

where C_e is the pan coefficient and E_p is the measured pan evaporation, usually expressed in mm/day (Brooks et al., 1991). PET is generally lower than evaporation values obtained by pan estimation; pan coefficients correct for this difference.

Pan coefficients differ for Class A evaporation pans and small pans, such as those used in this study (Pruitt, 1960; Chang, 1968; Wang and Felton, 1983). Small pans exchange heat with the air more quickly than do Class A pans. Heat transfer between soil and pan can accelerate or retard evaporation rates of pans resting on the soil, depending on whether the soil is warmer or colder that the pan. Small pans can over- or underestimate evaporation, depending on air and soil temperature and soil moisture conditions (Chang, 1968). Chang also reported that black pans exhibited 23% greater evaporative loss that did white pans. The impact of pan size on evaporative loss varies with relative humidity as well (Mather, 1959). Pan size greatly influenced evaporation rates when relative humidity was low, but had little impact on evaporation rates when relative humidity was high (Ibid., 1959). However, the net influence of these factors on small pan evaporation rates may not be as great as previously thought.

A recent Texas study found little difference in Class A and small pan evaporation rates (Parker et al., 1999). Parker et al. compared evaporation rates from 33cm x 23cm x 12cm translucent plastic pans, elevated 15cm above the ground on white and brown plywood benches, to that of a Class A evaporation pan. They reported that differences in evaporative loss from the small pans ranged between -7% and +16% of the Class A pan rate, with the mean percentage small pan evaporation for five trials being 4% greater than the Class A pan (Ibid., 1999). They reported no consistent difference in evaporation rates for small pans on white versus brown backgrounds compared to the Class A pan.

Class A evaporation pan coefficients can be estimated given knowledge of the relative humidity, winds, and fetch of unimpeded airflow at a site (Allen and Pruitt, 1991). Given typical growing season mean daily relative humidity values (50%-80% near Saginaw Bay; Michigan Department of Agriculture, Climatology office, unpublished data), growing season wind speed (10-78km/day in southern Michigan; Michigan Department of Agriculture, Climatology office, unpublished data), and Saginaw Bay coastal wet meadows fetches (conservatively, 10m-100m; see Chapter 3), Class A pan coefficients can be expected to range between 0.66 and 0.85 for Saginaw Bay coastal wet meadows (Allen and Pruitt, 1991, Table 5). This estimate is consistent with Lafleur (1990a), who, using the Bowen energy budget approach, estimated Class A pan coefficients to be 0.83 for "wet" sedge-dominated James Bay wetland sites, and 0.61 for "dry" sedge-dominated James Bay wetland sites.

Given these estimates, and given that pan coefficients of 0.7 to 0.75 are commonly used where they have not been experimentally determined (Eichenlaub et al., 1991; Brooks et al., 1991), a pan coefficient of 0.7 was used in this study.

The relationship between PET and ET is complex, dependent upon the vegetation present, vegetation rooting depths, available soil water, and the soil water capacity of the site under study (Brooks et al., 1991). ET nearly equals PET in soils wetted to field capacity (Ibid., 1991), and wetland soils are usually saturated to greater than field capacity, so pan evaporation estimates of PET should provide good estimates of ET in the wet meadow study sites.

Groundwater monitoring wells were installed at each site. Each well consisted of a PVC well screen (1.5m long, 5.1cm diameter, with 0.0254mm mesh) placed in 10cm diameter by 90-100cm deep bore hole. A 10-30cm deep sand filter pack was placed around each screen, and then the bore holes were back-filled with native soil cuttings. Groundwater monitoring wells were installed at each site in a rectangular grid with the long axis perpendicular to the Saginaw Bay shoreline. Details of well field layout can be found in Appendix B2.

Groundwater depths were determined using a remote-probe sump pump overflow alarm (Sonin Floodwatch® Model 30200). The factory-installed probe tip and connecting-cable were removed and replaced with an incrementally-labeled cable. Groundwater levels were measured (±0.1cm) from the well lip to the groundwater surface inside each well. The groundwater depth beneath the ground surface was calculated later by subtracting the height of the well lip above the ground from the groundwater measurement determined in the field. Groundwater measurements were collected at approximately the same time of day at each site to minimize variability resulting from diurnal ET fluctuations. Diurnal variation in evapotranspiration rates are known to cause cyclical groundwater fluctuations in cypress swamps (Heimburg, 1984; Ewel and Smith, 1992), and daily groundwater fluctuations of up to 20cm have been observed in experimental agricultural plots near the disturbed hydrologic study site (H. Belcher, pers. comm.).

Once the well fields and staff gauges were in place, a laser level (Spectra-Physics Model 650 Laser Level projector and Model 1175 Laser Eye detector) was used to determine the ground elevation at each well, the elevation of each well lip, the elevation of the top of each staff gauge, and the substrate level at each staff gauge with respect to a benchmark installed at each site. No effort was made to tie site benchmarks to Datum. The elevation data facilitated the study of patterns of surface water and groundwater fluctuation at each site. These patterns helped identify the factors driving surface water and/or groundwater flux in coastal wet meadows.

The percent soil moisture content of non-saturated soils was determined in June, July, August, and September 1996. Soil cores (2.5cm diameter) were collected from the top 4cm of the solum within 15m of, and at approximately the same elevation as, each groundwater monitoring well at the two sites. Fifty-four samples were collected on each date; three samples were collected near each disturbed-site well, and one near each reference-site well. Sample collection was undertaken in the early morning hours near sunrise, before the dew evaporated from the vegetation, and at least 48h after any measurable rainfall had occurred at the sites. The soil samples were dried 72h at 80°C, and the soil moisture content was determined gravimetrically (see Appendix B3). Soil moisture content provided a measure of the range of soil moisture conditions to be expected in wet meadows during the growing season.

Results

The study sites sloped very gradually from upland to Saginaw Bay (0.25% at the reference site, 0.15% at the disturbed site). Local topographical variations existed within each site, but these were minor and, in the reference wet meadow, did not significantly alter the surface water and groundwater flow paths. The ditch and swale at the disturbed site did alter drainage patterns somewhat. These impacts will be discussed below.

Saginaw Bay water levels at the reference site increased by 10-15cm between June-July 1996, and then gradually declined 15cm by the end of October (Figure 2-6a). Between April-July 1997, water levels increased 40cm from early spring levels, and then remained within 10cm of this level throughout September. Water levels only began to decline in October 1997.

Surface water hydroperiod differed at the disturbed site (Figure 2-6b). Water levels in both the ditch and drain fluctuated in response to precipitation events and dry spells, but in both years gradually decreased throughout the growing season. However, at any given time, water levels in the on-site ditch were elevated 10-30cm above those in the drain. The dike prevented excess water from draining off the site to Saginaw Bay, so it accumulated in the on-site ditch. As a result, the surface water elevation in the on-site ditch was higher than that of Saginaw Bay.

Storm surges were occasionally observed flooding non-inundated portions of the reference site and several other Saginaw Bay coastal wet meadows. Storm surges sometimes inundated only a small portion of a wet meadow for an hour or two, and at other times inundated the entire wet meadow for a day or more. On 8/21/97-8/22/97, strong northwest winds pushed 30-50cm of water onto the eastern shore of Saginaw Bay. This storm surge completely inundated several wet meadows for 6-12h, and inundated low-lying sections of the Sebewaing County Park for 4-6h (K. Stanley, pers. obs.).

Data from Essexville, MI (NOAA, 2000) indicated that between 3/1/97-10/31/97, Saginaw Bay water levels equaled or exceeded the maximum elevation of the Saginaw Bay wet meadow zone (177.3m AMSL in 1997, see Chapter 3) for one or more hours on 42 different days (Table 2-1). Depending on shoreline geomorphology and orientation with respect to the prevailing winds, various wet meadows may have been inundated numerous times during the 1997 growing season.

The elevated south shore at the reference site protected it from storm surges generated by the prevailing southwest winds, but northwest, north, or northeast winds could push water up onto the site. Storm surge inundation of portions of the reference site was observed on two occasions, and the presence of water-stained vegetation, flotsam, and drift lines on monitoring wells and the staff gauge indicated that similar events occurred on several other occasions. The dike at the disturbed site prevented storm surge inundation at that site.

Growing-season rainfall generally followed the long-term annual pattern, with the August-September period being the wettest time of the year (Figure 2-7). However, significant positive and negative departures from the 30-year mean monthly precipitation were recorded at both sites. The most notable departure from normal occurred in June 1996, when precipitation at both sites exceeded 17cm, more than twice the normal 7cm monthly rainfall.

There were also notable differences between sites for the same rainfall event (Figure 2-8). More than 6cm rainfall were recorded at the reference site on 6/13/96, when no measurable precipitation was recorded at the disturbed site. On 6/25/96, the disturbed site recorded more than 6cm rainfall at a time when only 0.8cm rain fell at the reference site.

Estimated ET ranged between 0.5-3mm/day at the two sites, with most mean monthly values falling between 0.5-2mm/day (Figure 2-9). Estimated ET at the nearest Class A evaporation pan, located in East Lansing, MI, approximately 130km southwest of the sites and 110km from the nearest Great Lakes shoreline, ranged between 1.8-4.4mm/day (Michigan Office of Climatology, unpublished data). Mean daily ET at the sites fell within the range of values reported for Great Lakes coastal wetlands (Souch et al., 1998), bogs (Campbell and Williamson, 1997) and James Bay sedge wetlands (Lafleur, 1990a; see also Lafleur, 1990b for additional wetland values). For the most part, mean daily ET not differ significantly between the two sites. Mean daily ET was significantly greater at the reference site only in July 1996 (t-test, $t = 2.335$, $df = 23$, Bonferroni-adjusted $P = 0.029$) and September 1996 (t-test, $t = 2.639$, $df = 9$, Bonferroni-adjusted $P = 0.027$).

ET sometimes exceeded precipitation during the growing season (Figure 2-10). For example, precipitation at the reference site totaled 2.2cm in July 1996, and no rainfall was recorded in August 1996. The mean daily estimated ET was 1.5mm/day in July 1996 and 0.3mm/day in August 1996. For the July-August period, total estimated ET equaled 5.5cm; for precipitation it was 2.2cm. ET exceeded precipitation by 3.3cm during the period.

Wet meadow groundwater levels followed the same annual pattern at both sites. Groundwater was at or near the ground surface during the winter and in the early growing season, then rapidly declined in late spring to some sub-surface summer level. Groundwater levels remained low until late summer, then returned to near-surface elevations in the fall.

Figure 2-11 illustrates the seasonal groundwater pattern across the elevation gradient at the reference site. The three lowest elevation wells (#201, #202, and #203) were inundated throughout the 1996 growing season. Water levels in these wells mirrored Saginaw Bay water levels. The next highest well (#204) was located 30m away from, and at an elevation 16cm above, the nearest of the low elevation wells (#203). The land surface elevation at #204 was above the mean elevation of Saginaw Bay in 1996, and this greatly influenced the seasonal groundwater profile observed at that well. Groundwater levels at #204 declined to approximately 20cm below ground between late May and mid-June. Except for a brief rebound in late June, they remained approximately 20cm below ground until August, when additional groundwater decline occurred, to nearly 60cm below ground. Groundwater elevations remained at this depth until mid-September, when they rebounded to within a few centimeters of the ground surface. Similar seasonal groundwater profiles were observed in wells located at higher elevation within the wet meadow (#205 and #206), though the magnitude of the groundwater decline was greater at higher elevations.

Groundwater rebound was observed in the upper wet meadow wells (#204-206) in late June. This rebound corresponded to a period in which more than 6cm precipitation and a 20cm seiche were recorded. However, this groundwater rebound was a short-lived event. By mid-July 1996, groundwater had once again declined to levels comparable to those in evidence before the rainfall and seiche occurred.

Three dimensional projection of the land surface and groundwater elevation data offered a clearer illustration of how groundwater elevations changed across the reference wet meadow as the 1996 growing-season progressed. In the early growing season, the wetland surface was entirely saturated, with groundwater contours mirroring land surface contours throughout the site (Figure 2-12a). There was 10-15cm standing water on the lower wet meadow, and groundwater within 5cm of the ground surface in the upper wet meadow.

By late June, upper wet meadow groundwater levels were declining, and appeared to be equilibrating with surface water levels in Saginaw Bay, which were themselves in the increasing phase of their annual hydroperiod (Figure 2-12b). However, groundwater levels continued to decline to as much as 100cm below the ground surface, and 65cm below the level of Saginaw Bay, at some points in the wetland by mid-July (Figure 2-12c). The site groundwater profile remained essentially unchanged thereafter until early September (Figure 2-13a), when groundwater levels rebounded site-wide to within a few centimeters of the ground surface within seven days (Figure 2-13b). More than 6cm precipitation, and a 35cm storm surge, occurred during that seven day period.

Similar groundwater profiles were observed at the disturbed site, but there were some important differences between the sites. Both sites were saturated to the ground surface in mid-May 1996, and groundwater decline had commenced at both sites by early June (Figure 2-14). By July 1, the reference and disturbed site groundwater tables had reached mid-summer levels. Thereafter, gradual draw down continued in un-inundated portions of both sites through early September (Figure 2-15). Groundwater recharge occurred within a few days in mid-September at the reference site, but required several months at the disturbed site to be completed (Figure 2-16). Also, at the disturbed site, wells closest to the on-site ditch recharged more rapidly than did wells further from the ditch. By contrast, recharge occurred at about the same rate at all elevations at the reference site. A detailed description of annual SF groundwater variation can be found in Appendix B4.

There were also differences in the soil moisture regime of the two sites. The mean percent soil moisture established by early June in all parts of the reference site did not change significantly for the remainder of the growing season (Figure 2-17). Also, differences in elevation had no impact on soil moisture content at this site. By contrast, mean percent soil moisture continued to decline as the growing season progressed at most sampling locations within the disturbed site, and soil moisture content generally declined as elevation increased across this site (Figure 2-18).

Mean percent soil moisture ranged from 71.7% at the disturbed site to 40.3% at the reference site. A typical loam soil at field capacity contains approximately 25% by volume water (Foth, 1990), so the soil moisture content at these two sites never fell below field capacity during the growing season.

Wet meadow soil moisture conditions varied significantly among years. Surface soils partially dried out at both sites for at least a portion of 1996, but all were inundated or completely saturated throughout the 1997 growing season.

Discussion

Reference wet meadow

Saginaw Bay coastal wet meadows occur in a zone beginning at, and extending approximately 60cm in elevation above, the mean annual Saginaw Bay high water mark (Keddy and Reznicek, 1986; and see Chapter 3). Surface water levels determined where coastal wet meadows occur on the landscape, so the elevation at which they occur varied with changes in Saginaw Bay water levels. In most years, the elevation of the wet meadow was greater than Saginaw Bay water levels, and in those years, precipitation and storm surge inputs, and evapotranspiration discharges, controlled wet meadow groundwater levels. In certain years, when Saginaw Bay water levels were increasing, the bay was higher than the wet meadow zone. When this occurred, surface water flooded the wet meadow and dominated site hydrology. When flooding persists for more than a few weeks or months, marsh vegetation begins to displace wet meadow species (Jaworski et al., 1979; Burton, 1985; Keddy and Reznicek, 1986), and the wet meadow zone shifts to a higher elevation, until it is once again above the mean annual high water mark.

Storm surges occasionally deposited large volumes of water on the surface of the reference wet meadow. While much of this water eventually returned to the lake basin, some infiltrated the wetland surface, re-wetting the substrate. These inundation events, with precipitation, helped keep soil moisture levels above field capacity in parts of the wet meadow above the nominal elevation of Saginaw Bay.

Year-to-year Saginaw Bay water level variations greatly influenced reference site soil moisture content. High water levels inundated site substrates for most of 1997. This occurred just a year after soil moisture levels as low as 40% were recorded at the reference site. These inter-annual water level differences are crucial to wet meadow vegetation. High water drown invading shrubs and trees, whereas low water desiccate invading marsh plants, allowing perennial sedges and grasses to dominate the wet meadow zone (Keddy and Reznicek, 1986; and see Chapter 3).

Growing season precipitation, seiche and storm surge inundation, and evapotranspiration interacted to determine groundwater levels in non-inundated portions of the reference site. As vegetation growth accelerated in the late spring, increasing ET exceeded precipitation and storm surge inputs, drawing down wet meadow groundwater levels. Similarly, in the late summer, ET began to slow when precipitation was at its annual high. Storm surge inundation and precipitation offset declining ET, triggering groundwater recharge.

During the late spring and late summer periods, small changes in either inputs or outputs resulted in noticeable changes in groundwater levels. For example, groundwater decline had begun at the reference site by early June 1996 (Figure 2-19a), but no groundwater decline was evident at the site seven days later (Figure 2-19b). Similarly, groundwater was completely recharged in a nine day period in mid-September 1996 (see Figure 2-13). Rainfall of 6.4cm, and a 20cm seiche, occurred during the June week, whereas a 6.8cm rainfall and 35cm storm surge occurred during the mid-September period. The water from these sources rapidly infiltrated the wetland, exceeded ET discharges, and brought groundwater levels back to the wetland surface.

A near-surface capillary fringe may be responsible for the rapid groundwater responses observed in the early and late growing season. Small water inputs are known to cause large water table responses when a near-surface capillary fringe is present (Gillham, 1984; Gerla, 1992). Gillham (1984) recorded a 30cm hydraulic head increase within 15 seconds of applying the equivalent of a 3mm rainfall to a fine sand soil. A 20cm water table increase lagged just a few seconds behind the hydraulic head response. He attributed this rapid response to a near-surface capillary fringe, and noted that the response would be more pronounced in finer-textured soils.

The minor impact that precipitation and seiches had on mid-summer groundwater levels may have been due to the absence of a near-surface capillary fringe. Soil moisture levels declined as groundwater levels declined in mid-summer. As the solum dried out, the capillary fringe withdrew from the soil surface. Once this occurred, sustained periods of precipitation or inundation, and a decrease in ET, were required to re-saturate the solum.

Similar patterns of ET-driven summer groundwater decline and inundation-driven fall groundwater recharge have been reported in northern Michigan shrub-carr wetlands (Parker, 1970), prairie potholes (Meyboom, 1966; Winter, 1989; Winter and Rosenberry, 1995) and Lake Michigan dune swales (Doss, 1993). ET is also an important driver of soil water movement in tidal marshes (Hemond and Fifield, 1982; Dacey and Howes, 1984), and is the critical pathway for pore water exchange in irregularly flooded tidal wetlands (Odum, 1988).

Standing water influenced wet meadow groundwater levels, but only over short distances. The smallest seasonal groundwater declines occurred in groundwater wells located closest to the on-site ditch at the disturbed site. Groundwater inflow from the ditch supported groundwater levels in these wells, which were only 10m from the ditch. However, groundwater levels in wells as little as 20m from Saginaw Bay at the reference site declined to more than 60cm below the bay surface elevation by mid-summer 1996 (see Figure 2-12c). These groundwater declines occurred even as Saginaw Bay was in the increasing phase of its annual hydroperiod.

Horizontal groundwater flow limitations have also been observed in tidal salt marsh substrates. Harvey et al. (1987) noted that salt-marsh soils drained horizontally through soil pores to nearby tidal creek-beds, but re-saturation occurred by vertical infiltration from the marsh surface following tidal inundation. Their modeling indicated that only 3% of sub-surface pore-water recharge occurred via groundwater inflow from tidal creek banks, and that when it did occur, horizontal pore-water flow occurred only over short distances (Ibid., 1987). Tide-driven horizontal pore-water fluxes were limited to a zone extending less than 15m from the creek-bed (Nuttle, 1986; Harvey et al., 1987). At greater distances, pore-water fluxes were mostly vertical, driven by ET and infiltration of tidal floodwaters (Hemond and Fifield, 1982; Harvey et al., 1987).

Doss (1993) observed similar horizontal flow limitations in Lake Michigan coastal dune swales. He noted that a 1m Lake Michigan lake level decline caused little measurable change in the surface water elevation of dune swale wetlands with documented sub-surface hydrologic links to the lake. The hydraulic gradient between the swales and Lake Michigan increased, but wetland surface water and groundwater levels barely changed. Doss suggested two possible explanations: that there might be relatively long lag times between lake level changes and groundwater responses, or that the swales were flow-through wetlands being maintained by groundwater flow from points inland.

Groundwater declined in the reference Saginaw Bay coastal wet meadow for the following reasons (Figure 2-20). Rainfall, snow melt, and storm surges saturated the wet meadow to the ground surface in late winter and early spring, when ET was low. As ET increased in late spring, the vegetation began removing water from wet meadow soils more rapidly than it was replenished by rainfall, storm surges, and groundwater inflow. The rate of infiltration and groundwater inflow decreased as soil moisture levels dropped below the saturation point, further reducing soil moisture content. A positive feedback loop developed; ET reduced soil moisture content, which slowed infiltration and groundwater recharge, driving groundwater levels lower. Groundwater decline resulted.

This pattern reversed in the fall. ET began to decline in September, when annual precipitation levels were at their highest. Soil moisture content increased as precipitation and storm surge inputs exceeded ET. Increased soil moisture content accelerated infiltration and groundwater inflow, further increasing soil moisture content. A positive feedback loop developed, accelerating groundwater recharge. Groundwater rebound resulted.

Disturbed wet meadow

Seasonal groundwater discharge/recharge patterns at the disturbed site were similar to those at the reference site. However, there were differences in how the individual hydrologic factors contributed to the overall seasonal pattern. Surface water hydrology at the disturbed site was quite different than that at the reference site, because the dike disrupted the direct surface connection between the disturbed site and Saginaw Bay. Seiche and storm surge impacts were completely eliminated by the dike. Saginaw Bay could only influence site hydrology indirectly, through groundwater infiltration beneath the dike.

While the dike eliminated seiche and storm surge flooding, it also inhibited site drainage. Surface and groundwater levels were often higher behind the dike than in the bay-level drain, particularly in the early growing season. The dike acted as a barrier to surface flow in either direction, either preventing site flooding or restricting site drainage, depending on meteorological conditions and the surface elevation of Saginaw Bay at any point in time.

Groundwater levels at the disturbed site rebounded more slowly in the fall than they did at the reference site. Several factors probably played a role in this delayed fall recharge. The dike eliminated seiche and storm surge inundation of the site, reducing inputs and slowing recharge. The lower water tables in the drained agricultural fields on either site of the disturbed site may have drawn groundwater away from the site. The ditch and swale system enhanced site drainage within the disturbed site. Efficient drainage reduced net infiltration, because standing water spent less time on the wet meadow surface after deposition. This also slowed groundwater recharge throughout much of the site.

Differences between the study sites in seasonal soil moisture trends reflected differences in site hydrology. The dike prevented seasonal and storm surge inundation of the disturbed site, while the drainage swale, on-site drainage ditch, and perhaps neighboring land uses facilitated drainage within the site. These factors allowed surface soils at the disturbed site to continue drying throughout the 1996 growing season. At the reference site, seiches and storm surges periodically inundated the wet meadow throughout the year, negating growing-season dry-down trends, and there was no nearby agricultural drainage to draw-down adjacent groundwater levels. Nonetheless, wet meadow soil moisture content never fell below field capacity in either wet meadow during the 1996 growing season.

In the absence of periodic inundation, groundwater inflow from sources of standing water became a more important factor in wet meadow groundwater recharge at the disturbed site, at least over short distances. Groundwater levels declined least at the disturbed site in the monitoring wells closest to the on-site drainage ditch. These wells were just 10m from the ditch, close enough that groundwater inflow could at least partially support the nearby groundwater table. However, groundwater inflow had only a minor influence on wet meadow groundwater levels at these wells, and no measurable impact at greater distances from standing water at either the disturbed or reference sites.

Several other factors might explain why groundwater recharge differed between the sites. As previously noted, differences in adjacent land use at the two sites may have impacted recharge rates. The disturbed site was flanked by agricultural fields which were tiled and mechanically-pumped to keep them dry. There was no such groundwater-lowering activity near the reference site. Groundwater outflow from the disturbed site to these fields may have occurred, slowing fall recharge. Glacial till subsoil was closer to the surface at the disturbed site, and may have slowed vertical soil water movement, so that horizontal pore-water flow became more apparent than at the reference site. Soils at the reference site were more permeable than at the disturbed site, and this may have resulted in more rapid re-saturation of reference site substrates. Groundwater recharge may simply have occurred at the reference site too rapidly to be detected using the methods applied in this study. Yet another possibility is that precipitation flowed off the disturbed wet meadow into the ditch and swale, and only then infiltrated back into the wetland from there.

The disturbed site generally retained more surface water in the winter and spring months, and then dried more thoroughly in the summer months, than did the reference site. Fall groundwater recharge required more time in the disturbed wet meadow than it did in the reference wet meadow. In these respects, disturbed site hydrology was more similar to inland wet meadow hydrology than it was to that of a coastal wet meadow.

Despite the differences in impact of individual hydrologic factors on the hydrology at the two sites, there were few differences in the seasonal groundwater discharge/recharge patterns of the reference and disturbed sites. Interruptions of seiche and storm surge flooding at the disturbed site were offset in the spring by increased detention of winter snow melt and spring precipitation, so early growing season hydrology was similar at the two sites. Once ET increased in late spring, groundwater levels declined at similar rates at both sites. It was only in the fall, when the dike prevented seiche or storm surge inundation at the disturbed site, that groundwater recharge was delayed.

Summary and Conclusions

Precipitation, seiche and storm surge inundation, and evapotranspiration controlled groundwater hydrology in the reference and disturbed wet meadow study sites.

Groundwater declines of up to 100cm below the wet meadow surface occurred during the June-August growing period at both sites, driven by evapotranspiration averaging 0.5-2mm/day. Early and late growing-season groundwater recharge occurred when precipitation, or at the reference site, seiche and storm surge inputs, exceeded evapotranspiration and re-saturated wet meadow soils. ET withdrawals exceeded surface water, groundwater, and precipitation inputs in mid-summer, driving wet meadow groundwater levels downward.

The reference wet meadow was occasionally inundated by precipitation and seiches or storm surges during the growing season. Such inundation maintained wet meadow soils at a saturation level suitable for wet meadow vegetation. By contrast, the dike at the disturbed wet meadow prevented seiche and storm surge flooding, and inundation during high water years, while detaining excess water on the site in the early growing-season. The ditch and swale at the disturbed site enhanced drainage as surface water and groundwater levels declined in the summer, permitting soils at the site to continue drying down in the late growing season. The dike, ditch, and swale altered the annual hydroperiod at the disturbed site to resemble that of an inland wet meadow rather than a coastal wet meadow.

Precipitation and Saginaw Bay were the principal sources of wet meadow groundwater at these sites. Low wet meadow slopes (0.15-0.25%) and the lack of adjacent uplands at the reference and disturbed site limited groundwater inputs from nearby uplands. Groundwater inflow from adjacent uplands may contribute water, nutrients and pollutants to other coastal wet meadows. Studies of groundwater chemistry or stable isotope ratios would provide useful insights into the source and fate of wet meadow groundwater, and the contributions made by upland sources to the overall wet meadow water balance.

It is not known how similar these patterns of evapotranspiration, precipitation, and inundation may be to those found in other Saginaw Bay coastal wet meadows. Differences among sites in shoreline aspect and geomorphology, exposure to prevailing winds, storm surge frequency and amplitude, bay circulation and sedimentation patterns, substrate composition, and groundwater inflow from adjacent uplands have undetermined impacts on wet meadow hydrology. Further study would be required to determine if these findings apply to other Saginaw Bay coastal wet meadows, or to Great Lakes coastal wet meadows outside the Saginaw Bay basin.

Having defined the hydrologic regime of the coastal wet meadow, the question arises at to the manner in which this hydrologic regime influences wet meadow vegetation structure and composition. That question is addressed in Chapter Three.

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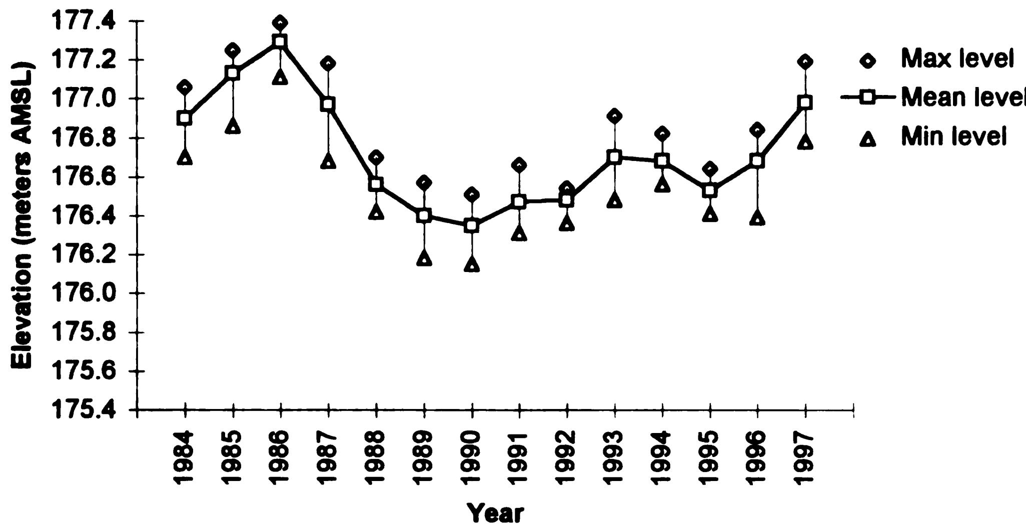


Figure 2-1. Maximum, mean, and minimum annual water levels of Lake Huron: 1984-1997. Data from the Detroit District, US Army Corps of Engineers.

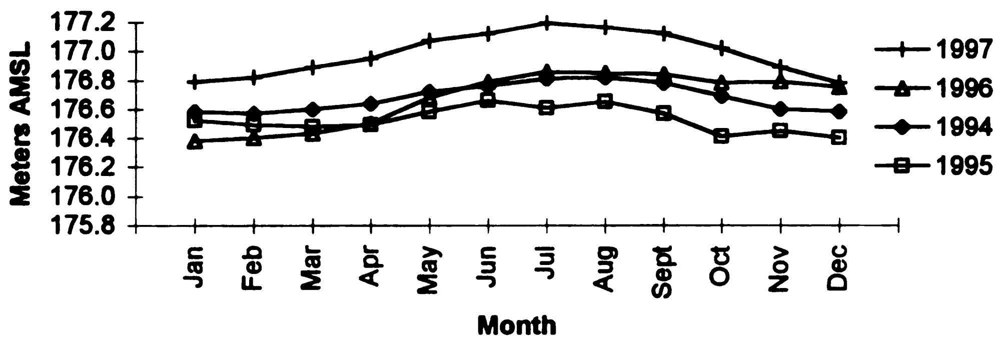


Figure 2-2. Mean monthly Lake Michigan-Huron water levels: 1994-1997. Data from the Detroit District, US Army Corps of Engineers.

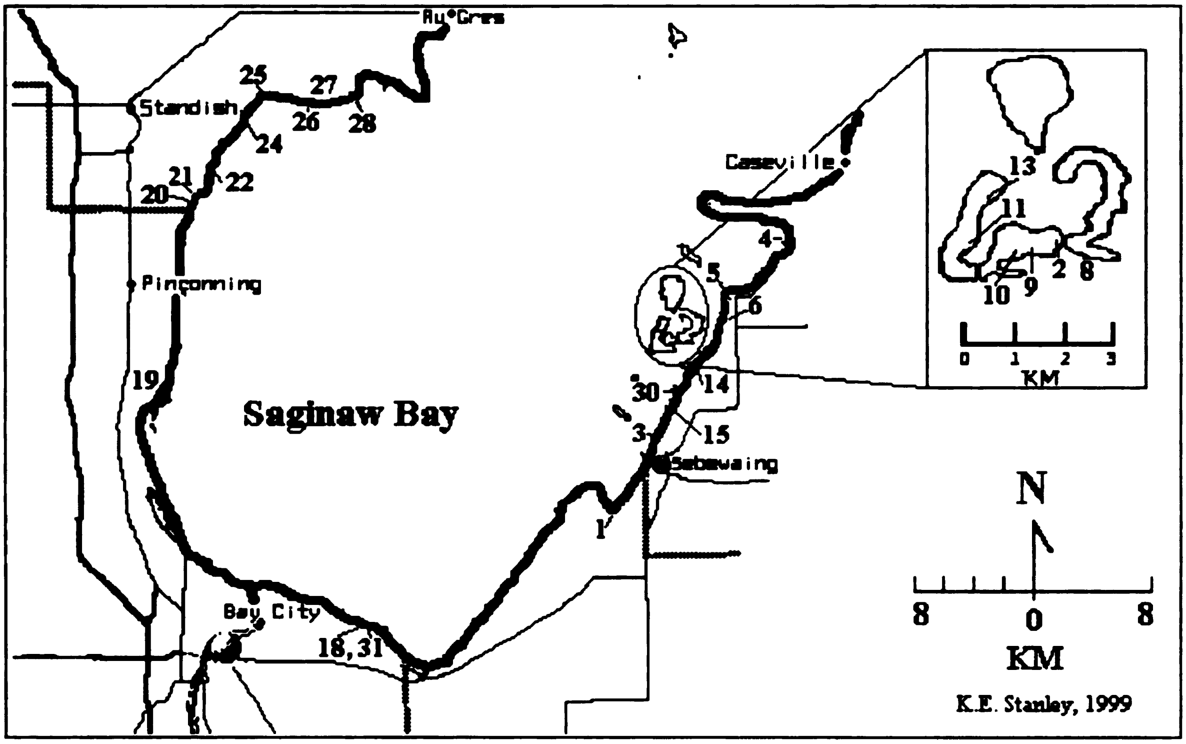


Figure 2-3. Map of the Saginaw Bay region. The location of the reference hydrologic study site (Site 2; see inset) and the disturbed hydrologic study site (Site 1) are indicated. These were two of 31 coastal wet meadows bordering Saginaw Bay in 1997. Wet meadow vegetation was examined at the two hydrologic study sites, and 23 other wet meadows. Sites 7, 12, 16, 17, 23, and 29 were not used in the study and are not shown (see Figure 1-2 for location of these sites). Map data from US Census Bureau TIGER database and Michigan Department of Natural Resources.

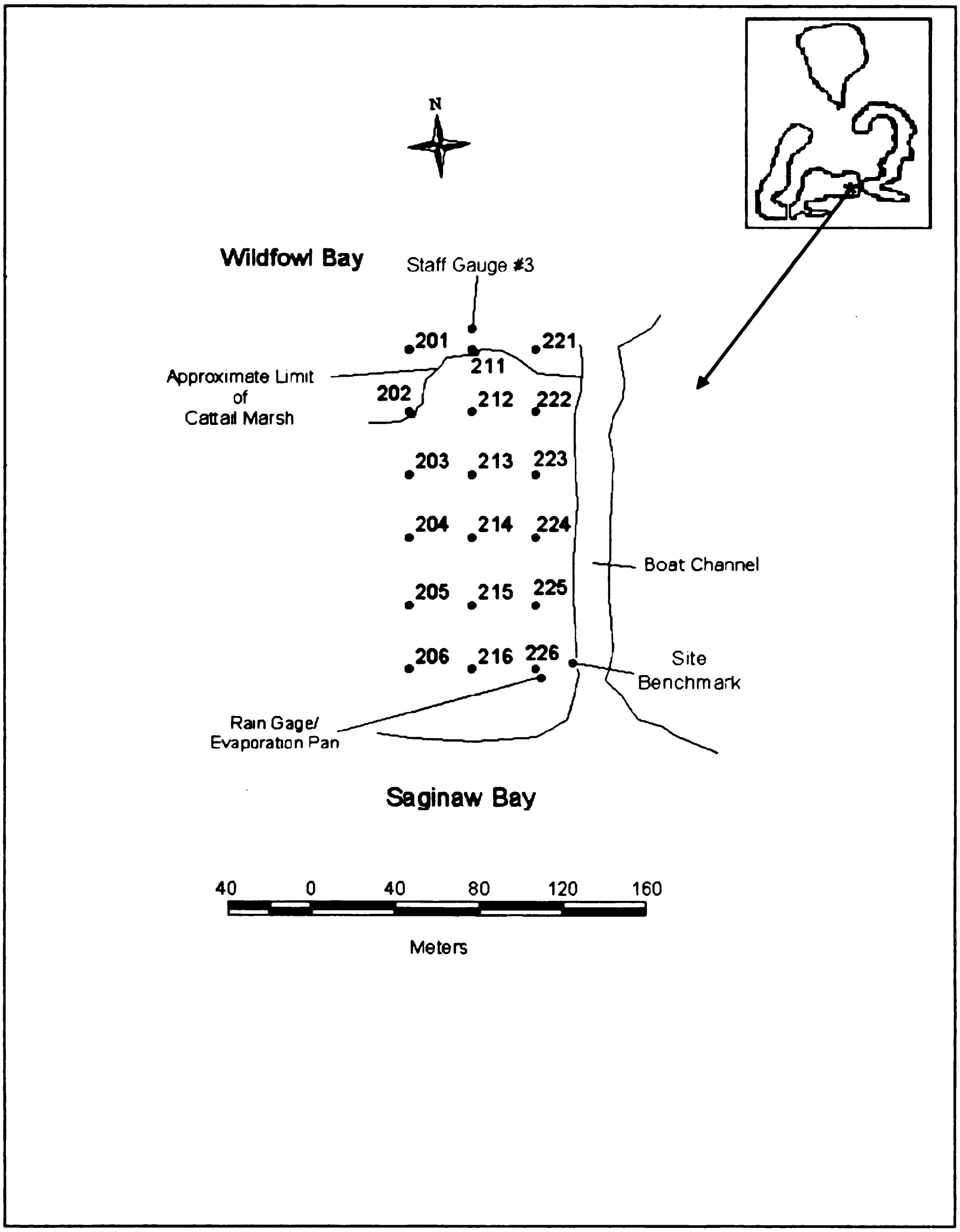


Figure 2-4. Map of the reference hydrologic study site, located 12km north of Sebewaing, MI and 2km off the coast in the Wildfowl Bay State Game Area. The site sloped from high ground on the south shore to cattail marsh on the north. The wet meadow-cattail marsh boundary fluctuated annually depending on the level of Saginaw Bay. The boat channel was excavated prior to 1938. The numbers identify groundwater monitoring wells.

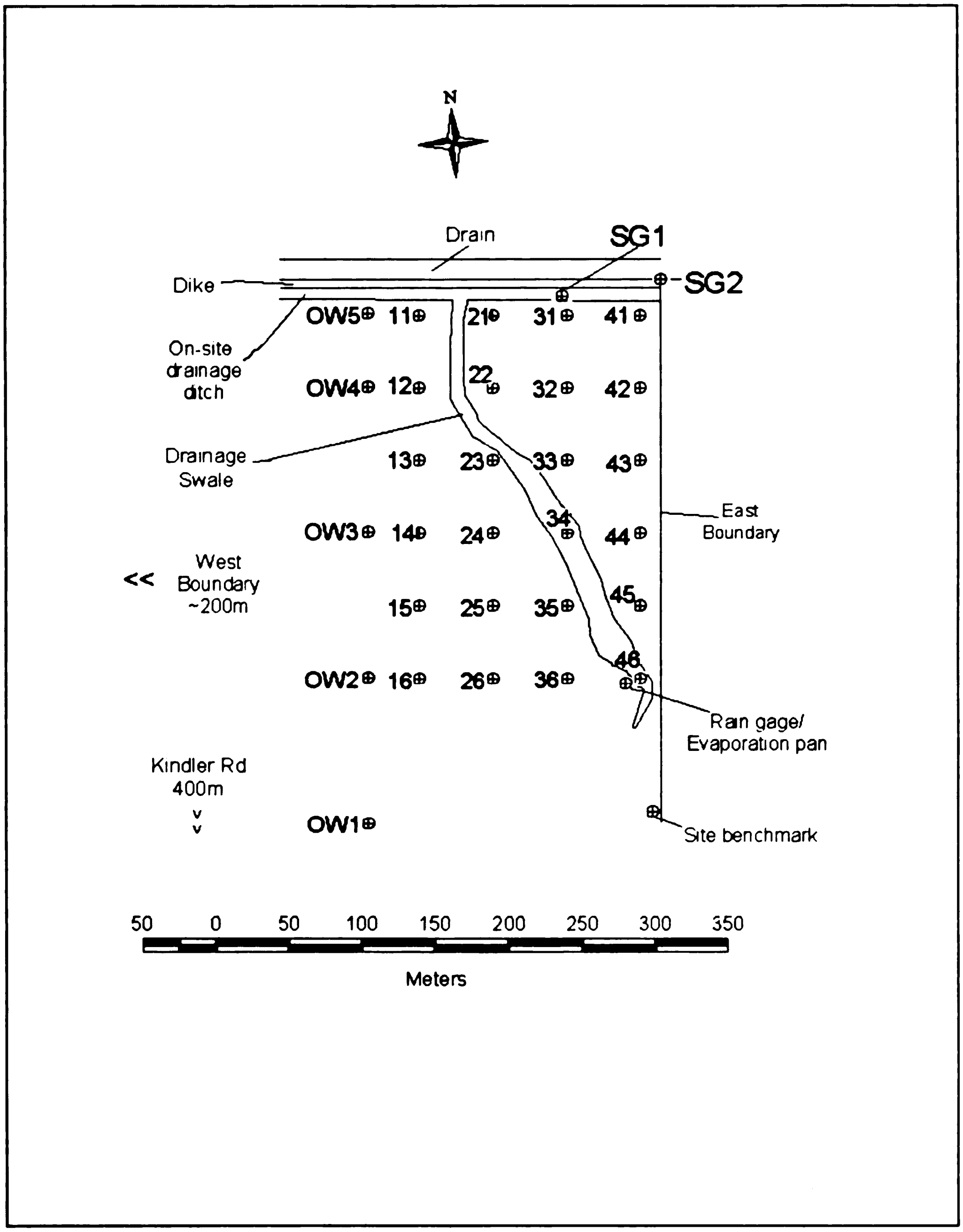
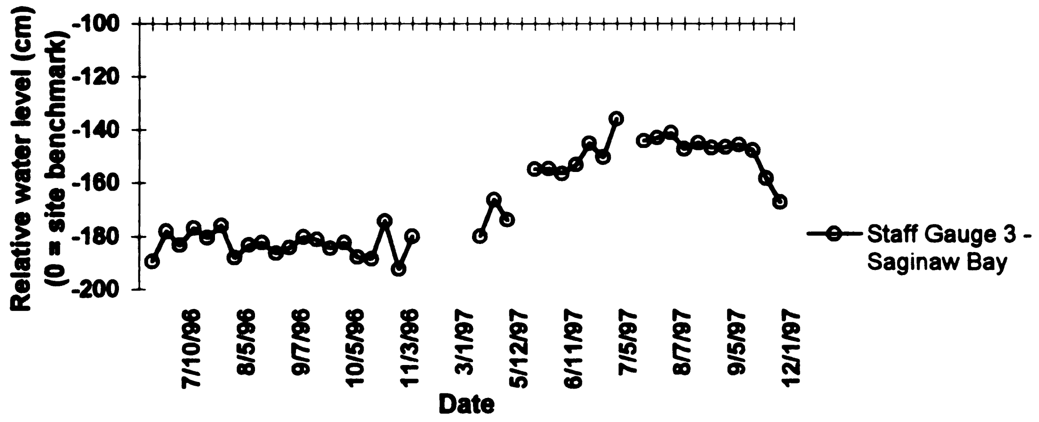
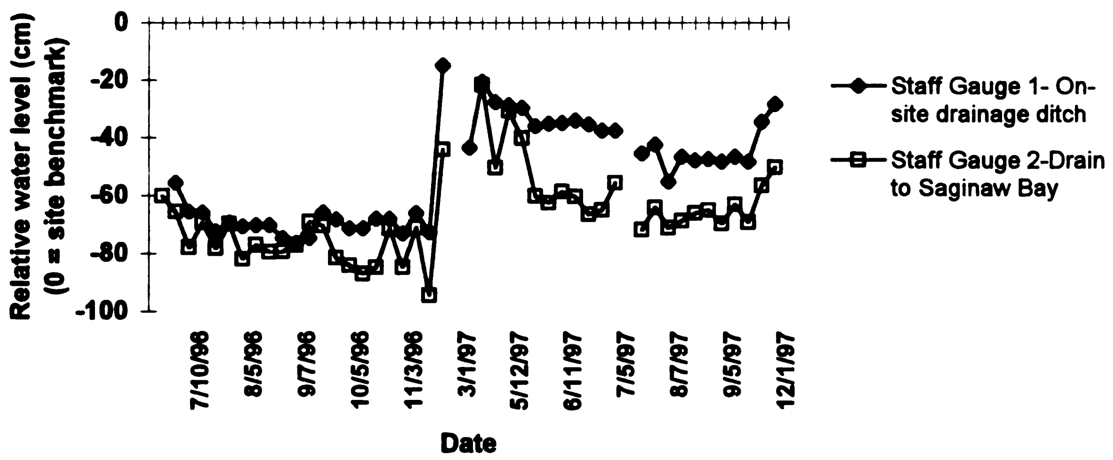


Figure 2-5. Map of the disturbed hydrologic study site, located 19km southwest of the reference site on Saginaw Bay's eastern shore. The site was either cultivated or grazed for an 80-100 year period ending in the late 1980's. The dike, constructed between 1941-1949, severed the direct surface connection with Saginaw Bay. The drain discharged into Saginaw Bay (not shown). The numbers and "OW" labels identify groundwater monitoring wells, the "SG" labels staff gauges.



A. Reference site.



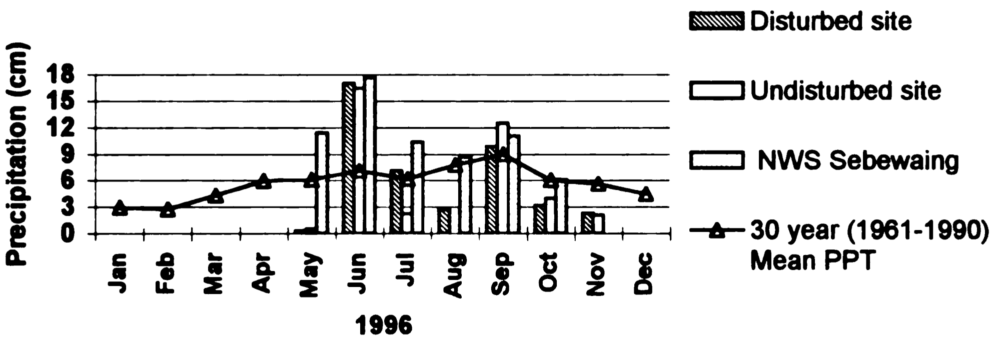
B. Disturbed site.

Figure 2-6. Change in surface water levels at the reference and disturbed hydrologic study sites: 1996-1997. Staff Gauge 1 was in the on-site ditch at the disturbed site. Staff Gauge 2 was in an agricultural drain at the disturbed site that discharged to Saginaw Bay. Staff Gauge 3 was in Saginaw Bay at the reference site. Surface water levels for each site were referenced to site benchmark, not to Datum, and are not directly comparable. Staff gauge readings were not collected in winter when the gauges were encased in ice.

Table 2-1. Occurrence of water levels greater than or equal to 177.3m AMSL at Essexville, MI: 3/1/97-10/31/97. 177.3m AMSL was the maximum elevation of the Saginaw Bay wet meadow zone during 1997. Data from NOS-NOAA.

Date	Number of hours water level ≥177.3m AMSL	Peak water level (m AMSL)	Date	Number of hours water level ≥177.3m AMSL	Peak water level (m AMSL)
5/3	11	177.47	8/2	2	177.33
5/24	2	177.39	8/3	2	177.32
5/25	8	177.49	8/4*	3	177.45
5/26	1	177.33	8/5*	7	177.44
5/27	1	177.30	8/10*	3	177.40
6/2	5	177.35	8/11*	1	177.33
6/14	2	177.31	8/17	11	177.37
6/16	1	177.33	8/20*	6	177.50
6/17	1	177.35	8/21*	15[(a)]	177.55
7/4	2	177.33	8/22	18	177.44
7/6	6	177.42	9/2	7	177.41
7/8*	4	177.54	9/3	8	177.41
7/9*	3	177.47	9/7	3	177.33
7/18	4	177.43	9/10	9	177.42
7/19	9	177.53	9/20	3	177.31
7/21	4	177.33	9/23	1	177.30
7/22	10	177.38	9/25	2	177.36
7/23	6	177.33	9/26	2	177.31
7/28*	7	177.37	9/30	1	177.39
7/29*	7	177.38	10/1	5	177.47
			10/26*	5	177.61
			10/27*	6	177.69

* - Indicates that the event was continuous during the two days.
(a) - Only ten hours were continuous with the previous day (8/20).



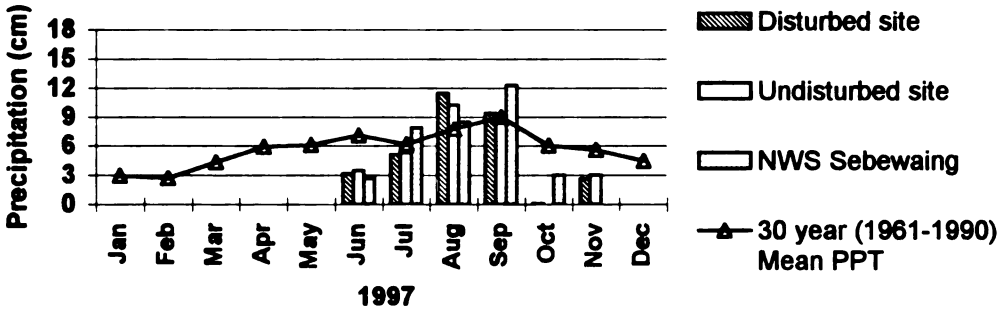


Figure 2-7. Monthly precipitation at the reference and disturbed hydrologic study sites, and the National Weather Service climatological reporting station at Sebewaing, MI: 1996-1997. The line describes the 30 year (1961-1990) mean monthly precipitation for NWS-Sebewaing. Rainfall data were not collected in winter months.

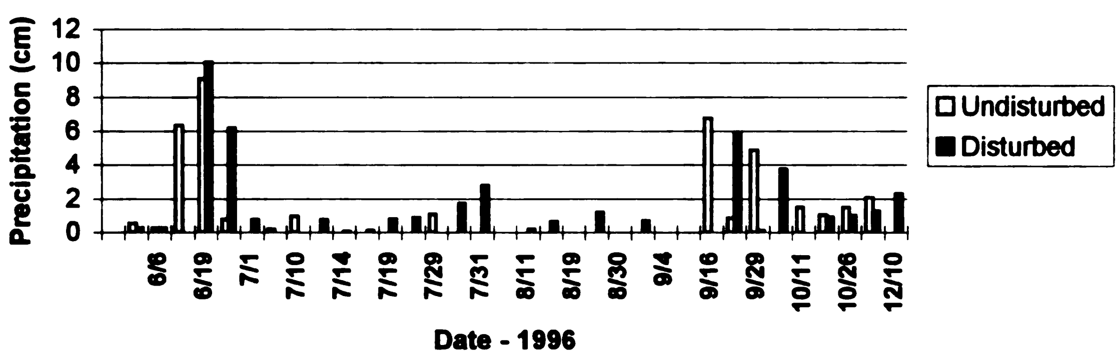


Figure 2-8. Precipitation recorded at the reference and disturbed hydrologic study sites: 1996. Rainfall data were not collected in winter months.

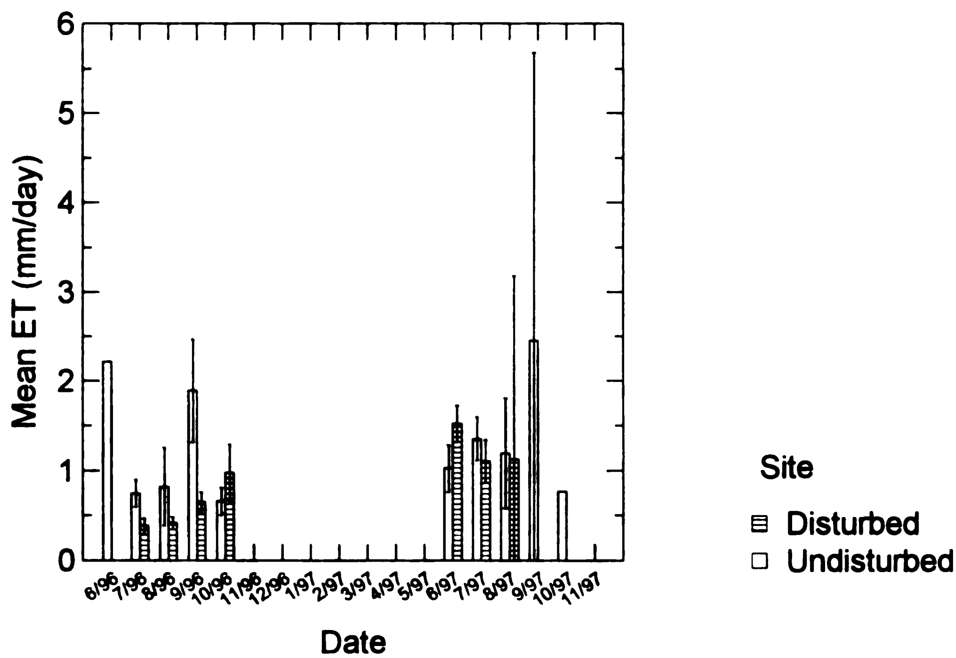


Figure 2-9. Monthly mean daily evapotranspiration (ET) for the reference and disturbed hydrologic study sites: 1996-1997. ET estimated from pan evaporation measured at the sites. Data were not available from the disturbed site in June 1996, and September and October 1997. Error bars denote ±1SE of the mean.

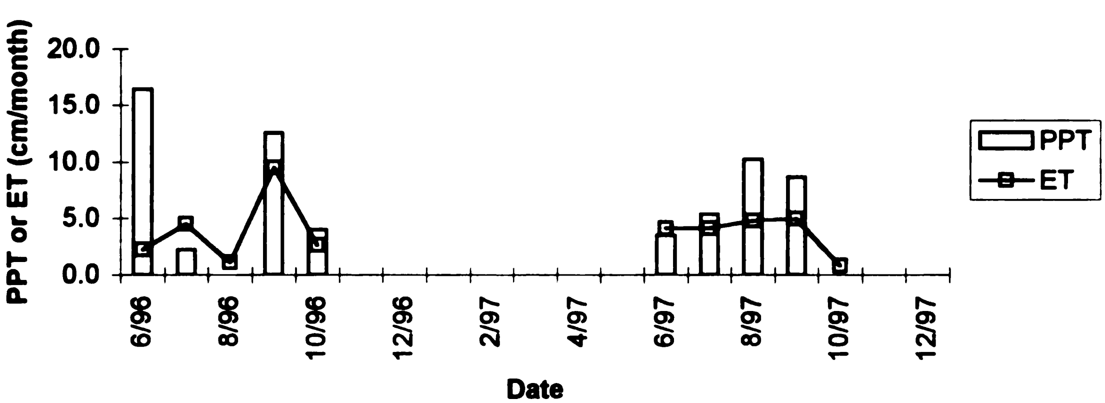


Figure 2-10. Monthly precipitation (PPT) and estimated evapotranspiration (ET) at the reference hydrologic study site: 1996-1997. Rainfall and pan evaporation data were not collected in winter months.

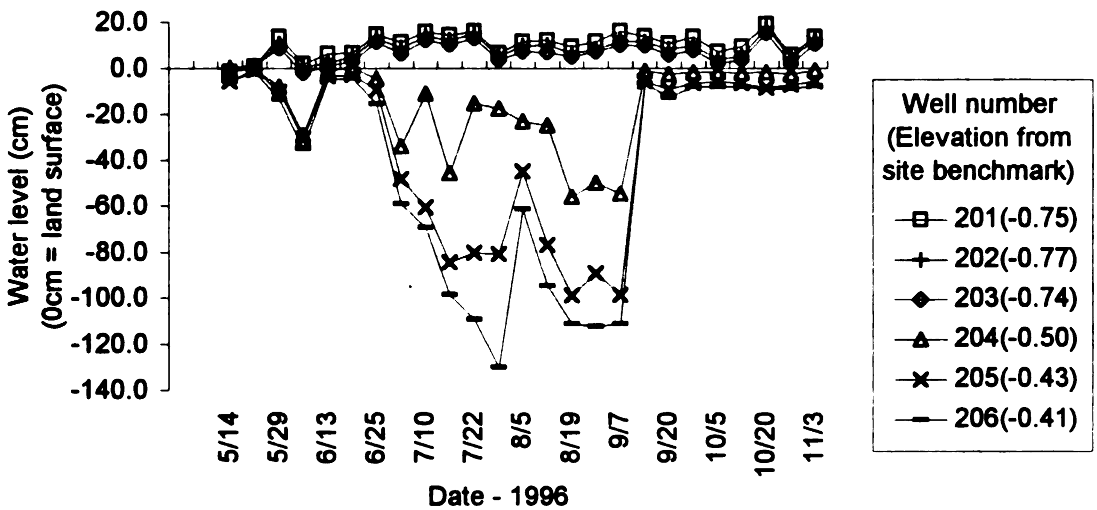
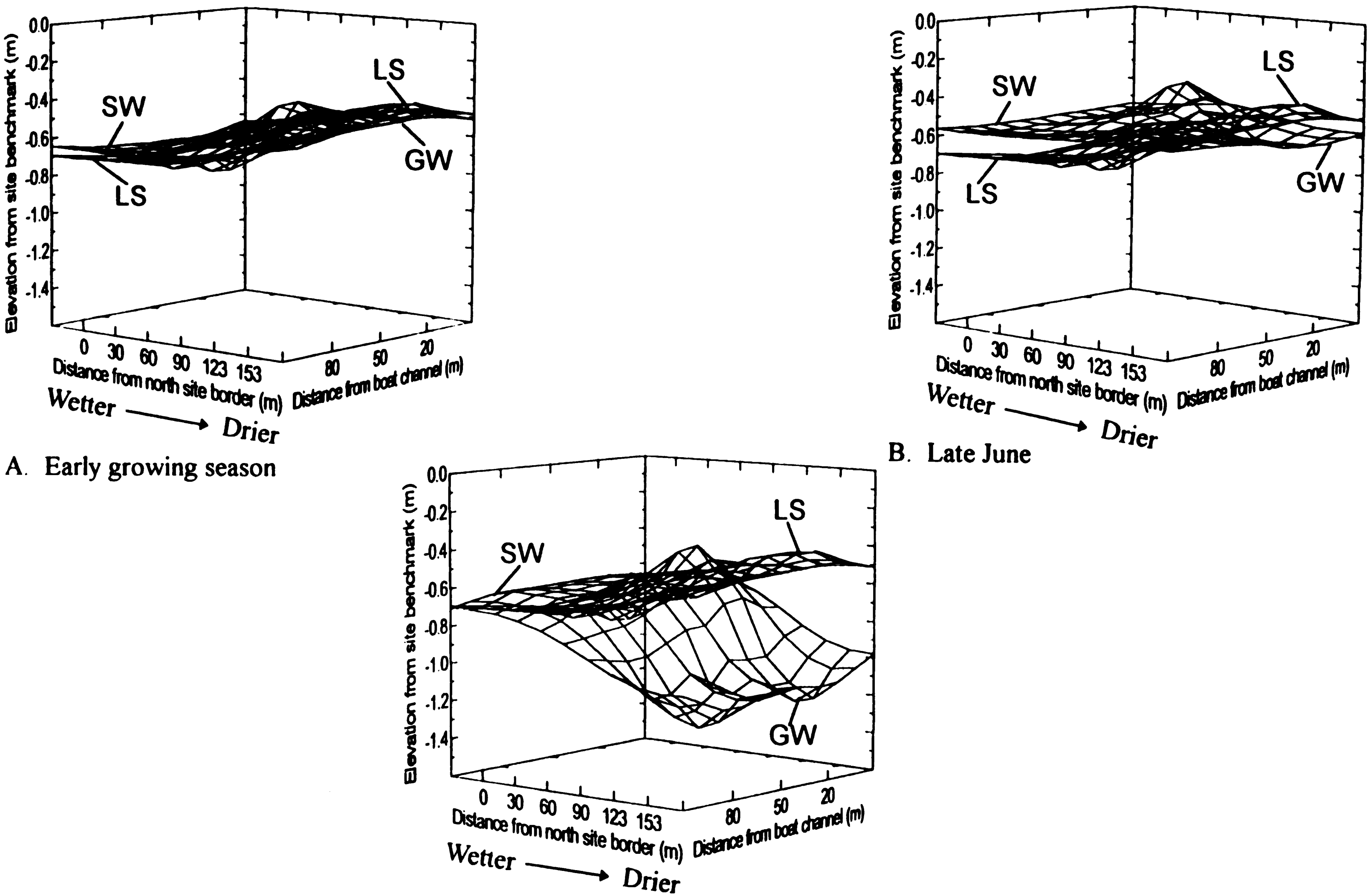


Figure 2-11. Surface water and groundwater profiles for monitoring wells #201-#206 at the reference hydrologic study site during the 1996 growing season. Wells were in line order ranging from lowest (#201) to highest elevation (#206). Elevations indicate ground level at each well with respect to the site benchmark. Each well was 30m from the next well in line. Wells #201, 202, and 203 were inundated throughout the growing season. Wells #204, 205, and 206 remained free of standing water for most of the growing season.

Figure 2-12. Groundwater levels declined at the reference hydrologic study site in 1996. A. In the early growing season, the wetland surface was entirely saturated, and there was 10-15cm water standing in the lower wet meadow. B. By late June, groundwater levels in the upper wet meadow appeared to be equilibrating with surface water levels in Saginaw Bay. C. By mid-July, groundwater levels had dropped sharply in the upper wet meadow to levels as much as 100cm below the ground surface, or 65cm below the level of Saginaw Bay. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay. The east site border was the boat channel. Elevation increased, and the site became drier, as one moved away from the north site border. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the southwest.



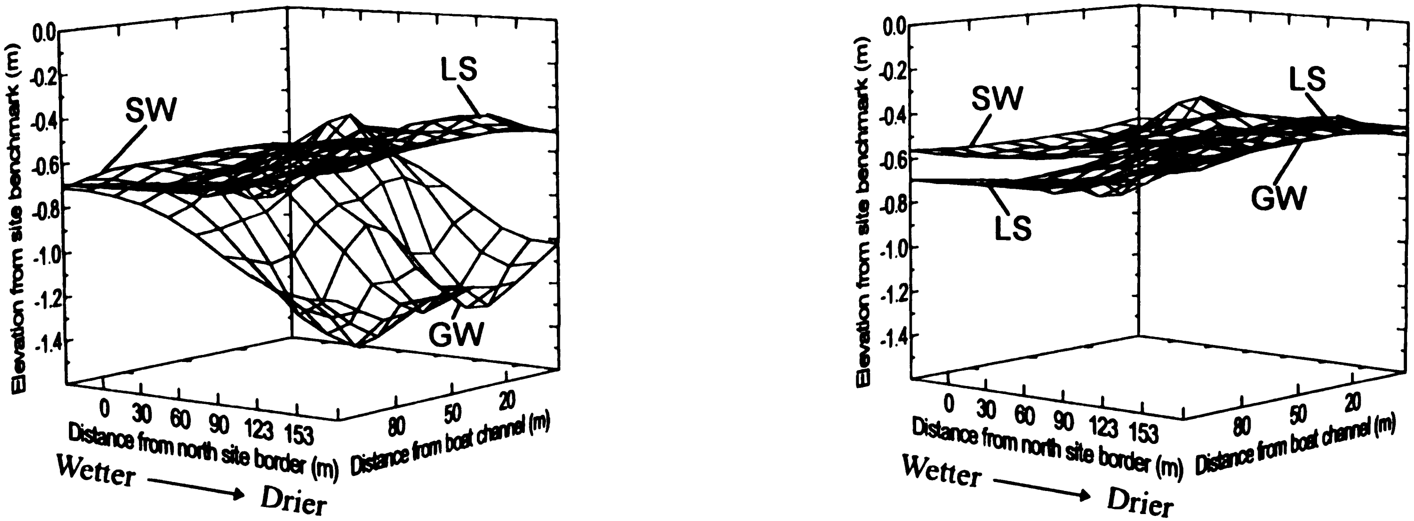
A. Early growing season

B. Late June

C. Mid-July

Figure 2-12.

Figure 2-13. Groundwater levels rebounded in late summer 1996 at the reference hydrologic study site. A. Mid-summer groundwater profiles remained unchanged until early September 1996. B. Within seven days in mid-September, groundwater levels in the upper wet meadow rebounded to within a few centimeters of the ground surface, while the lower wet meadow had been inundated to a depth of 15cm. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay. The east site border was the boat channel. Elevation increased, and the site became drier, as one moved away from the north site border. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the southwest.



A. Mid-summer

B. Mid-September

Figure 2-13.

Figure 2-14. Comparison of early growing season groundwater levels at the reference and disturbed hydrologic study sites. Similar groundwater profiles were observed at the sites in the early growing season. Both sites were saturated to the ground surface in mid-May 1996, and groundwater decline had commenced at both sites by early June. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay, at each site. The east site border was the boat channel at the reference site, and an agricultural field at the disturbed site. Elevation increased, and the sites became drier, as one moved away from the north site border of each site. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the east.

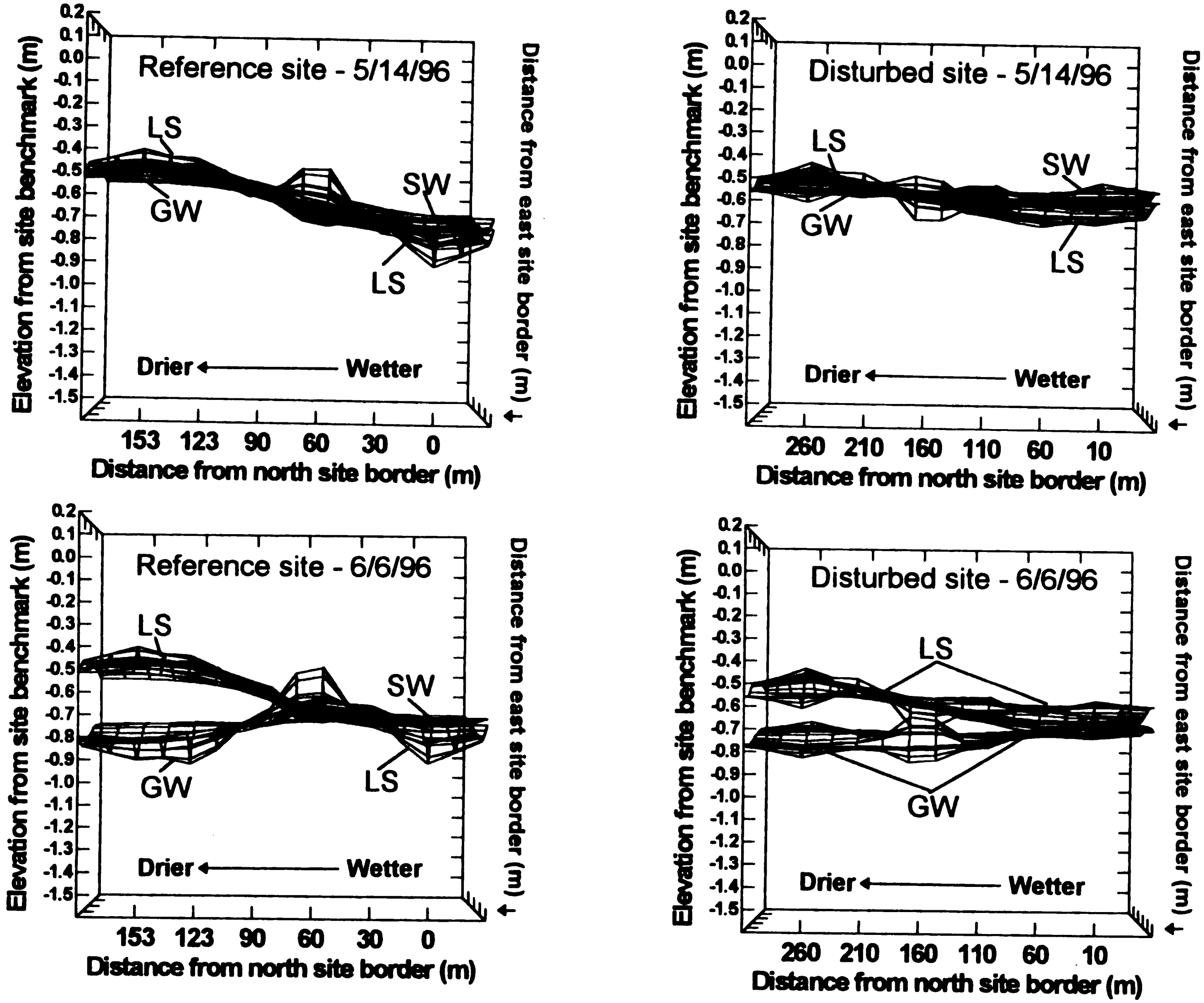

Reference site - 5/14/96
Disturbed site - 5/14/96
Reference site - 6/6/96
Disturbed site - 6/6/96
LS
SW
GW
Drier ← Wetter
Elevation from site benchmark (m)
Distance from north site border (m)
Distance from east site border (m)
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1.0
-1.1
-1.2
-1.3
-1.4
-1.5
153 123 90 60 30 0
260 210 160 110 60 10

Figure 2-14.

Figure 2-15. Comparison of mid-summer groundwater levels at the reference and disturbed hydrologic study sites. By July 1, 1996, the reference and disturbed site groundwater tables had reached mid-summer levels. Thereafter, gradual draw down continued in un-inundated portions of both sites through early September. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay, at each site. The east site border was the boat channel at the reference site, and an agricultural field at the disturbed site. Elevation increased, and the sites became drier, as one moved away from the north site border of each site. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the east.

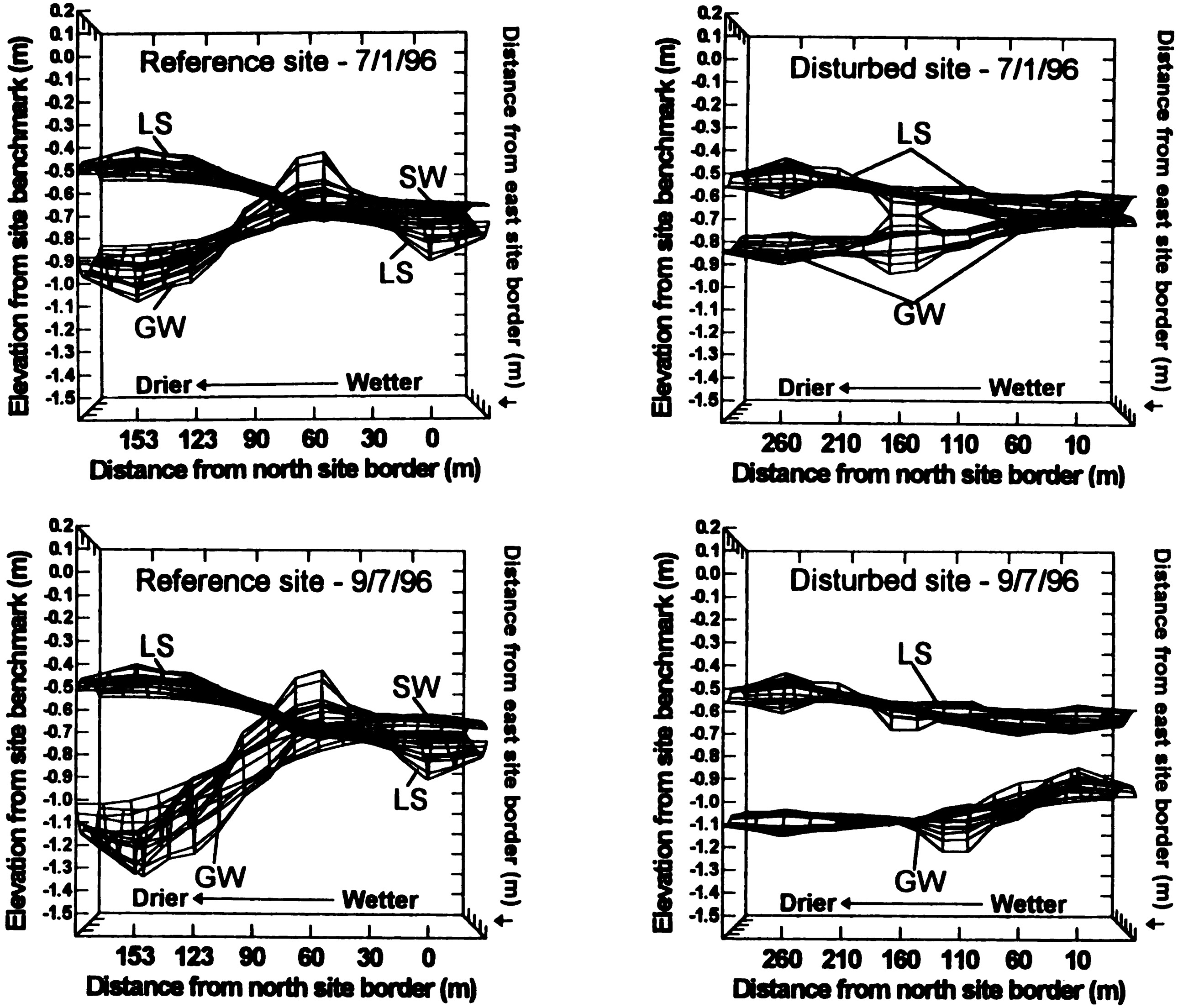
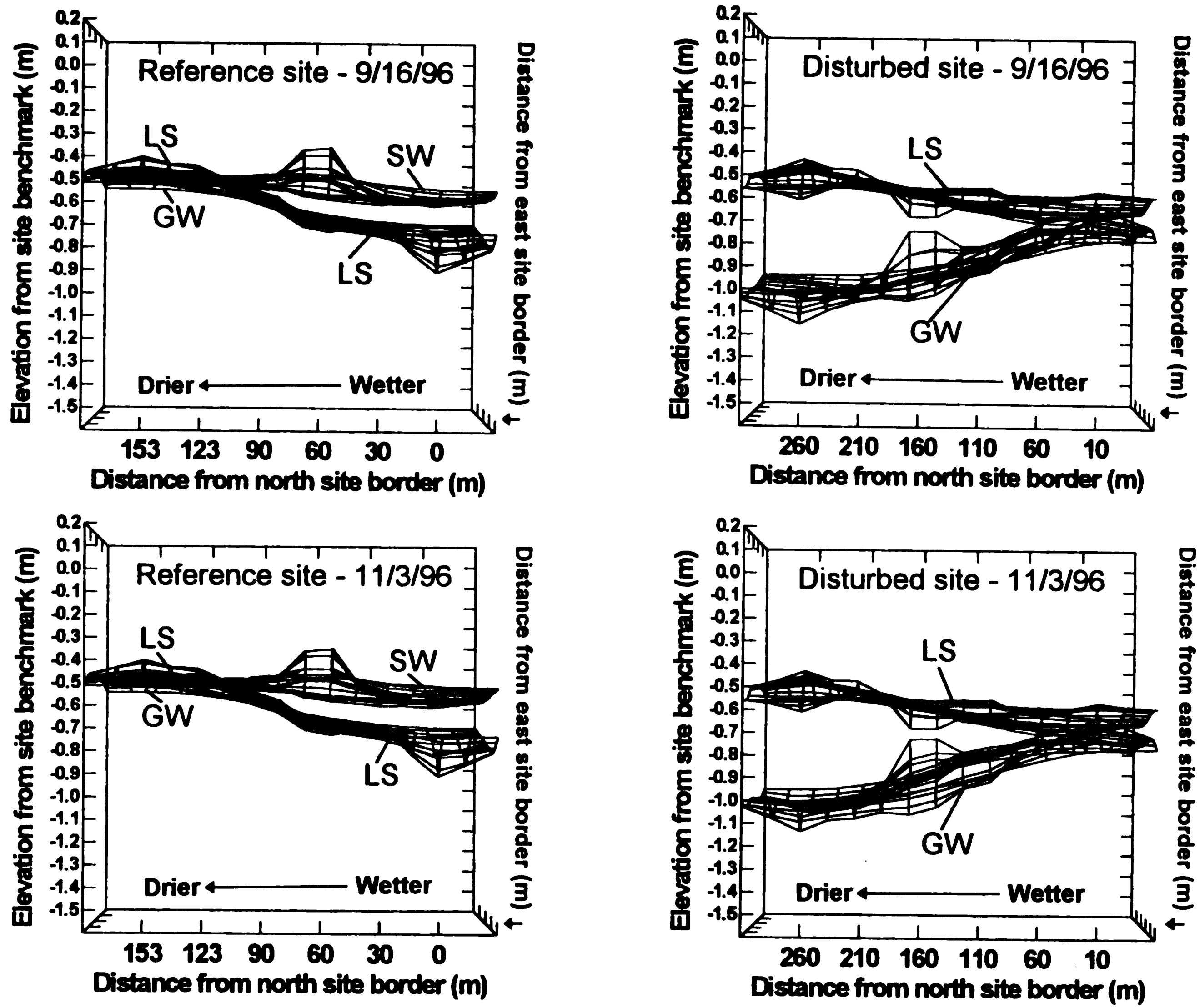

Reference site - 7/1/96
Disturbed site - 7/1/96
Reference site - 9/7/96
Disturbed site - 9/7/96
LS
SW
GW
Drier
Wetter
Elevation from site benchmark (m)
Distance from north site border (m)
Distance from east site border (m)
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
-1.0
-1.1
-1.2
-1.3
-1.4
-1.5
153
123
90
60
30
0
260
210
160
110
10

Figure 2-15.

Figure 2-16. Comparison of late summer groundwater levels at the reference and disturbed hydrologic study sites. Groundwater recharge occurred within a few days in mid-September at the reference site, but required several months at the disturbed site to be completed. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay, at each site. The east site border was the boat channel at the reference site, and an agricultural field at the disturbed site. Elevation increased, and the sites became drier, as one moved away from the north site border of each site. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the east.



Reference site - 9/16/96
Disturbed site - 9/16/96
Reference site - 11/3/96
Disturbed site - 11/3/96
LS
SW
GW
Drier ← Wetter
Elevation from site benchmark (m)
Distance from north site border (m)
Distance from east site border (m)
153 123 90 60 30 0
260 210 160 110 60 10
0.2 0.1 0.0 -0.1 -0.2 -0.3 -0.4 -0.5 -0.6 -0.7 -0.8 -0.9 -1.0 -1.1 -1.2 -1.3 -1.4 -1.5

Figure 2-16.

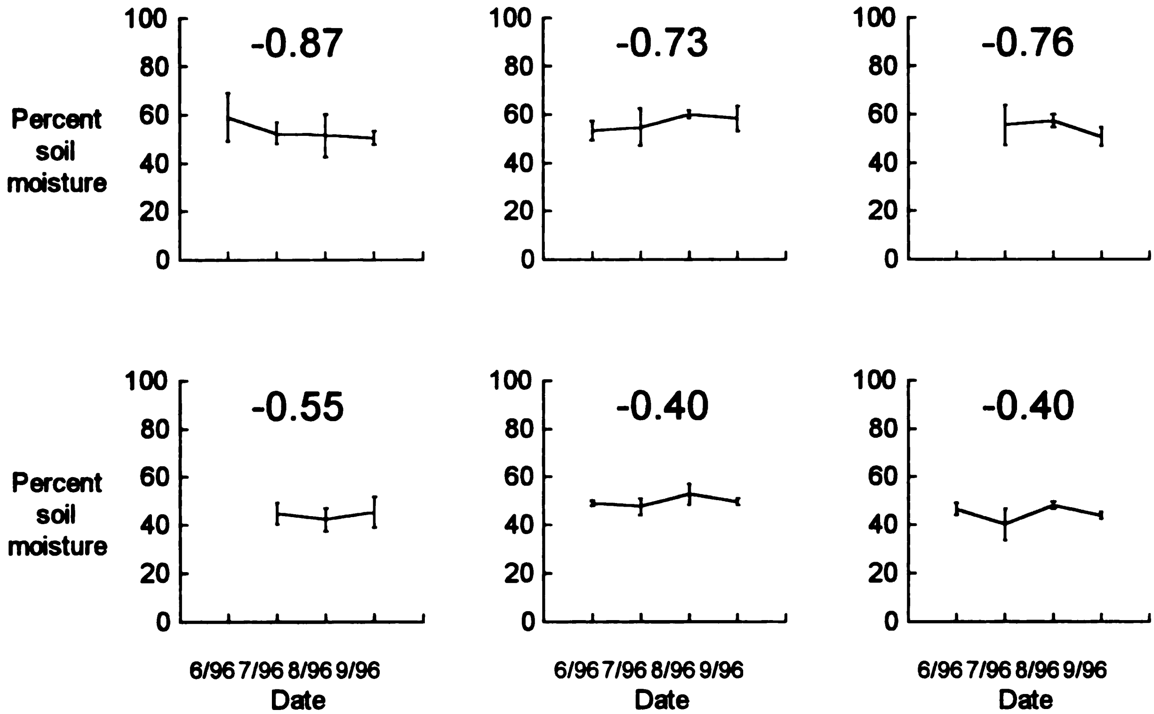


Figure 2-17. Percent soil moisture content of non-saturated soil in various locations at the reference hydrologic study site: 1996. The large numbers above the graphs indicate the elevation (in cm with respect to the site benchmark) at which the soil samples were collected. Error bars denote ±1SE of the mean.

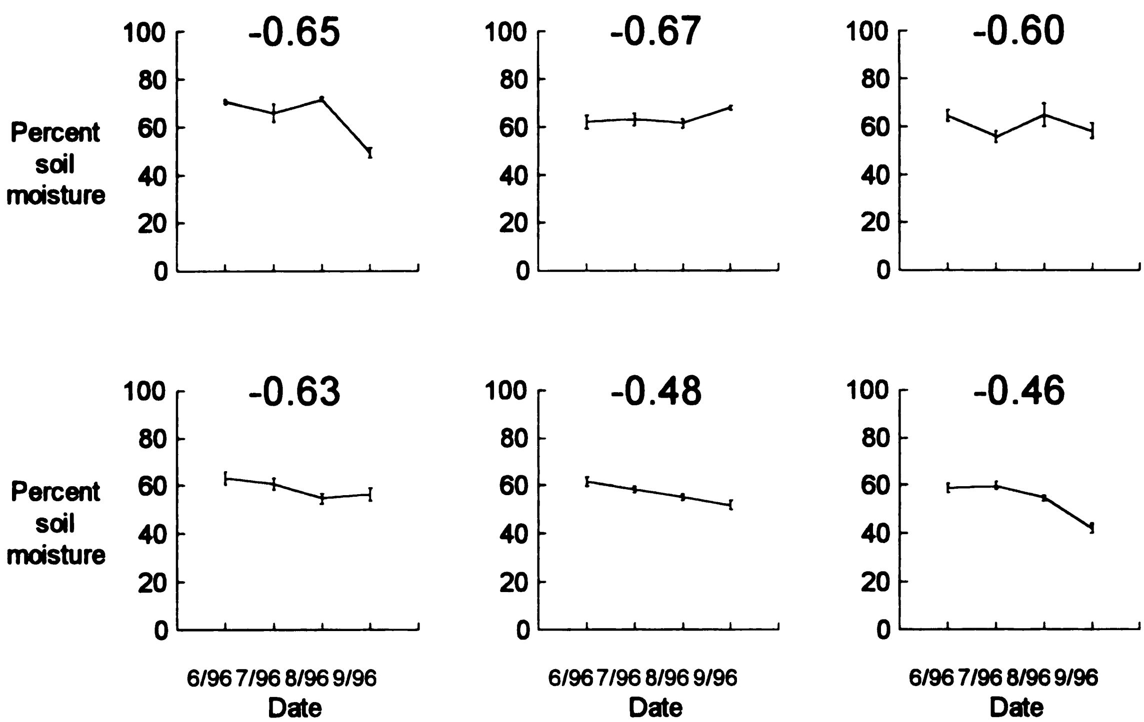
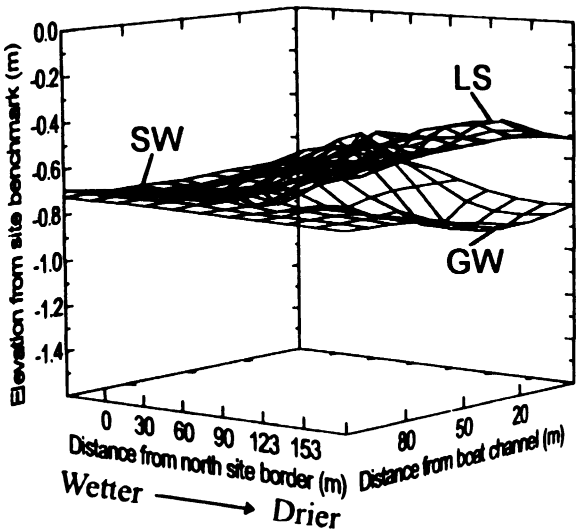
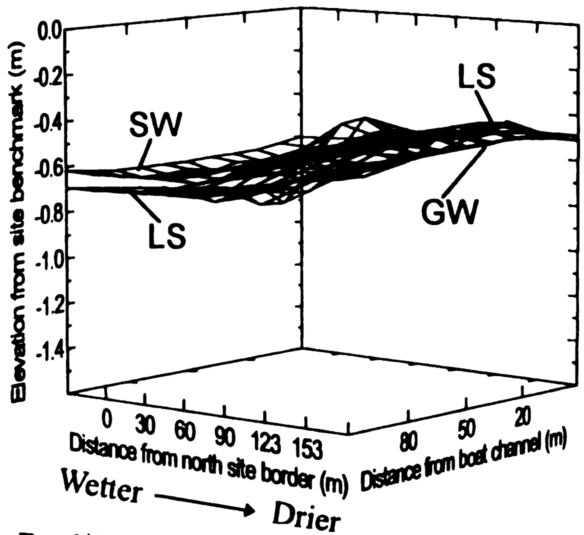


Figure 2-18. Percent soil moisture content of non-saturated soil in various locations at the disturbed hydrologic study site: 1996. The large number above the graphs indicates the elevation (in cm with respect to the site benchmark) at which the soil samples were collected. Error bars denote ±1SE of the mean.

Figure 2-19. Groundwater levels rebounded in mid-June 1996 in response to heavy rainfall and seiche activity. A. Groundwater decline had begun by 6/6/96 at the reference hydrologic study site. B. Groundwater measurements collected on 6/13/96 indicated no evidence of groundwater decline at the site. A total of 6.35cm precipitation, and a 20cm seiche, occurred between 6/6/96 and 6/13/96. The rainfall and surface water rapidly infiltrated and recharged the declining groundwater surface, bringing it back to near the wetland ground surface. LS = land surface; GW = groundwater surface; SW = Saginaw Bay surface elevation. The north site border was the wet end of the site water level gradient, and closest to Saginaw Bay. The east site border was the boat channel. Elevation increased, and the site became drier, as one moved away from the north site border. Elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contours between the monitoring wells were estimated using an inverse squared distance smoothing function (SPSS, Inc., 1996). View point is from the southwest.



A. 6/6/96



B. 6/13/96

Figure 2-19.

Figure 2-20. Seasonal discharge and recharge pattern observed at the reference hydrologic study site. In late winter and early spring, wet meadow substrates were completely saturated. Evapotranspiration discharged groundwater more rapidly than it was replenished by precipitation and storm surge inputs in late spring and early summer, causing groundwater decline. Precipitation and storm surge inputs exceeded ET discharges in late summer, recharging wet meadow groundwater.

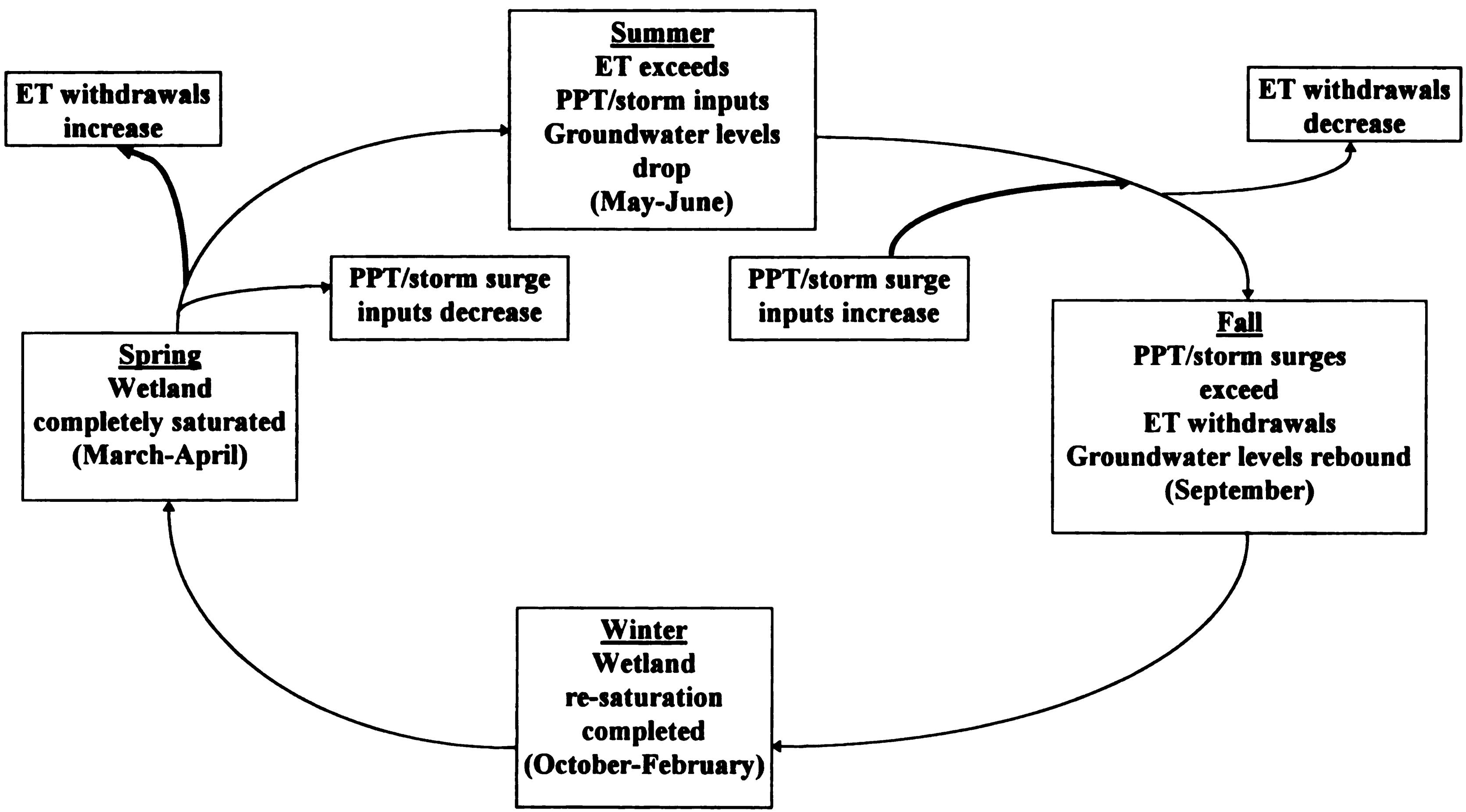

ET withdrawals increase
Summer
ET exceeds
PPT/storm inputs
Groundwater levels
drop
(May-June)
ET withdrawals decrease
PPT/storm surge inputs decrease
PPT/storm surge inputs increase
Spring
Wetland
completely saturated
(March-April)
Fall
PPT/storm surges
exceed
ET withdrawals
Groundwater levels rebound
(September)
Winter
Wetland
re-saturation
completed
(October-February)

Figure 2-20.

Chapter 3 - The structure and composition of Saginaw Bay coastal wet meadow vegetation

Introduction

Saginaw Bay coastal wet meadows are the herbaceous, graminoid-dominated vegetation zone occurring between forested beach ridges and Lake Huron cattail/bulrush marshes and bounded by the yearly mean and yearly maximum elevation of Lake Huron (see Chapters 1 and 2). This vegetation association shelters threatened and endangered plants, including *Asclepias hirtella* (Pennell) Woodson, *Rumex maritima* L., *Cacalia plantaginea* (Raf.) Shinners, and *Astragalus neglectus* (T.&G.) Sheldon (Albert et al., 1988, 1989), and supports the greatest plant diversity of any Great Lakes wetland type (Keddy, 1990). Yet few ecological studies of these wet meadow plant communities have been undertaken.

The pre-1900 studies of Saginaw Bay's natural history were simple catalogues of the region's geology and biota (see Ruthven, 1911). Between 1900-1920, the Michigan Geological and Biological Survey organized the first ecological studies of Saginaw Bay coastal wetland vegetation (Davis, 1900; Davis, 1908; Michigan Geological and Biological Survey, 1911; Dodge, 1920). Interest in the plant ecology of the Saginaw Bay coastal zone flagged after 1920, and did not increase again until the 1970's. Since then, numerous Saginaw Bay and Great Lakes coastal wetland studies have been produced (Hayes, 1964; Stuckey, 1975; Tilton et al., 1978; Jaworski and Raphael, 1979; Jaworski et al., 1979; Herdendorf et al., 1981; Albert et al., 1988, 1989; Prince and Burton, 1995; Minc, 1997; Minc and Albert, 1998). However, these studies have generally centered on wet meadow species composition or extent, rather than on the ecological factors controlling vegetation structure and composition.

Abiotic factors influencing wet meadow structure

Abiotic factors guide the development of Great Lakes coastal wet meadow vegetation. The most important of these factors is hydrology (Keough et al., 1999; Wilcox and Whillans, 1999). Periodic lake level fluctuations control vegetation zonation in Great Lakes marshes (Burton, 1985; Kelley et al., 1985; Keddy and Reznicek, 1986; Keough, 1990; Batterson et al., 1991, Keough et al., 1999). Other hydrologic factors, such as precipitation, groundwater inflows, and evapotranspiration, also play an important role in coastal wet meadow hydrology (see Chapter 2).

Geomorphic setting impacts the vegetation structure and composition of coastal wet meadows (Minc, 1997; Minc and Albert, 1998; Keough et al., 1999; and see Chapter 1). Site geomorphology influences the depth, duration, and frequency of inundation, intensity of wave and current action, degree of ice scour, and rate of erosion and sedimentation at that site. These factors, in turn, impact the distribution patterns and persistence of plant species at a site (Keough et al., 1999).

Soil type, sediment quantity or quality, and organic matter content influence the distribution of Great Lakes coastal wetland vegetation (Tilton et al., 1978; Wilcox, 1995). Wetland plant community composition is determined in part by substrate type, with many plant species showing a preference for either sandy, organic, or lacustrine clay soils (Tilton et al., 1978; Mitsch and Gosselink, 1993; Wilcox, 1995). Substrate preferences reflect, among other things, a species' particular nutrient requirements and its ability to compete with other species for available soil resources. These abilities and requirements function as filters or sieves (*sensu* van der Valk, 1981) to sort the plant community into recognizable vegetation associations.

Vegetation attributes

The species composition of Saginaw Bay coastal wetland vegetation is well documented (Davis, 1900; Davis, 1908; Michigan Geological and Biological Survey, 1911; Dodge, 1920; Herdendorf et al., 1981; Albert et al., 1988, 1989; Prince and Burton, 1995; see also Table 3-4). However, species lists reveal only one attribute of a vegetation association. Information about community structure, and the species richness, evenness, diversity and dominance relationships among plant community members are also needed to fully understand the ecology of wet meadow vegetation.

Vertical vegetation stratification, the vertical distribution of plant species above the ground surface, characterizes the canopy architecture of a vegetation assemblage. Detailed study of wet meadow canopy architecture may increase our understanding of the factors controlling species distribution within the wet meadow zone, and aid in identifying the conditions defining wet meadow boundaries.

Goals and Objectives

The goals of this chapter were to describe above-ground wet meadow vegetation structure and composition, and to examine the manner in which hydrology, soils, and plants species composition act and interact to determine vegetation structure and composition. The specific objectives were:

1. to describe horizontal and vertical vegetation structure;
2. to characterize plant species composition;
3. to describe wet meadow soil attributes, including texture, organic matter content, and major mineral components; and
4. to determine how hydrology, soils, and plant species composition act and interact to influence vegetation structure, composition, and distribution within the wet meadow.

Sites

Vegetation sampling was performed in 1996 at the two hydrologic study sites (see Chapter 2) to determine how hydrology impacted species distribution at those sites. During 1997, vegetation and soil sampling were performed at these two sites and 23 additional sites distributed throughout the Saginaw Bay coastal zone to define the vegetation structure and composition of the region's coastal wet meadows. The 1997 sampling encompassed all of the intact coastal wet meadows in the region (see Figure 1-2). A description and list of study sites can be found in Chapter 1 and Appendix A2.

Methods

Elevation determination

1996 sampling

Elevation surveys were undertaken at the two hydrologic study sites after all hydrologic sampling devices were installed (see Chapter 2 for details). These data were used to construct site contour maps, from which surface and groundwater elevations throughout the two sites could be estimated. Locating sample plots on the maps allowed estimation of sample plot surface and groundwater elevation at each sample plot.

1997 sampling

Most sites were inundated during the 1997 sampling period, so water depth in sample plots was used to determine plot elevation. Water depth at a specific date and time was recorded (±0.1cm) at each sample plot. Saginaw Bay water levels, measured at six minute intervals and referenced to International Great Lakes Datum (IGLD 1985), were obtained from the National Ocean Service of the National Oceanographic and Atmospheric Administration (NOS-NOAA, 1999). Plot elevation in meters above mean sea level (m AMSL) was determined by matching plot and NOAA water level data by date and time.

Data collection

1996 sampling

In 1996, vegetation data were collected in 0.25m^2 (50cm by 50cm) sample plots at the two hydrologic study sites. Sampling was undertaken during July and August, the period of peak above-ground biomass in the region (Barko et al., 1977; Kelley, 1985; and see Chapter 4). Vegetation sampling was stratified across the elevation gradient at each site to ensure the adequacy of sampling at all elevations within each site. Species frequency of occurrence, stem density, and above-ground biomass was determined for each species in each plot.

1997 sampling

Vegetation data were collected in twelve 0.25m^2 (50cm by 50cm) sample plots at each site during July-August 1997. The vertical vegetation stratification, species identity, and the above-ground species and plot biomass, species and plot stem density, and species frequency of occurrence were determined for each plot. Litter depth, peat depth, hummock heights in any plot containing hummocks, and a field estimation of surface substrate texture were also determined for each plot. The texture, organic matter content, and major mineral components of the top mineral soil layer were determined by laboratory analysis of soil aliquots collected at each site.

Vegetation sampling

1996

Species stem density, frequency, and biomass values were determined using the harvest method. All living and dead standing plant material in each plot was clipped at the substrate surface and sorted into living (green) and dead (brown) material. The living material was sorted by species and counted to determine species stem densities. No attempt was made to identify or sort dead material to species. Once stem counts were completed, the living material from each plot was bagged by species and the dead material was bagged *en masse*. Above-ground biomass by species was determined by weighing the contents of each bag after oven-drying 72h at 60°C (see Chapter 4). Individual species stem-density and biomass values were summed to determine plot stem-density and biomass.

Vegetation sampling was stratified by elevation at both hydrologic study sites. Eight strata, or zones, were established at the reference site, 13 at the disturbed site. Zones were laid out parallel to the local Saginaw Bay shoreline, which was perpendicular to the site elevation gradient. Each zone was 20m in length (parallel to the elevation gradient), and sufficiently wide to span the groundwater well field installed at the site. The first zone began at the wet meadow-marsh boundary at the reference site, and at the ditch and dike forming the north border of the disturbed site, and extended 20m up the elevation gradient. Additional zones were added until sampling zones spanned the well field at each site.

Sample plots were distributed randomly within each sampling zone. Vegetation sampling continued in each zone until a species-area curve for that zone reached its apparent asymptote.

1997

Vertical vegetation stratification was measured at four points within each plot using a welding rod marked at centimeter intervals. The rod was positioned perpendicular to the ground surface in the plot. Then, for all live plant contacts with the rod, the species identity, the height above the substrate, and whether the contact was a leaf, stem, or inflorescence were recorded. These data revealed the vegetation canopy architecture, and provided an estimate of wet meadow leaf area index (LAI), the single surface leaf surface area per unit ground area (m^2/m^2).

Stem density, frequency, and biomass values were determined using the harvest method. The techniques and procedures were unchanged from 1996 (see above).

Vegetation sampling was stratified by elevation at each site, four plots each at three different elevations, to examine how differences in depth and duration of inundation impacted vegetation composition. Water depth, the proxy for plot elevation, was stratified into eight depth classes to facilitate sampling: -10-0.1cm (-10-0.1cm being the only sub-surface water level class), 0.0-9.9cm, +10-19.9cm, +20-29.9cm, +30-39.3cm, +40-49.9cm, +50-59.9cm, and +60-69.9cm.

The three water-depth classes sampled at a site were determined by site geomorphology and statistical requirements. Shoreline geomorphology varied among sites. The wet meadow zone was narrow and steeply sloped at some sites, broad and very gradually sloping at other sites. There were more depth classes to choose from in the latter group of sites. Also, an attempt was made to collect enough data in each depth class to permit valid statistical analysis of the data set. The depth classes sampled at a site depended on which classes were available at that site, which classes were representative of that site, and which of the available depth classes were least represented in previous vegetation sampling.

Line-intercept transect sampling (Brower and Zar, 1977) was performed at all sites in August-September 1997 to verify that plot sampling fairly represented site species assemblages. Transects were established from upland to marsh across the wet meadow, and the identity and tally of plant species intersecting the plane of the transect was recorded every 0.5m.

Line-intercept sampling continued at a site until a species-distance curve indicated that no new species were being encountered along the transect. A species-distance curve differs from a species-area curve only in that cumulative distance rather than cumulative area is plotted on the x-axis.

Voucher botanical specimens were deposited in the Beal-Darlington Herbarium at Michigan State University. Botanical nomenclature follows Voss (1972, 1985, 1996) for vascular plants, and Gleason and Cronquist (1991) for vascular cryptogams.

Soil sampling

Soil samples were collected in 1997 from each of the 25 study sites and used to determine the mineral soil texture, pH, the Phosphorus (P), Potassium (K), Calcium (Ca), Magnesium (Mg), and nitrate-N (NO_3-N) plus Ammonium-N (NH_4-N) nitrogen levels, and percent organic matter content (%OM) of wet meadow substrates. Three to five replicate soil samples were extracted from the mineral soil surface at each site, thoroughly mixed, and an aliquot of this mixture was collected for analysis. When visually apparent differences in mineral soil color or texture were noted within a site, a soil aliquot was collected from each soil type. In all, 33 aliquots were collected from the 25 sites and delivered to the Michigan State University Soil and Plant Nutrient Laboratory for analysis.

To determine soil bulk density, a 90ml undisturbed mineral soil sample was collected at each site using a slide-hammer soil core sampler. Samples were dried 72h at $80^{O}C$ and weighed. Sample bulk density (g/ml) was calculated on a dry weight per unit volume basis.

Statistical procedures

1996 sampling

The relative stem density, relative biomass, and relative frequency data were summed to generate importance values for each species in each plot (Curtis and McIntosh, 1951; Brower and Zar, 1977). Several variables exhibited non-normal or heteroscedastic distributions. $Log_{10}(X+1)$ transformation of species biomass data, importance values, and species richness data resolved most problems with the distribution of these variables. Kruskal-Wallace ANOVA was used to test hypotheses involving stem density, which could not be transformed to meet parametric assumptions.

Mean mid-summer groundwater depths were determined by averaging groundwater measurements at each monitoring well for the period 7/1/96 through 9/4/96. This period reflected the length of time that groundwater levels remained at their stable mid-summer levels (see Chapter 2). Mid-summer groundwater levels were the deepest observed during the growing season. At other times of the year, groundwater levels were either at or near the wetland surface, or rapidly fluctuating between near-surface and mid-summer levels.

Groundwater contour maps were used to estimate mean groundwater depths of the sample plots. Groundwater contours were linear and perpendicular to the elevation gradient at the reference site, and varied at most by approximately 5cm within any vegetation sampling zone, so groundwater depths were blocked by zone for analysis at the reference site. At the disturbed site, surface and groundwater contours were complex, so groundwater levels were blocked in 10cm intervals for analysis.

1997 sampling

The relative stem density, relative biomass, and relative frequency were summed to generate importance values for each species in each plot. Shannon-Wiener diversity was calculated for each site (Brower and Zar, 1977). Mean species richness/m^2 was estimated for each site by performing five replicate cumulative species counts of four randomly-selected $0.25m^2$ plots from each site.

Several variables exhibited non-normal or heteroscedastic distributions, but mathematical transformation remedied most data distribution problems. $Log_{10}(X+1)$ transformation of species biomass data, importance values, and species richness data, and square-root transformation of peat depth, litter depth, leaf, stem, and inflorescence height, and mean LAI data resolved problems with the distribution of these variables.

Pearson product-moment correlation matrices were constructed to examine associations among plant species and among environmental factors. Correlation and Principal Components Analysis (PCA) were used to examine associations among plant species and environmental factors.

Analysis of variance (ANOVA) was used to test hypotheses involving normally distributed or transformed variables. Similarly, correlation and PCA were performed on normally distributed or transformed variables. Kruskal-Wallace ANOVA was used to test hypotheses involving data which could not be transformed to meet parametric assumptions.

Results

Water level, vegetation, and soil at the reference and disturbed hydrologic study sites

At the reference site, mean mid-summer water levels ranged between +0.34m (34cm standing water) and -0.85m (85cm below ground) among plots. Total plot stem densities were highest when mean water levels ranged between approximately 10cm above and 10cm below the wetland surface (Figure 3- 1). Total plot stem density in these plots was significantly greater than that of plots with either greater mean standing water depths or greater groundwater depths (ANOVA, $F_{(0.05, 5, 151)} = 22.015$, $P<0.001$). Total plot biomass was significantly greater in plots with the deepest mean standing water levels (+34cm and +24cm) compared to plots with shallower standing water or deeper groundwater depths (ANOVA, $F_{(0.05, 5, 151)} = 6.492$, $P<0.001$). The significantly greater biomass of the emergent marsh species *Typha angustifolia* in inundated plots (ANOVA, $F_{(0.05, 5, 151)} = 19.125$, $P<0.001$) accounted for this difference.

Plot species richness was greatest in the plots with the deepest mean water depths. This was due to the presence of marsh species (e.g., *Typha angustifolia, Sagittaria latifolia, Sparganium eurycarpum*) in addition to wet meadow species in these plots. However, in plots lacking marsh species, wet meadow species richness increased as standing water levels declined until mean mid-summer plot water levels were below ground, after which plot species richness did not change significantly with increasing groundwater depth (ANOVA, $F_{(0.05, 5, 151)} = 14.682$, $P<0.001$).

There was a significant association between mean mid-summer water levels and the National Wetlands Inventory (NWI) classification of the species found in plots. As surface water depths and groundwater levels declined, fewer obligate (OBL) and facultative wetland (FACW) species, and more facultative (FAC) and facultative upland (FACU) species occurred in plots (Somer's D, d = 0.163, N = 812, asymptotic SEE = 0.020; range of d = +1.0 to -1.0). FACU species only occurred in plots with mean mid-summer water levels below the ground surface.

Fourteen species (*Calamagrostis canadensis, Carex sartwellii, Typha angustifolia, Eleocharis smallii, Carex bebbii, Campanula aparinoides, Polygonum amphibium, Calystegia sepium, Cladium mariscoides, Lathyrus palustris, Juncus balticus, Carex comosa, Leersia oryzoides,* and *Carex lacustris*; hereafter "major species") exhibited IV ≥1% of the total IV of all species in all plots at the reference site. Each major species exhibited a preference for certain water levels within the reference site (Figures 3-2 through 3-5). Four species (*C. comosa, E. smallii, Leerzia oryzoides,* and *T.*

angustifolia) exhibited greater IV in plots where mean mid-summer water levels were above ground, five species (*C. canadensis, C. sepium, C. aparinoides, C. bebii,* and *L. palustris*) exhibited greater IV in plots where water levels were below ground, and two species (*C. lacustris,* and *P. amphibium*) exhibited no water level preference. Three of the fourteen major species (*C. sartwellii, C. mariscoides,* and *J. balticus*) had their greatest IV in plots with mean water levels ranging between 10cm above and 10cm below the wetland surface.

At the disturbed site, mean mid-summer water levels ranged between -0.04m (4cm below ground) and -0.65m among plots. There was a significant difference in plot stem density (ANOVA, $F_{(0.05, 20, 166)} = 2.037$, $P = 0.008$) and plot biomass (ANOVA, $F_{(0.05, 20, 166)} = 1.918$, $P = 0.014$) across the site water level gradient (Figure 3-1). The increased presence of certain large wetland species (e.g., *Carex lacustris* and *Phalaris arundinacea*) at shallow groundwater depths (<-20cm) and certain other large species (e.g., *Aster dumosus* and *Phalaris arundinacea*) in deeper groundwater plots (>-50cm) accounted for the significantly higher biomass in these plots. Significantly greater stem densities occurred in plots with intermediate mean mid-summer water levels (-30cm to -50cm). The maximum stem densities of the major species *Calamagrostis canadensis, Carex stricta, Carex sartwellii, Calystegia sepium, Potentilla anserina,* and *Spartina pectinata* occurred in these plots.

Species richness was significantly greater (ANOVA, $F_{(0.05, 20, 166)} = 2.505$, $P = 0.001$) in intermediate depth groundwater plots (-30cm to -50cm) compared to the shallowest groundwater plots (0cm to -10cm). Species richness did not significantly differ between plots with intermediate groundwater levels and deeper groundwater levels, or between plots with the shallowest and the deepest groundwater levels.

There was a significant association between mean mid-summer groundwater levels and the NWI classification of the species observed in disturbed site plots. As at the reference site, fewer OBL and FACW species, and more FAC and FACU species, occurred as mean groundwater depth increased (Somer's D, d = 0.135, N = 1154, asymptotic SEE = 0.022). However, unlike at the reference site, FAC and FACU species were found in small quantities at all groundwater levels at the disturbed site.

Fifteen species (*Phalaris arundinacea, Calamagrostis canadensis, Carex stricta, Aster dumosus, Calystegia sepium, Carex bebbii, Spartina pectinata, Carex sartwellii, Polygonum amphibium, Carex lacustris, Anemone canadensis, Lathryus palustris, Galium obtusum, Potentilla anserina,* and *Lycopus americanus*) each contributed ≥1% of total disturbed site vegetation IV. Most of these major species exhibited a water level preference within the disturbed site (Figures 3-6 through 3-9). *C. bebbii, C. lacustris, C. sartwellii, L. americanus,* and *P. amphibium* exhibited greater IV in plots with the shallowest mean mid-summer groundwater levels, whereas *A. canadensis, A. dumosus, C. sepium,* and *G. obtusum* exhibited greater IV where groundwater was deepest. Four species (*C. canadensis, C. stricta, P. anserina,* and *Spartina pectinata*) exhibited greater IV at intermediate (-30cm to -50cm) groundwater depths, whereas the IV of *L. palustris* did not vary with groundwater levels at this site. *Phalaris arundinacea* had lower IV at intermediate groundwater levels, and higher IV in plots with either shallow or deep groundwater levels.

There were differences in soil structure and composition between the sites. Soil calcium, magnesium, percent organic matter, cation exchange capacity, ammonium nitrogen, phosphorus, and clay content were all significantly greater at the disturbed site compared to the reference site. Soil pH, potassium, nitrate nitrogen, sand, silt, and bulk density did not vary significantly between sites (Table 3-1).

There were two visually distinct surface soil types at the reference site. For the most part, reference site surface soils were black loamy sand, but a tan fine sand soil occurred where mean water levels ranged between +10cm and -10cm depth. Soil analysis indicated that this sand soil had lower clay, silt, potassium, and calcium content, and greater sand content and bulk density, than the adjacent loamy sands. There were no visually distinct soil types at the disturbed site. All soil samples collected at the disturbed site were black sandy loam soils, and these soils were uniformly underlain by glacial till at approximately 45cm depth. Soil analysis indicated that the soil structure and composition at the disturbed site was relatively homogenous, as might be expected of an historically tilled soil.

Physical attributes of Saginaw Bay coastal wet meadows

Saginaw Bay coastal wet meadow vegetation occurred at elevations ranging between 176.7-177.3m AMSL (mean $\pm$1SEM = 177.0$\pm$0.125m AMSL) during the study period. The wet meadow vegetation zone extended from the annual mean high water mark (176.67m AMSL) upward approximately 0.6m in elevation to a point approximately 0.1m below the maximum Saginaw Bay high water mark.

The depth and duration of inundation of any part of the wet meadow varied from year to year with the inter-annual variation in Saginaw Bay water levels, and seasonally with annual water level variations (Figure 3-10). The entire wet meadow zone was above the mean elevation of Saginaw Bay throughout the 1995 growing season, but most of the zone was inundated for some portion of the 1997 growing season. Between 1988 and 1996, approximately 80% of the wet meadow zone was above Saginaw Bay's mean monthly elevation for the entire growing season. However, this did not mean that wet meadow substrates were dry.

Portions of the wet meadow located above the bay's nominal surface elevation were often inundated by seiches and storm surges (Figure 3-11; and see Chapter 2). The monthly maximum Saginaw Bay water elevation averaged 36cm higher than the monthly mean elevation during the 1997 growing season, and ranged as high as +67cm in October 1997 (NOS-NOAA, 1999). Seiche- or storm surge-related water levels increases were great enough to inundate the entire wet meadow zone on 42 different days during the 1996 growing season, and great enough to do so at least monthly in 1997 (see Chapter 2).

The mean(±1SEM) width of the wet meadow zone was 123.9(15.8)m (Table 3-2). The zone ranged from 11-545m wide, with half the values falling between 65-147m. The wet meadows sloped very gradually toward the bay (median slope = 0.27%), with half the values ranging between 0.10-0.39%. Three sites with shallower-than-average slopes (0.092-0.099%) were wider than the median site width, and six sites with steeper-than-average slopes (0.70-2.25%) were narrower than the median site width.

Wet meadow soils generally consisted of a 1-16cm peat or muck "O" horizon overlying a sandy mineral "A" horizon. However, several sites lacked "O" horizons, instead having only black sandy loam or loamy sand "A" horizons. Mechanical soil analysis indicated that 24 of 25 wet meadow "A" horizons were either sandy loam, loamy sand, or sand soils. The mineral soil pH ranged from 6.1 to 8.5, with 75% of the values >7.0 (Appendix C1).

Field texture determinations indicated that 49% of plot surface substrates were peat or muck, 20% were fine sand, and 11% were gravelly sand. Altogether, over 90% of plot surface substrates were organic soils or sandy mineral substrates. Marl, clay, silt or gravel substrates were only very rarely encountered during sampling.

Sub-surface soil composition was not systematically examined in this study, but bore holes excavated at three study sites (Sites 1, 2, and 3; see Figure 1-2) provided some information about sub-surface soil stratigraphy to a depth of 1m. At Site 1, sandy loam gave way to glacial till below 45cm depth, with a 10cm band of sand and gravel commonly being encountered at approximately 90cm depth. Substrates at Sites 2 and 3 were 15-25cm sandy loam or loamy sand layer over medium to fine sand to 1m depth. Gray clay fines commonly lined the soil pores in the sub-surface substrates. While no clay layers were encountered in these bore holes, lacustrine or till clays lined the bottom of canals and Saginaw Bay adjacent to the sites, suggesting that these sands rested on clay substrates.

Channels, ditches, and shore line erosion permitted examination of sub-surface mineral substrates in several other wet meadows. Glacial till or lacustrine clay substrates occurred below the mineral surface layer at these sites.

The peat thickness ranged between 0-16cm among sites, with mean($\pm$1SEM) site values ranging between 0.4(0.1)-11.0(0.8)cm (Table 3-2). Peat depth exhibited a strong negative correlation with wet meadow elevation (r = -0.644, n = 2384; Table 3-3a), the thickest peat occurring at low elevation, thinner peat at higher elevation.

Litter depths, determined at 18 study sites, varied between 1-45cm, with mean(±1SEM) site values ranging between 8.7(2.0)-30.5(7.0)cm. Litter depths were negatively correlated with soil texture (r = -0.196, n = 2384) and elevation (r = -0.159, n = 2384). Deeper litter was associated with finer-textured soils and lower elevation, shallower litter depths with coarser soils and higher elevation.

Carex stricta Lam. hummocks occurred in 12 study sites. Where present, hummocks ranged between 11-62cm height, and mean(±1SEM) site hummock heights varied between 18(0.0)-38.0(6.4)cm. Hummock height exhibited a significant negative correlation with wet meadow elevation (r = -0.258, n = 382; Table 3-3b). Taller hummocks were associated with lower elevation, short hummocks with higher elevation.

Hummocks served as growth platforms for other vegetation. Several forbs (*Galium obtusum* Bigelow, *Campanula aparinoides* Pursh, and *Impatiens capensis* Meerb., among others) were observed growing on the sides and tops of hummocks, above the level of standing water, in flooded study sites.

Ants also colonized hummocks, or constructed earthen anthills, at some sites. Wet meadow ants apparently utilize subterranean galleries during low water periods, and live in the upper, un-flooded portion of these structures when wet meadows are flooded (Bruskewitz, 1981).

Vegetation attributes

A total of 93 plant species, representing 34 families and 63 genera, were encountered during vegetation sampling (Table 3-4). The best-represented families were Cyperaceae (16 species), Poaceae (10), Asteraceae (9), Lamiaceae (7), and Rosaceae (6). The best-represented genus was *Carex*, with nine species. Fifteen species (three grasses, five sedges, one cattail, and six forbs) each contributed ≥1% of total vegetation importance value (Table 3-5). Thirteen of the 15 major species were native perennial plants (Reed, 1988), and 12 of the 15 were rhizomatous species (Gleason and Cronquist, 1991). Some (e.g., *Phragmites australis* (Cav.) Steudel, and several sedges) rarely produce viable seeds (Ibid., 1991). Seven of the major species were emergent wetland species (Reed, 1988), adapted to growing in standing water (Niering, 1985). Eleven of the major species were NWI Region 3 obligate wetland species (OBL), three were FACW+ species, and one was a FAC species (Reed, 1988).

The 15 major species comprised 84.0% of the total species importance value. Conversely, 27 species occurred in only one of the 300 sample plots. (See Appendix C2 for species stem density data). Four species dominated the vegetation. The grass *Calamagrostis canadensis* (Michaux) Beauv. and three sedges, *Carex aquatilis* Wahl., *Carex sartwellii* Dewey, and *Carex stricta*, contributed 60.1% of total wet meadow IV. *C. canadensis* alone contributed 31.1%, and two species, *C. canadensis* and *C. aquatilis*, by themselves contributed 45.7% of total IV.

Mean (±1SEM) wet meadow species richness equaled 15.4(0.5)spp./m^2 and ranged between 9.0-27.2spp./m^2 among study sites (Table 3-6). The mean value fell within the range of values for similar vegetation assemblages (Table 3-7a). Similarly, mean wet meadow leaf-area index (LAI) was 5.0(0.1)m^2/m^2, ranged between 3.1-7.7m^2/m^2 among sites, and fell within the range of values published for wet meadows (Table 3-7b). Shannon-Wiener diversity averaged 1.53(0.03), ranging between 1.31-1.71, mean Evenness was 0.77, ranging between 0.59-0.86, and mean Dominance was 0.23, ranging between 0.14-0.41.

Pearson product-moment correlation of the major species IV revealed significant associations among the major species (Table 3-8). *Calamagrostis canadensis* exhibited significant negative association with *Carex stricta, Carex sartwellii,* and two physically small species (*Cladium mariscoides* (Muhl.) Torrey, and *Galium obtusum*). *Campanula aparinoides* was negatively associated with *Phalaris arundinacea*, *Polygonum amphibium* with *Galium obtusum* and *Stachys tenuifolia*, and *Carex lacustris* with *Carex sartwellii* and *Lythrum salicaria*. *Galium obtusum* was positively associated with *Carex stricta* and *Stachys tenuifolia*, and *Carex sartwellii* with *Cladium mariscoides*.

Vertical vegetation stratification

Wet meadow vegetation was composed of grasses, sedges, and forbs 1.2-1.5m tall, though in some places cattails and the taller grasses exceeded 2m in height. The median vegetation height was 62cm (mean±1SEM = 61.49±0.001cm), attaining a maximum of 223cm. Half the stem, leaf, and inflorescence contacts occurred between 43cm-84cm above the substrate surface. Shrubs, trees, and woody seedlings were rarely encountered, and when they were, they occurred near the wetland-upland boundary, or at topographic high points within the wet meadow. Where shrubs or trees did become established, the herbaceous vegetation exhibited a reduction in height, stem density, and species richness.

The vegetation canopy exhibited a three layer architecture, based on the median and maximum heights of species comprising each layer. These layers were canopy emergent species, canopy species, and understory species. A fourth group, clingers/climbers, filled a role similar to that of lianas in a forested ecosystem (Table 3-9).

Canopy emergent species exhibited median heights >90cm and maximum heights >2m. They extended above the general level of the wet meadow vegetation canopy. Only two species, *Typha angustifolia* L. and *Phragmites australis*, were canopy emergent species. *T. angustifolia* occurred in the lower, wetter portions of the wet meadow, whereas *P. australis* exhibited no significant elevation preference. These species were usually the dominant species in the plots in which they occurred. Yet, despite the apparent ability to dominate wet meadow vegetation, they only occurred in scattered patches in the wet meadow, except at the wet meadow-marsh boundary, where *T. angustifolia* became the dominant species.

Canopy species exhibited median heights of 40-90cm, and maximum heights of up to 2m. The dominant wet meadow grasses and sedges, and a number of the taller forbs, were canopy species. The majority of plant stem and leaf contacts occurred in this height class (Appendix C3).

Understory species were those with median heights <40cm, and, in most cases, maximum heights <50cm. Components of this group included herb and shrub seedlings, and low-stature grasses, sedges and forbs.

Three species (*Calystegia sepium* (L.) R. Br., *Campanula aparinoides*, and *Galium obtusum*) were Clingers/climbers. The stems of Clingers/climbers were too weak to support their own weight. These species wrapped themselves around the stems of other plants (*C. sepium*), or used downward-pointing hairs or bristles (*C. aparinoides* and *G. obtusum*) to cling to and climb vine-like up the stems of taller plants into the canopy layer.

Biotic/abiotic interactions

There was no significant difference in plot biomass (ANOVA, $F_{(0.05,7,292)} = 1.510$, $P = 0.163$; and see Chapter 4), or plot stem density (Kruskal-Wallace ANOVA, KW = 9.231, df = 7, P = 0.236) across the wet meadow elevation gradient. However, species richness was significantly lower in plots located below 177.0m AMSL compared to plots located above that elevation (ANOVA, $F_{(0.05,7,292)} = 9.472$, $P<0.001$). There were fewer species present in low elevation plots, but those tended to be the taller wetland emergent species with higher per-stem biomass (see Chapter 4). Plot LAI did not differ across the elevation gradient (ANOVA, $F_{(0.05,7,292)} = 1.104$, $P = 0.361$), but the height at which leaves occurred in the canopy did increase significantly as elevation decreased (ANOVA, $F_{(0.05,7,6699)} = 148.59$, $P<0.001$).

Pearson product-moment correlation of plot elevation, peat depth, litter depth, soil texture, and the major species IV revealed significant associations between species IV and abiotic factors (Table 3-10). The larger, taller wetland emergent species (e.g., *C. lacustris, C. aquatilis*) were associated with thicker peat and greater litter depths, and the smaller, shorter species (e.g., *C. stricta, G. obtusum, C. aparinoides*) were associated with thinner peat and litter depths.

All 15 major species also exhibited a preference for certain elevations within the wet meadow zone (Tables 3-11 and 3-12, and Figures 3-12 through 3-15). The smaller, shorter plants (e.g., *C. stricta, C. sepium, C. aparinoides, S. tenuifolia*) exhibited significant positive correlation with higher wet meadow elevations (see Table 3-10), whereas the taller, larger wetland emergent species (e.g., *C. aquatilis, C. lacustris*) were positively correlated with lower elevations. Some species were positively associated with sandy substrates (*C. aparinoides, C. mariscoides, G. obtusum*), and some (*C. lacustris, C. sepium, P. arundinacea*, and *P. amphibium*) exhibited a significant positive correlation with muck substrates.

Galium obtusum and *Lythrum salicaria* were significantly negatively correlated with hummock height (Table 3-13). Hummocks occurred in only 17% (51 of 300) sample plots. The lack of significant correlation with other species may have been an artifact of sample size.

PCA illustrated the nature of the relationship among the species and abiotic factors (Figure 3-16). The first principal component axis (PC1) was the best-fit line describing the association among the abiotic factors. The relatively small angular offset of the elevation interval, soil texture, peat depth, litter depth, and hummock height factors from PC1, and the relatively long distance that these factors plotted from the graph origin, indicated the strength of the association between these factors and PC1. Species located near the negative end of PC1 (e.g., *C. stricta, G. obtusum*) were associated with higher elevation, thinner peat and litter mats, shorter hummocks, and coarse-textured substrates. Those located near the positive end of PC1 (e.g., *C. aquatilis, C. lacustris*) were associated with lower elevation, thicker peat and litter mats, taller hummocks, and fine-textured substrates.

The greater the distance and angular offset of a species from PC1, the weaker the linkage between that species and the suite of abiotic factors comprising PC1. *C. sepium, C. sartwellii,* and *C. mariscoides* plotted away from PC1 because they did not fit the pattern of association dictating the orientation of PC1. *C. sartwellii* and *C. mariscoides* were associated with lower elevations and thicker peat, but also with coarse-textured substrates and low hummock heights. Similarly, *C. sepium* was associated with higher elevation plots and thinner peat mats, but fine-textured soils. In each case, the species plotted at a nearly a right angle to PC1.

PC1 accounted for 21% of the variance explained, whereas PC2 accounted for 12% of the variance explained in this PCA. Together, these two PCs accounted for 33% of the variance among the variables explained by the analysis.

Discussion

Relationship of vegetation, water level, and soil at the reference and disturbed hydrologic study sites

At the reference site, vegetation stem density and species richness peaked in plots with mean mid-summer water level between +10cm and -10cm depth. Plots in this range experienced more frequent inundation/exposure cycles than higher or lower elevation plots at the reference site. Frequent water level variation and moderate disturbance regimes result in the greatest plant diversity in Great Lakes wetlands (Keough et al., 1999) and these factors exert their greatest influence on vegetation in upper elevation Great Lakes wetlands (Ibid., 1999), which includes the wet meadow zone.

At the reference site, plot biomass was minimal and plot stem density was maximal in plots with mean mid-summer water level between +10cm and -10cm. Large stem densities of small, low biomass/stem plant species (e.g., *Eleocharis smallii, Cladium mariscoides,* and *Juncus balticus*; see Chapter 4 for biomass data) occupied plots in this water level range. By contrast, large emergent marsh species (e.g., *Typha angustifolia, Sparganium eurycarpum*) increased plot biomass and reduced stem density in the deepest standing water plots. A similar pattern was observed in the disturbed site, even though there was little standing water on the site. The smaller species had their greatest stem densities in plots with intermediate groundwater levels. The tall species *Carex lacustris* and *Phalaris arundinacea* dominated the plots with the shallowest groundwater, and the similarly large species *Aster dumosus* and *Phalaris arundinacea* did the same in the deepest groundwater plots. The mechanism controlling this species distribution was unclear, but in addition to water level preferences, may have included light competition (Keddy, 1989; Leps, 1999), space competition (Auclair et al., 1973), litter deposition and smothering (Wilcox et al., 1985), and anthropogenic disturbance (see below).

Standing water reduced wet meadow species richness. In plots not being invaded by marsh plants, species richness increased significantly as standing water levels dropped at the reference site. However, once the mean mid-summer water level was below ground, species richness did not change significantly. At the disturbed site, where all mean water levels were below ground, species richness increased significantly only between the shallowest groundwater plots (4cm below ground) and intermediate level plots. There was no significant difference in species richness within either site once plot mean mid-summer groundwater levels dropped below -10cm.

Changes in species NWI classification were significantly correlated with increasing groundwater depths at both sites. The occurrence of OBL species decreased as groundwater depths increased, and the occurrence of FACU species increased with groundwater depth. However, over 20% of OBL species occurrences at both sites were recorded in plots where mean mid-summer groundwater depths exceeded 50cm. The major wet meadow species were tolerant of summer draw-down conditions, and appear to be dependent on occasional draw-downs in order to maintain local vegetation dominance.

At the reference site, FACU species did not occur where mean mid-summer water levels were above the substrate surface. However, FACU species were recorded at almost all water levels at the disturbed site. The dike separating the disturbed site from Saginaw Bay prevented storm surge and seiche inundation of the disturbed site, allowing it to dry down more thoroughly than the reference site during the growing season (see Chapter 2). The broader distribution of FACU species at the disturbed site may have been facilitated by the elimination of site inundation by Saginaw Bay.

The elimination of occasional inundation during the growing season may also have contributed to the increased presence of shrubs and trees at the disturbed site. Shrubs and trees (principally *Cornus amomum, Cornus foemina, Cornus stolonifera, Fraxinus pennsylvanica, Populus deltoides,* and *Salix petiolaris*) occurred within 1m of 40% (75 of

187) sample plots at the disturbed site. Only 1.3% (2 of 157) sample plots at the reference site were within 1m of shrubs, and those shrubs were seedlings less than 20cm tall. Davis (1900) had observed that Saginaw Bay wet meadow soils were alternately too wet for tree growth and too dry for tree seedling establishment during the growing season. He noted that the lower limit of tree growth was the upper limit of annual flooding, and concluded that flooding was the factor limiting tree invasion in Saginaw Bay wetlands. Davis also reported considerable shrub and tree growth in formerly treeless wet meadows within five years of the beginning of agricultural ditching in 1897 (Ibid., 1900). The elimination of periodic inundation at the disturbed site permitted shrub-scrub and forest succession to begin at the site, providing further evidence that the natural Saginaw Bay hydroperiod, with its occasional storm surges and high water years, was important in preventing succession from occurring in these wet meadows.

Historic land use patterns altered soil structure and composition at the disturbed site. The higher calcium, magnesium, phosphorus, percent organic matter content, and cation exchange capacity of disturbed site soils reflected historic use of the site as a pasture. The uniform surface soil texture may be attributable to past cultivation.

Soil texture may have influenced species distribution at the reference site. *Carex bebbii, Carex sartwellii, Cladium mariscoides,* and *Juncus balticus* generally favor open, sandy shore line habitats (Voss, 1972), and many of the plots exhibiting maximum IV of these species also had tan, sandy substrates. Soil particle size has been shown to impact seed germination and seedling recruitment on lake shores, particularly when water levels were at least 4cm below ground (Keddy and Constabel, 1986). They attributed this to the comparatively rapid drying of coarse substrates, which accelerated seed and seedling desiccation (Ibid., 1986).

Differences in soil fertility might also have impacted species composition at the reference site. The sand soil was lower in silt, clay, calcium, and potassium than the adjacent loamy sand soils. Competitive asymmetry increases with soil fertility, accelerating exclusion of competitively inferior wetland species (Keddy et al., 1997). The relatively short *Carex bebbii, Carex sartwellii, Cladium mariscoides,* and *Juncus balticus* may have been excluded from the more fertile loamy sand plots by taller species that were more successful light or space competitors, and so occupied the relatively infertile sand plots by default.

Small-scale water level fluctuations may also have been involved in sorting species in the sand plots. Daily seiche amplitudes range between 20-40cm in southern Saginaw Bay (Batterson et al., 1991). The sand plots occurred where mean mid-summer water levels ranged between -10cm and +10cm. Seiches could have alternately inundated and exposed these plots on a daily basis. Disturbance caused by these inundation/exposure cycles may have created exploitable gaps or otherwise caused the competitive advantage to shift to the small species (Keddy, 1984).

At both sites, the major species exhibited water level preferences. Species classified as obligate wetland species occurred at all wet meadow water levels, but most exhibited greater plot IV where water levels were less than 10cm below the ground surface. Emergent wetland species (e.g., *Typha angustifolia,* and *Carex lacustris*) typically occurred where mean water levels were at or above ground. Most FACW species exhibited their greatest plot IV where mean mid-summer water levels were at or below ground. One exception to this rule was *Phalaris arundinacea*, a FACW+ species that occurred only at the disturbed site. It exhibited a bi-modal distribution with respect to water levels (see Figure 3-6). *P. arundinacea* had maximum plot IV both in plots with the shallowest mean mid-summer groundwater and in plots with the deepest groundwater levels.

The unusual distribution pattern displayed by *Phalaris arundinacea* (Reed Canary grass) was probably the result of its deliberate introduction as a forage crop. *P. arundinacea* was for many year recommended for use as a forage or hay crop on poorly drained soils because it grows well under saturated conditions and tolerates extended periods of inundation (Harmer, 1941; Heath and Hughes, 1951; Tesar and Shepherd, 1963). At least one of the 1997 study sites (Site #21) had been seeded in *P. arundinacea* during the 1950's on the recommendation of the county agricultural extension agent (W. Grobsky, pers. comm.; and see Chapter 5), and a long-time local resident confirmed that a prior owner of the disturbed site had at one time experimented with *P. arundinacea* as a forage crop at the site (K. Wildner, pers. comm.).

Physical attributes

Fluctuating wet meadow groundwater and surface water levels were the key factors determining coastal wet meadow vegetation structure and composition. Fluctuating water levels periodically de-saturated or re-saturated wet meadow substrates, eliminating non-wet meadow species and spatially sorting wet meadow species (*sensu* van der Valk, 1981) according to inundation and saturation tolerance. Fluctuating water levels also significantly impacted peat and litter depths, soil texture, and hummock heights. These abiotic factors influenced wet meadow species distribution as well.

While Saginaw Bay surface fluctuations display a certain periodicity (see Chapter 2), bay water levels vary literally minute-by-minute. Stochastic changes in precipitation and evapotranspiration enhance this variability, resulting in unpredictable short-term and long-term changes in wet meadow surface water and groundwater levels. Given the extremely dynamic nature of Saginaw Bay hydrology, it was impractical to estimate the amount of time that any particular point in the wet meadow was inundated. However, plots located at similar elevations exhibited similar physical and vegetation attributes, so plot elevation with respect to the mean high water mark was a good integrator of the net impact of these hydrologic variations on the wet meadow.

The wet meadow zone extended 60cm in elevation above the mean annual Saginaw Bay high water mark. Keddy and Reznicek (1986) reported that Lake Erie wet meadows developed in this elevation range, and attributed the grass and sedge dominance of wet meadow vegetation to a hydrologic regime that was alternately too wet for woody plants and too dry for marsh plants (Keddy and Reznicek, 1986).

From a vegetation standpoint, the most significant elevation in the wet meadow may have been the mean elevation of the wet meadow zone (177.0m AMSL in 1996-1997). There was a significant decrease in species richness as elevation decreased below this level, and the 177.0m AMSL elevation contour delineated the approximate boundary between upper and lower wet meadow vegetation.

The 177.0m AMSL contour was approximately 33cm above the mean annual Saginaw Bay high water level. Seiches exhibit a 24hr periodicity in southern Saginaw

Bay, with daily fluctuations ranging between 20-40cm (Batterson et al., 1991). Batterson et al. linked aquatic macrophyte and periphyton distribution within Saginaw Bay bulrush marshes to these fluctuations. Periodic precipitation and storm surge inundation maintain wet meadow soil moisture conditions that are favorable for wet meadow vegetation (see Chapter 2). Daily seiche inundation may have had similar impacts on wet meadow vegetation during calm, dry weather, and may define the upper limit of the lower wet meadow.

It is important to note that the elevation of the wet meadow zone is not fixed on the landscape. It moves land-ward and lake-ward from time to time with changes in Saginaw Bay water levels (Minc and Albert, 1998; Keough et al., 1999). 176.67m AMSL, or 177.0m AMSL, or any other fixed elevation are not absolute values with respect to the location of Saginaw Bay coastal wet meadows. These elevations simply represent important reference points during 1996 and 1997.

Coastal wet meadow soils generally consisted of an organic layer up to 16cm thick deposited over a sandy mineral substrate. Glacial till or lacustrine clay deposits were encountered wherever lower soil layers were examined. Earlier investigators reported that the organic layer thickness ranged from a "few centimeters" (Albert et al., 1988) to as much as 20cm in Saginaw Bay wetlands (Davis, 1908). Coons (1911) reported 5cm of fine silt and un-decomposed organic matter at one site, and "black, amorphous peat" of almost 60cm depth at another nearby site. The underlying mineral substrates have been described as "gravelly or clayey" loam, clay, or sand soils and "stiff, bouldery till clay"(Davis, 1908), firm sandy substrates (Coons, 1911), and sandy or clayey material of lacustrine or glacial origin (Albert et al., 1988). Davis reported sharply-defined alternating strips of "clayey", "gravelly", and "organic soils" lying parallel to the Saginaw Bay shore line as he moved inland from the coast. Albert et al. (1988) linked the predominance of fen species in several Saginaw Bay coastal wet meadows to the calcareous soils occurring at those sites.

Though an organic surface layer was a common feature in most wet meadows, several sites lacked an "O" horizon. Some of these sites were former agricultural fields. In these sites, cultivation-induced soil homogenization and oxidation of organic matter exposed by tillage probably accounted for the lack of a distinct "O" horizon. In sites with no agricultural disturbance history, wave action or ice scour most likely explained the absence of "O" horizons (Tilton et al., 1978; Geis, 1985).

Peat and litter thickness varied greatly within and among sites, but were negatively correlated with plot elevation. Ambient temperature, oxygen status, and nutrient availability are most important in determining peat and litter decomposition rates (Godshalk and Wetzel, 1978; Brinson et al., 1981; Kelley, 1985; Mitsch and Gosselink, 1993). Peat forms most rapidly in waterlogged sites protected from wave disturbance, where anoxic sediments and reduced decomposition rates accelerate peat accumulation (Tilton et al., 1978; Godshalk and Wetzel, 1978; Brinson et al., 1981; Mitsch and Gosselink, 1993). The warm, damp, exposed conditions associated with rapid organic matter oxidation were more likely to be found in the upper wet meadow, and probably accounted for the thinner upper wet meadow litter and peat mats in most years. Wave action or ice scour may have removed peat or litter from the upper wet meadow in high water years (Tilton et al., 1978; Geis, 1985).

Greater peat and litter depths were positively correlated with fine-textured substrates. Decomposing organic matter increases the fine-particle fraction of underlying mineral substrates (Foth, 1990). Thicker peat and litter mats may also have absorbed wave energy, reducing wave-induced sorting of soil particles. Such sorting preferentially removes fine-textured particles from the substrate (Ibid., 1990).

Tall vegetation hummocks occurred most often in the lower wet meadow. Oddly though, the hummock-building wetland emergent species *Carex stricta* was negatively (though not significantly) correlated with hummock height ($r = -0.220$, $n = 51$). There are two possible explanations for this. First, *C. stricta* may not have formed all of these hummocks; *Calamagrostis canadensis* reportedly forms hummocks in some Saginaw Bay wetlands (Albert et al., 1988). Second, *C. stricta* was positively correlated with plot elevation, so was more likely to be found in the upper wet meadow, where hummocks were shorter and less common. Widely fluctuating water levels trigger hummock production in *C. stricta* (Costello, 1936), so the depth and frequency of inundation in the upper wet meadow was apparently insufficient to stimulate much hummock production in *C. stricta*. Where *C. stricta* occurred in the lower wet meadow, it may have adapted a hummock habit in response to the greater inundation depths and frequencies found there.

Other annual and perennial plants also occupied the hummocks. These plants, generally the shorter, physically smaller wet meadow species, utilized the hummocks as safe sites. They became established on the hummocks at the optimal elevation (for them) above that year's wetland water surface. These species utilized the hummocks to colonize, either by seed germination or rhizome extension, suitable micro-sites within the wetland.

Vegetation attributes

Saginaw Bay coastal wet meadows supported a diverse and stable assemblage of native grasses, sedges and forbs. The species composition of these wet meadows was very similar to that previously reported for Saginaw Bay and other Great Lakes coastal wet meadows (Davis, 1900; Davis, 1908; Coons, 1911; Dodge, 1920; Hayes, 1964; Stuckey, 1975; Tilton et al., 1978; Jaworski and Raphael, 1979; Jaworski et al., 1979; Herdendorf et al., 1981; Albert et al., 1988, 1989; Prince and Burton, 1995). Many of the dominant and sub-dominant species reported by Davis (1900, 1908) and Coons (1911) were still present as dominant and sub-dominant species 90-100 years later.

Saginaw Bay coastal wet meadows were grass- and sedge-dominated vegetation assemblages. The four most important species included a grass and three sedges, and eight of the 15 major wet meadow species were grasses or sedges. Grass and/or sedge dominance is an emergent property of this vegetation assemblage, one held in common with inland wet meadows (Curtis, 1959).

These coastal wet meadows also resembled inland wet meadows in other respects. The vegetation structure and species composition was quite similar to that described for inland wet meadows, in some cases even with respect to the identity of the dominant species (Stout, 1914; Curtis, 1959; van der Valk and Bliss, 1971). Hydrology was similar as well (Curtis, 1959; and see Chapters 1 and 2). Both inland and coastal wet meadows develop at or just above the local water table, and both experience one or more draw-down and re-saturation cycles during the growing season.

Species richness varied significantly across the coastal wet meadow elevation gradient. The shorter major species had much lower importance values at lower wet meadow elevations, and several species were not encountered at all in the lower wet meadow. The thicker peat and litter mats, and the greater depth and duration of inundation occurring at lower elevations comprised a less-hospitable growing environment for these species. The wet meadow emergent species, taller and better adapted to prolonged inundation, persisted in the lower wet meadow. Lower species richness resulted.

Sandy substrates and the variable Saginaw Bay hydroperiod probably played a role in determining wet meadow species richness. Wetland plant species richness is greatest on sand or gravel substrates (Keddy, 1989), and at or just above the water line (Keddy, 1984). Fluctuating water levels enhance species richness in lacustrine wetlands (Wilcox and Meeker,1991; Wilcox, 1995).

Fluctuating water levels and sandy substrates also promote wetland plant species diversity. Sandy substrates produced higher plant species diversities and propagule densities than organic substrates in Long Island ponds, with the highest diversities occurring in non-flooded zones subject to periodic inundation (Schneider, 1994). In the Great Lakes, the greatest plant diversities generally occur in gently-sloping upper elevation wetlands subject to intermediate levels of disturbance (Keough et al., 1999). Occasional flooding is thought to increase herbaceous wetland plant species diversity by transporting nutrients and propagules into the wetland and eliminating woody vegetation from it (Keddy and Reznicek, 1986; Schneider, 1994).

Leaf-area index did not vary across the elevation gradient because wet meadow vegetation physiognomy did not change with elevation. Only species composition changed, and then only gradually. The dominant species, which contributed most to LAI and vegetation physiognomy, remained the same throughout the wet meadow.

While LAI may not have changed across the elevation gradient, the height at which leaves occurred in the canopy did increase as elevation decreased. Inundation often triggers stem elongation in wetland plants (Ernst, 1990). Increased leaf heights in the lower wet meadow were probably a response to increased inundation depth and duration.

Species interactions

Competitive exclusion, occurring in wet meadows via light competition (Keddy, 1989; Leps, 1999), space competition (Auclair et al., 1973), litter deposition and smothering (Wilcox et al., 1985), and antibiosis (Leibundgut, 1952, cited in Auclair et al., 1973) may explain the negative correlation in the importance values of the physically large and small major wet meadow species. The intensity of above-ground wetland plant competition is known to increase with standing crop biomass (Twolan-Strutt and Keddy, 1996). However, it does not necessarily follow that biomass determines species richness. Environmental variables accounted for 89% of the variation in species richness in one study of Louisiana flood plain wetlands (Gough et al., 1994). Biomass became the best predictor of species richness only after abiotic stressors were factored out of the analysis (Ibid., 1994). Keddy (1989) suggested that water levels, soil fertility, and disturbance determined to what extent competition influenced vegetation structure in lacustrine wetlands. Grace and Pugesek (1997) concluded that species richness in Louisiana's Pearl River flood plain was about equally impacted by abiotic influences and biomass, with disturbance playing a secondary role.

Abiotic factors were important mediators of competition in Saginaw Bay coastal wet meadows. *Typha angustifolia* and *Phragmites australis* demonstrated the ability to dominate wet meadow vegetation in some lower wet meadow plots, yet these species occurred only occasionally in the wet meadow. *T. angustifolia* and *P. australis* are wetland emergent plants, and *T. angustifolia* was one of the dominant species of the adjacent coastal marshes. However, these species were not tolerant of the annual substrate de-saturation that occurred in the wet meadow. So, even though they were capable of successfully competing with wet meadow grasses and sedges for light and space, hydrologic factors limited the ability of these two species to dominate wet meadow vegetation.

Inundation frequency was also the principal factor determining affinities among certain major wet meadow species. *Carex stricta* and *Galium obtusum* were positively associated with one another, and with less frequently inundated upper wet meadow elevations. The impact of inundation on the growth habit of *C. stricta* may also have influenced the association among these species. In the drier upper wet meadow, *C. stricta* grew in tufts, leaving gaps in the turf that could be occupied by this other relatively short species. In the more frequently inundated lower wet meadow, *C. stricta* hummocks provided safe sites for *G. obtusum* when water levels rose.

Both competitive factors and abiotic control were probably involved in determining species richness, species composition, and species distribution in Saginaw Bay coastal wet meadows. The relative impact of competition and environmental factors were not determined in this study, but it seems likely that abiotic factors dominated the process.

Depth and duration of inundation impacted species distribution within the wet meadow. Inundation depth and duration also influenced rates of peat development, litter accumulation, and hummock development throughout the wet meadow. Adaptation to specific combinations of these abiotic factors determined which species could compete most successfully, exclude less competitive species, and become dominant at any particular elevation within the wet meadow.

Using the available abiotic and species interaction data, the major wet meadow species could be separated into three groups. The first group of species (*Campanula aparinoides, Carex stricta, Galium obtusum*, and *Stachys tenuifolia*) more commonly occurred in higher elevation plots that had lower peat and litter depths, and a relatively large number of species per $0.25m^2$ plot (Table 3-14). Higher elevation could mean either plots above the 177.0m AMSL elevation contour in the upper wet meadow, or on the sides and tops of hummocks in the lower wet meadow. One sedges and three forbs comprised this group of upper wet meadow species. The plants comprising this group were all among the smaller, shorter major plant species.

A second group of lower wet meadow species (*Calamagrostis canadensis, Carex aquatilis, Carex lacustris, Phragmites australis,* and *Polygonum amphibium*) more commonly occurred below the 177.0m AMSL elevation contour in plots containing deeper peat, thicker litter mats, taller hummocks, and fewer species per plot compared to the upper wet meadow. These species, excepting *C. canadensis*, were wetland emergent species, and all were of average to above-average height, and often were the dominant or co-dominant species in the plots in which they occurred.

Six species, *Calystegia sepium, Cladium mariscoides, Carex sartwellii, Lythrum salicaria, Phalaris arundinacea,* and *Typha angustifolia*, comprised the last group. These species could not be easily classified as either upper or lower wet meadow species. *P. arundinacea* was a native grass seeded into wet meadows as a forage crop, *C. sepium* and *L. salicaria* were introduced exotic species (Reed, 1988), and *T. angustifolia* was the dominant species of the adjacent cattail marshes. These species were either deliberately introduced agricultural species (*P. arundinacea*), recent additions to the vegetation assemblage (*C. sepium* and *L. salicaria*), or relicts from a time when different hydrologic conditions existed at these sites (*T. angustifolia*). *C. sartwellii* and *C. mariscoides* were native wet meadow species that did not fit the pattern of association that defined the two groups. *C. sartwellii* favored intermediate to lower elevation plots with thicker peat layers, but also coarse surface substrates and low hummocks. Similarly, *C. mariscoides* favored intermediate to lower elevation plots, thicker peat, and coarse surface substrates.

Vertical vegetation stratification

The wet meadow canopy exhibited a three layer architecture (canopy emergent species, canopy species, and understory species), with a fourth group (Clingers/climbers) ranging among the other three layers. Similar canopy architecture has been observed in Canadian wet meadows (van der Valk and Bliss, 1971). They reported that three canopy layers existed in these wetlands, an upper layer (0.75-1.0m height) occupied by the dominant sedges and forbs, a middle layer (0.25-0.50m) occupied by herbs and grasses, and a ground layer occupied by vascular cryptogams. van der Valk and Bliss (1971) made no mention of vine-like climbing species.

The Saginaw Bay wet meadow vegetation canopy was commonly 1.2-1.5m tall, with 50% of the leaves occurring between 43-84cm above the substrate. This was taller than either the Canadian wet meadows or Dutch wet grasslands, which, like their Canadian counterparts, had a maximum height of about 1m (Fliervoet and Werger, 1984). Dutch Senecioni-Bromentum wet grasslands exhibited a vertical profile similar to that of Saginaw Bay wet meadows, but with peak leaf densities occurring 20-50cm above the ground. Fliervoet and Werger (1984) reported that while standing crop varied considerably among years, the vertical distribution of phytomass and LAI differed very little from year to year in these wetlands.

Summary and conclusions

Saginaw Bay coastal wet meadows are the grass- and sedge-dominated herbaceous vegetation assemblage that occur in a zone extending from the mean annual Saginaw Bay high water mark to approximately 60cm in elevation above that level. A combination of predictable and stochastic hydrologic inputs and outputs are the primary determinants of the landscape position and species composition of the wet meadow zone.

Mean mid-summer plot water level impacted plot biomass, stem density, and herbaceous species distribution at both a reference and disturbed hydrologic study site. Plot stem density at the reference site peaked when mean mid-summer water levels ranged between +10cm and -10cm. Plot stem density and biomass also varied across the groundwater gradient at the disturbed site, even though a dike eliminated wave action and storm surge inundation at that site. The elimination of inundation permitted succession of shrub and forest species to begin at the disturbed site. Species richness at both sites increased significantly as water levels decreased, until mean mid-summer water levels were below ground, after which species richness did not change. Historic land use, soil texture, and soil fertility may also have impacted species distribution within the reference and disturbed study sites, and the presence and distribution of *Phalaris arundinacea* at the disturbed site was linked to anthropogenic factors.

Fifteen wet meadow species contributed 84% of all vegetation importance value in Saginaw Bay coastal wet meadows. Four species (*Calamagrostis canadensis, Carex aquatilis, Carex lacustris,* and *Carex stricta*) contributed 60% of total IV, with the grass *Calamagrostis canadensis* by itself contributing over 31% of the total. By contrast, 27 of the 93 species encountered occurred in only one of 300 sample plots.

Coastal wet meadow vegetation was 1.2-1.5m tall, with half the leaf, stem, and inflorescence contacts occurring between 43-84cm above the substrate surface. The vegetation exhibited a three-layer canopy architecture (canopy emergent species, canopy species, and canopy understory species) with certain climbing species (clingers/climbers) comprising a fourth vertical stratification group. Canopy layers could be identified by examining the median and maximum height of the species occupying the layers.

There were three vegetation sub-groups within the wet meadow zone: upper wet meadow vegetation, lower wet meadow vegetation, and species that could not easily be classified as either upper or lower wet meadow vegetation. The upper and lower wet meadow sub-groups could be distinguished by the affinity of constituent species for certain combinations of biotic and abiotic factors. The upper wet meadow could generally be recognized by the presence of significantly thinner peat (mean = 1.1cm) and litter (mean = 8.9cm) mats, shorter hummocks (mean = 23.4cm), higher number of species per plot (mean = 7.3spp./0.25m^2), higher elevation (mean = 177.09m AMSL), and small to average size plants (e.g., *Campanula aparinoides, Carex stricta, Galium obtusum*, and *Stachys tenuifolia*). The lower wet meadow could generally be recognized by the presence of significantly thicker peat (mean = 5.4cm) and litter (mean = 18.4cm) mats, taller hummocks (mean = 33.2cm), lower number of species per plot (mean = 4.9spp./0.25m^2), lower elevation (mean = 176.88m AMSL), and relatively tall wetland emergent species (e.g., *Calamagrostis canadensis, Carex aquatilis, Carex lacustris, Phragmites australis,* and *Polygonum amphibium*).

Extrapolation of these findings beyond Saginaw Bay to other Great Lakes wet meadows must be undertaken with caution. Lake size, shoreline geomorphology, exposure to prevailing winds and storm surges, circulation and sedimentation patterns, substrate composition, groundwater inflow from adjacent uplands, and species distribution vary greatly from site to site, and have uncertain impacts on the developmental trajectory of coastal wet meadow vegetation. Further study would be required to determine if these findings apply to other Great Lakes coastal wet meadows, or fringing wetlands in smaller lakes.

These findings highlight the importance of a variable hydroperiod in the development and maintenance of coastal wet meadow habitat in Saginaw Bay. The continued existence of this ecosystem hinges on the continuation of undisturbed natural variations in Great Lakes water levels.

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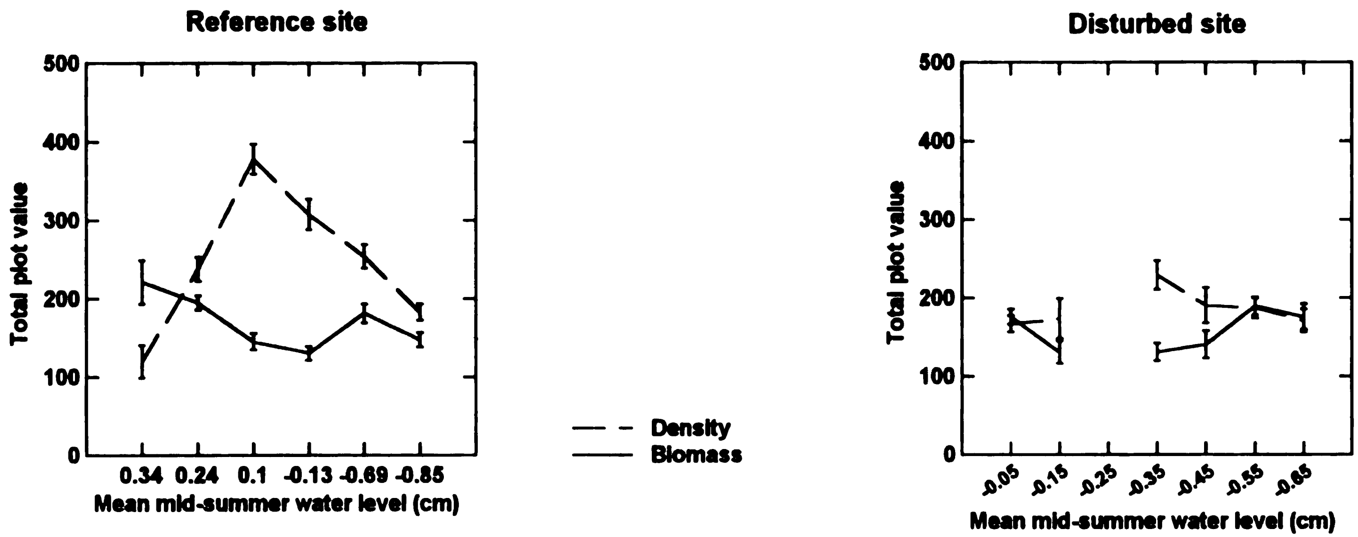

Figure 3-1. Changes in total plot biomass ($g/0.25m^2$) and stem density ($stems/0.25m^2$) across the water level gradient at the hydrologic study sites: 1996. Negative water level values indicate groundwater depth. Error bars equal ±1SEM.

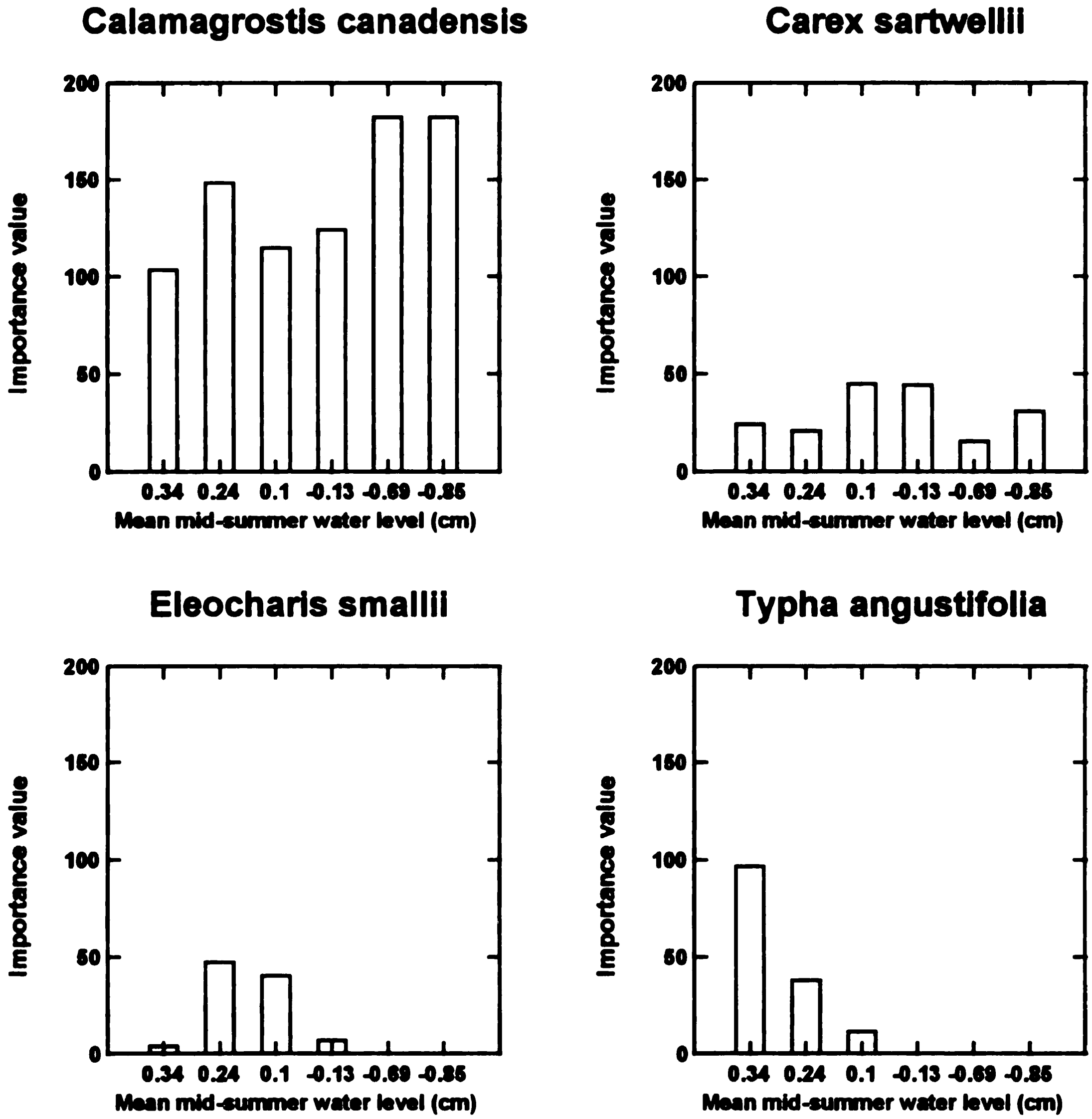

Figure 3-2. Change in importance value of *Calamagrostis canadensis, Carex sartwellii, Eleocharis smallii,* and *Typha angustifolia* across the water level gradient at the reference hydrologic study site: 1996. Positive water levels represent standing water depths, negative values represent groundwater depths. Maximum possible IV = 300.

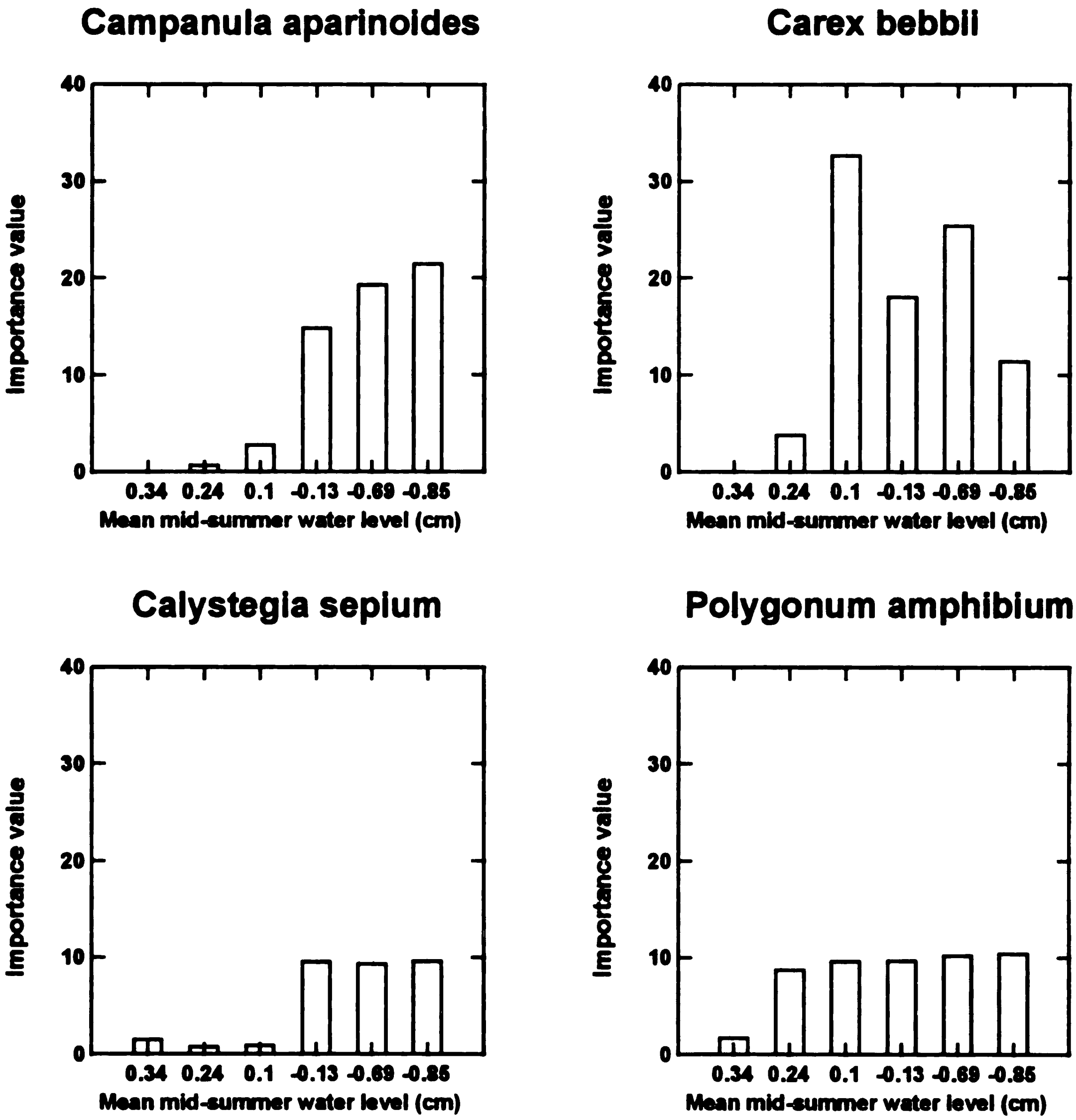

Figure 3-3. Change in importance value of *Campanula aparinoides, Carex bebbii, Calystegia sepium,* and *Polygonum amphibium* across the water level gradient at the reference hydrologic study site: 1996. Positive water levels represent standing water depths, negative values represent groundwater depths. Maximum possible IV = 300.

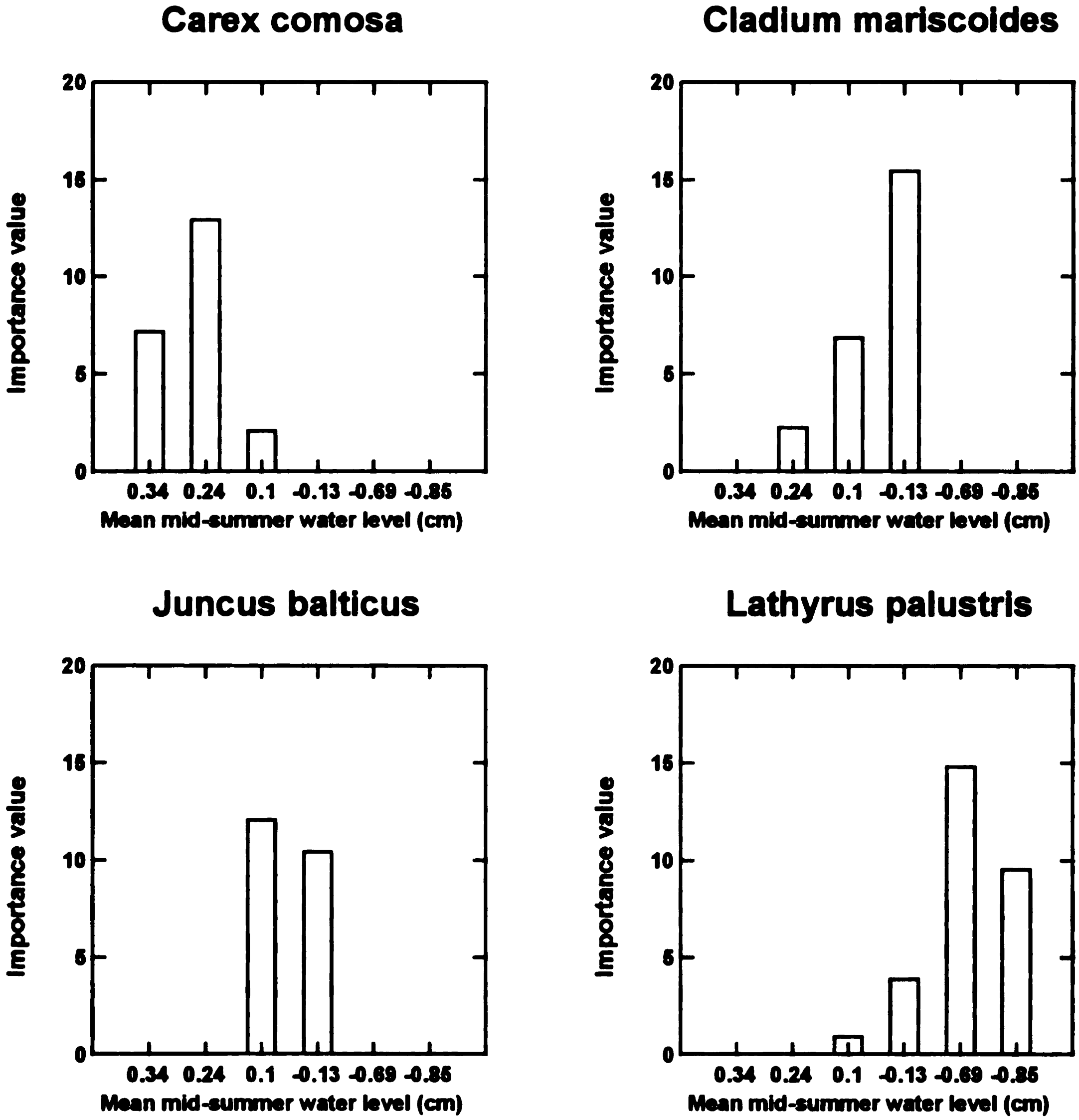

Figure 3-4. Change in importance value of *Carex comosa, Cladium mariscoides, Juncus balticus,* and *Lathyrus palustris* across the water level gradient at the reference hydrologic study site: 1996. Positive water levels represent standing water depths, negative values represent groundwater depths. Maximum possible IV = 300.

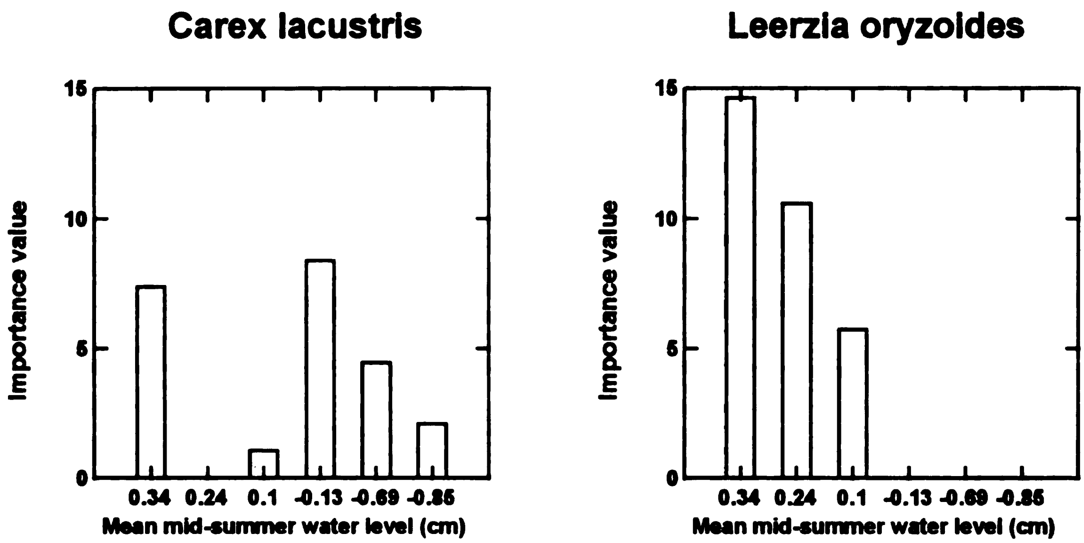

Figure 3-5. Change in importance value of *Carex lacustris*, and *Leerzia oryzoides* across the water level gradient at the reference hydrologic study site: 1996. Positive water levels represent standing water depths, negative values represent groundwater depths. Maximum possible IV = 300.

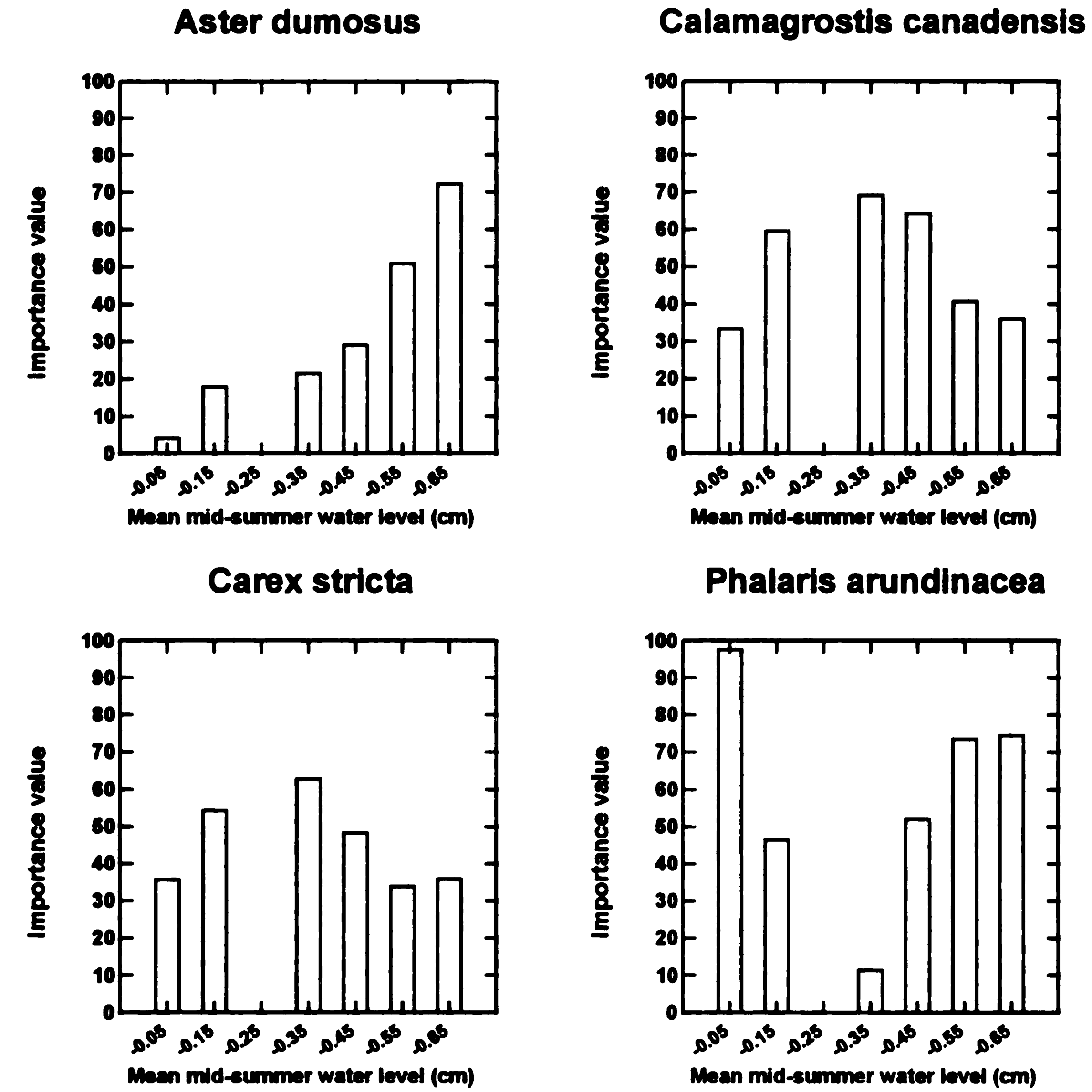

Figure 3-6. Change in importance value of *Aster dumosus, Calamagrostis canadensis, Carex stricta,* and *Phalaris arundinacea* across the water level gradient at the disturbed hydrologic study site: 1996. Negative water levels represent groundwater depths. Maximum possible IV = 300.

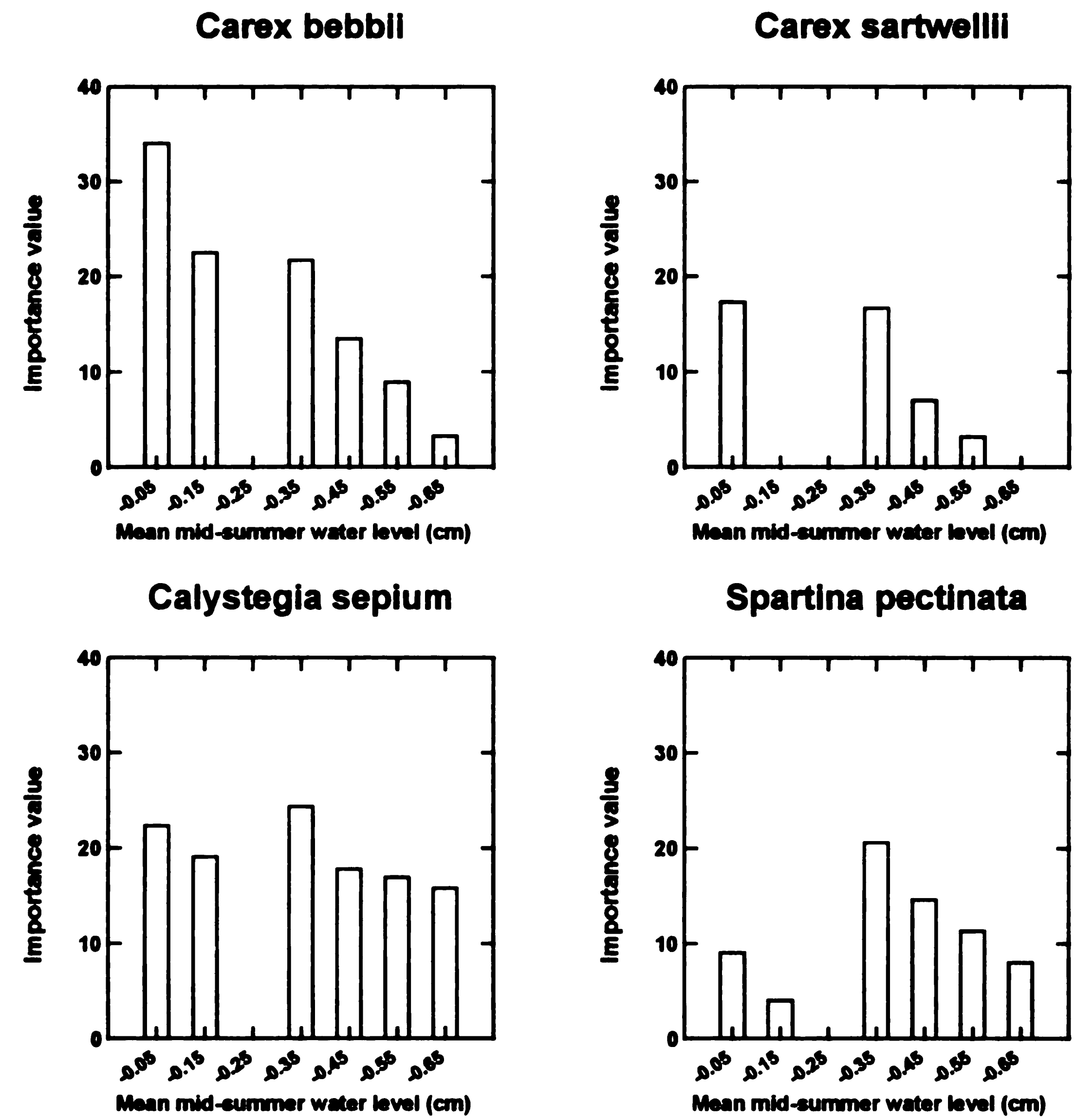

Figure 3-7. Change in importance value of *Carex bebbii, Carex sartwellii, Calystegia sepium,* and *Spartina pectinata* across the water level gradient at the disturbed hydrologic study site: 1996. Negative water levels represent groundwater depths. Maximum possible IV = 300.

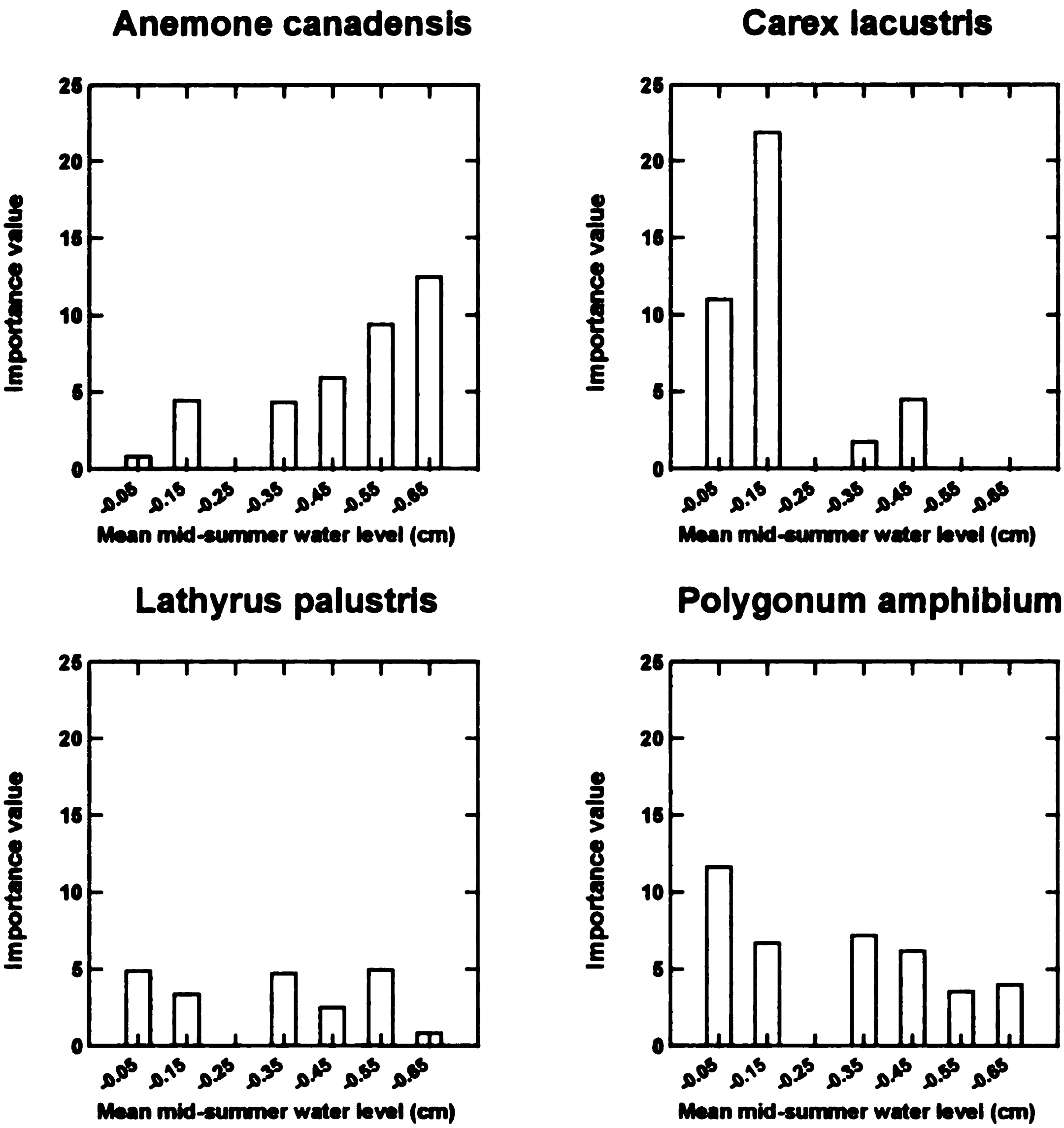

Figure 3-8. Change in importance value of *Anemone canadensis, Carex lacustris, Lathyrus palustris,* and *Polygonum amphibium* across the water level gradient at the disturbed hydrologic study site: 1996. Negative water levels represent groundwater depths. Maximum possible IV = 300.

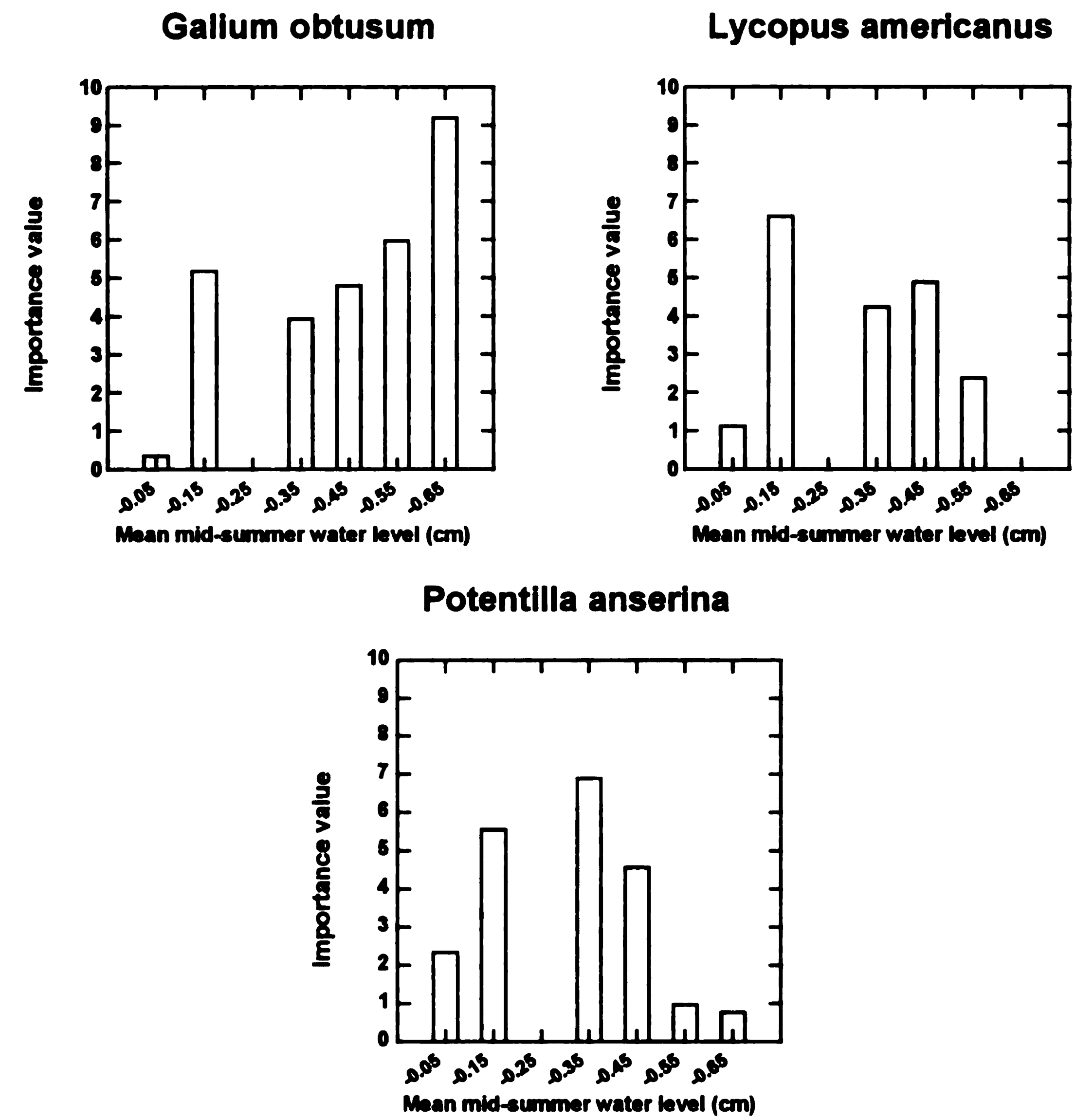

Figure 3-9. Change in importance value of *Galium obtusum*, *Lycopus americanus*, and *Potentilla anserina* across the water level gradient at the disturbed hydrologic study site: 1996. Negative water levels represent groundwater depths. Maximum possible IV = 300.

Table 3-1. Comparison of soil variables measured at the hydrologic study sites. Significantly different P-values are indicated in boldface and with an asterisk. P-values were determined using the Mann-Whitney U test. PPM equals parts per million, Meq/100ml equals milli-equvalents per 100ml soil.

Soil variable	Reference site Mean(±1SEM)	Disturbed site Mean(±1SEM)	P-value
Samples analyzed per site	3	4	N/A
pH	7.4(0.2)	7.0(0.1)	0.108
P (PPM)	9.5(2.1)	25.6(3.6)	**0.034***
K (PPM)	29.8(10.7)	57.9(11.2)	0.154
Ca (PPM)	2182.0(714.2)	5693.5(116.4)	**0.034***
Mg (PPM)	243.0(91.0)	850.3(13.6)	**0.032***
Organic matter (%)	4.9(1.5)	35.0(4.1)	**0.032***
Cation exchange capacity (Meq/100ml)	13.0(3.8)	35.7(0.7)	**0.034***
NO_3-N (PPM)	2.5(1.1)	8.9(2.4)	0.077
NH_4-N (PPM)	3.3(1.2)	8.1(1.4)	**0.034***
SAND (%)	74.9(11.3)	68.0(2.7)	0.480
SILT (%)	20.6(8.4)	17.1(2.2)	0.593
CLAY (%)	4.6(3.4)	14.9(0.9)	**0.034***
Bulk density (g/ml)	0.8(0.2)	0.4(0.0)	0.289

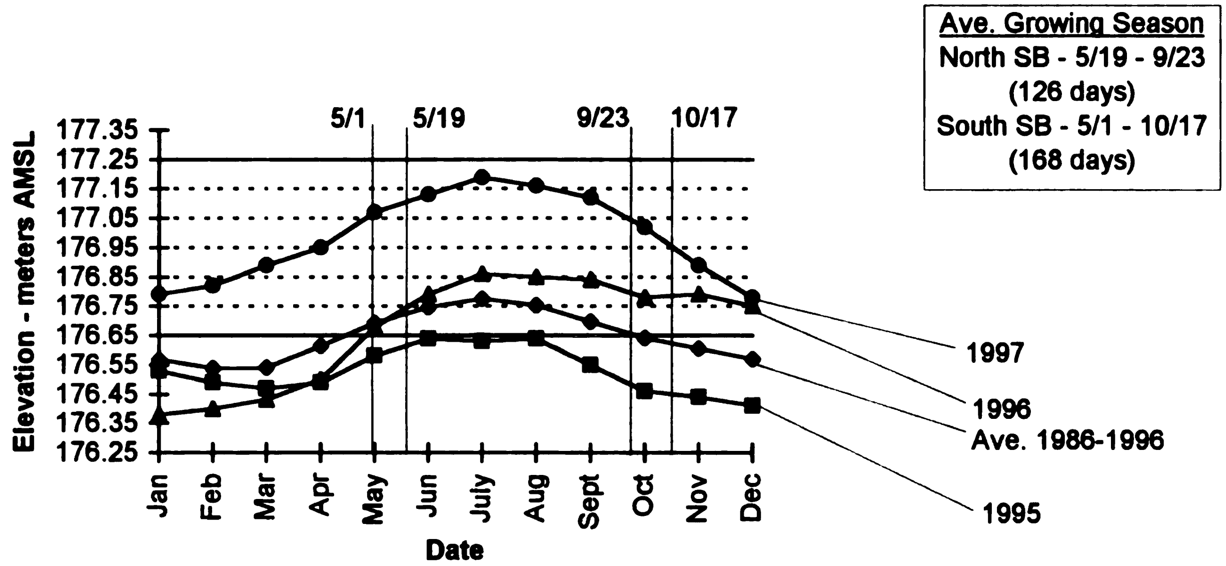

Figure 3-10. Saginaw Bay hydrographs for 1995-1997, and the average hydrograph for 1986-1996. The solid horizontal lines delimit the elevation of the Saginaw Bay coastal wet meadow zone. The dotted horizontal lines indicate 10cm intervals within the wet meadow. Vertical lines indicate growing season length for northern and southern Saginaw Bay.

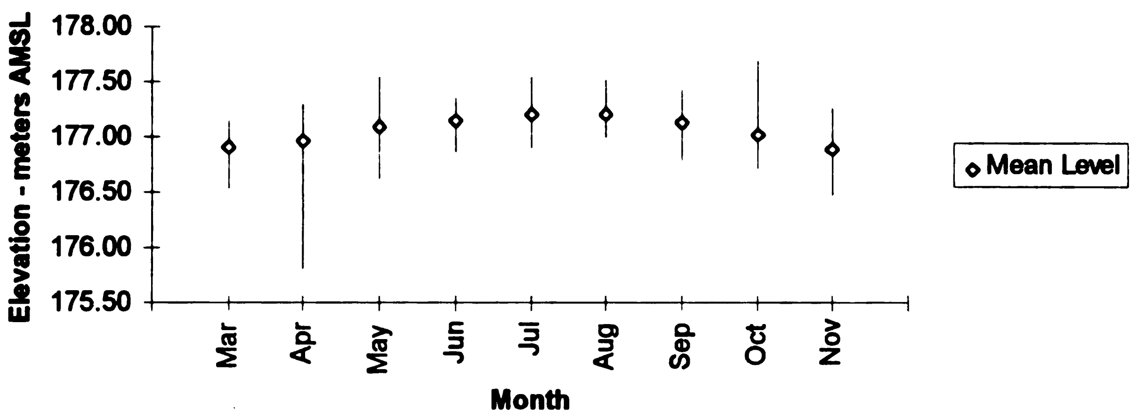

Figure 3-11. Monthly mean and range of Saginaw Bay water levels recorded during the 1997 growing season. Monthly maximums averaged 36cm higher that monthly means, and ranged as high as +67cm in October.

Table 3-2. Wet meadow width, slope, peat and litter depth, and hummock height by site for Saginaw Bay coastal wet meadows.

Site	Site width (m)	Slope (%)	Peat depth (cm) mean(±1SEM)	Litter depth (cm) mean(±1SEM)	Hummock Height (cm) mean(±1SEM)
1	265.	0.12	2.2(0.6)	14.3(1.5)	N/A(2)
2	119.	0.36	4.4(0.9)	15.4(5.3)	38.0(6.4)
3	133.	0.28	3.3(0.4)	*(1)	N/A
4	100.	0.32	3.0(0.6)	*	N/A
5	257.	0.10	5.1(1.3)	13.0(1.7)	28.0(6.4)
6	11.	2.00	4.0(0.8)	11.5(1.3)	N/A
8	147.	0.27	4.8(1.0)	17.4(1.5)	N/A
9	210.	0.11	0.4(0.1)	*	35.9(3.2)
10	105.	0.24	2.3(0.6)	*	25.7(5.5)
11	197.	0.15	4.3(0.9)	*	N/A
13	92.	0.26	4.3(0.8)	13.1(1.4)	N/A
14	110.	0.34	3.3(0.7)	12.6(1.8)	N/A
15	252.	0.10	2.0(0.3)	*	N/A
18	25.	1.08	3.3(0.9)	10.1(2.1)	N/A
19	31.	0.97	4.6(0.7)	19.0(1.0)	30.7(2.9)
20	50.	0.40	3.2(0.5)	*	N/A
21	45.	0.82	4.4(0.7)	17.3(1.6)	N/A
22	12.	2.25	3.8(1.0)	14.5(1.0)	18.0(0.0)
24	65.	0.15	2.3(0.6)	16.3(1.4)	37.4(3.5)
25	115.	0.13	7.4(1.0)	18.7(0.9)	21.0(0.0)
26	65.	0.71	5.5(1.2)	8.7(2.0)	24.5(1.5)
27	545.	0.09	8.8(0.9)	30.5(7.0)	27.7(2.5)
28	95.	0.12	11.0(0.8)	23.8(0.8)	19.0(0.0)
30	128.	0.13	3.1(0.7)	10.2(0.9)	N/A
31	100.	0.30	8.4(2.0)	17.6(1.9)	19.3(7.4)
All	123.9(15.8)	0.27(3)	4.4(0.2)(4)	15.4(0.5)(5)	30.3(1.6)(6)

(1) - Asterisk indicates that no litter measurement was collected at that site.
(2) - N/A indicates that Hummocks did not occur at that site.
(3) - Median value.
(4) - N = 300.
(5) - N = 215.
(6) - N = 5i.

Table 3-3. Pearson product-moment correlation matrix of Saginaw Bay coastal wet meadow abiotic factors. Peat depth and litter depth were square-root transformed to meet parametric assumptions. Boldface values marked with an asterisk were significant (Bonferroni-corrected P<0.05).

(A) Hummock height data were non-normally distributed, and could not be transformed to meet parametric assumptions, and so was excluded from the analysis. N = 2384.

Variable	Peat depth	Litter depth	Soil texture	Plot elevation
Peat depth	1.000			
Litter depth	-0.042	1.000		
Soil texture	0.021	**-0.196***	1.000	
Plot elevation	**-0.644***	**-0.159***	**0.220***	1.000

(B) Hummock height data were normally distributed when cases were excluded in which hummocks were not present, or where hummock data was not collected. N = 382.

Variable	Peat depth	Litter depth	Soil texture	Plot elevation
Hummock height	-0.018	0.101	-0.026	**-0.258***

Table 3-4. Importance values (IV) for plant species encountered in Saginaw Bay coastal wet meadows in 1997. Importance value is the sum of the relative above-ground biomass, relative stem density, and relative frequency of occurrence of each species in the wet meadow (Brower and Zar, 1977). A total of 300-0.25m^2 sample plots were collected in 25 coastal wet meadows. Percent frequency of occurrence was determined from the number of sample plots in which the species was found. N equals the number of plots in which a species occurred.

Species	Family	Frequency of Occurrence (%)	Contribution to Total IV (%)	Species IV	N
Acorus calamus L.	Acoraceae	0.3	<0.1	0.1	1
Agropyron repens (L.) Beauv.	Poaceae	2.7	0.2	0.6	8
Alisma plantago-aquatica L.	Alismataceae	0.3	<0.1	0.1	1
Anemone canadensis L.	Ranunculaceae	8.3	0.6	1.9	25
Apocynum canabinum L.	Apocynaceae	5.3	0.3	1.0	16
Asclepias incarnata L.	Asclepiadaceae	1.7	0.1	0.3	5
Aster borealis (T. & G.) Prov.	Asterdaceae	7.3	0.4	1.3	22
Aster dumosus L.	Asterdaceae	10.3	0.9	2.7	31
Calamagrostis canadensis (Michaux) Beauv.	Poaceae	92.0	31.1	93.2	276
Calystegia sepium (L.) R. Br.	Convovulaceae	20.0	1.2	3.7	60
Campanula aparinoides Pursh	Campanulaceae	47.0	4.5	13.4	141
Carex aquatilis Wahl.	Cyperaceae	50.0	14.6	43.7	150
Carex bebbii (Bailey) Fern.	Cyperaceae	6.3	0.9	2.7	19
Carex buxbaumii Wahl.	Cyperaceae	3.7	0.9	2.7	11
Carex comosa Boott	Cyperaceae	0.7	<0.1	0.1	2
Carex hystericina Willd.	Cyperaceae	0.3	<0.1	0.1	1
Carex lacustris Willd.	Cyperaceae	19.0	2.9	8.8	57
Carex sartwellii Dewey	Cyperaceae	53.7	8.9	24.6	161
Carex stricta Lam.	Cyperaceae	23.3	5.5	16.5	70
Carex vulpinoidea Michaux	Cyperaceae	0.3	<0.1	0.1	1
Cicuta bulbifera L.	Apiaceae	1.3	0.1	0.2	4
Cicuta maculata L.	Apiaceae	1.7	0.1	0.3	5

Table 3-4 (cont'd).

Species	Family	Frequency of Occurrence (%)	Contribution to Total IV (%)	Species IV	N
Circium arvense (L.) Scop.	Asteraceae	10.0	0.6	1.8	30
Cladium mariscoides (Muhl.) Torrey	Cyperaceae	34.3	2.5	7.6	103
Cornus amomum Miller	Cornaceae	3.0	0.2	0.5	9
Cornus stolonifera Michaux	Cornaceae	7.0	0.4	1.3	21
Eleocharis rostellata Torrey	Cyperaceae	0.7	0.1	0.2	2
Eleocharis smallii Britton	Cyperaceae	8.7	1.0	2.9	26
Epilobium hirsutum L.	Onagraceae	1.0	0.1	0.2	3
Equisetum arvense L.	Equisetaceae	0.3	<0.1	1.0	1
Equisetum hyemale L.	Equisetaceae	0.3	<0.1	0.1	1
Eupatorium maculatum L.	Asteraceae	1.7	0.1	0.4	5
Eupatorium perfoliatum L.	Asteraceae	2.3	0.1	0.4	7
Fragaria virginiana Miller	Rosaceae	0.7	<0.1	0.1	2
Fraxinus pennsylvanica Marshall	Oleaceae	<0.1	<0.1	<0.1	1
Galium obtusum Bigelow	Rubiaceae	12.7	1.2	3.5	38
Geum laciniatum Murray	Rosaceae	0.3	<0.1	0.1	1
Helenium autumnale L.	Asteraceae	0.7	0.1	0.2	2
Hypericum kalmianum L.	Clusiaceae	1.0	0.1	0.2	3
Impatiens capensis Meerb.	Balsaminaceae	8.7	0.5	1.5	26
Iris versicolor L.	Iridaceae	2.3	0.3	0.7	7
Juncus balticus Willd.	Juncaceae	9.3	0.9	2.6	28
Juncus brevicaudatus (Englem.) Fern.	Juncaceae	4.3	0.5	1.6	13
Juncus effusus L.	Juncaceae	0.3	<0.1	0.1	1
Lathyrus palustris L.	Fabaceae	17.3	1.0	3.0	52
Leerzia oryzoides (L.) Sw.	Poaceae	4.3	0.3	0.8	13
Lobelia kalmii L.	Campanulaceae	0.7	<0.1	0.1	2
Lycopus americanus W.P.C. Barton	Lamiaceae	5.7	0.3	1.0	17
Lysmachia quadriflora Sims	Primulaceae	4.7	0.4	1.3	14
Lysmachia terrestris (L.) BSP.	Primulaceae	1.0	0.1	0.2	3
Lysmachia thrysiflora L.	Primulaceae	3.7	0.2	0.7	11
Lythrum alatum Pursh	Lythraceae	0.7	<0.1	0.1	2

Table 3-4 (cont'd).

Species	Family	Frequency of Occurrence (%)	Contribution to Total IV (%)	Species IV	N
Lythrum salicaria L.	Lythraceae	12.3	1.4	4.3	37
Mentha arvensis L.	Lamiaceae	5.7	0.4	1.0	17
Onoclea sensibilus L.	Polypodiaceae	0.3	<0.1	0.1	1
Panicum spp.	Poaceae	<0.1	<0.1	<0.1	1
Panicum virgatum L.	Poaceae	1.7	0.2	0.5	5
Phalaris arundinacea L.	Poaceae	14.7	3.0	9.0	44
Phragmites australis (Cav.) Steudel	Poaceae	6.7	1.3	3.8	20
Poa palustris L.	Poaceae	1.3	0.1	0.3	4
Poa spp.	Poaceae	<0.1	<0.1	<0.1	1
Polygonum amphibium L.	Polygonaceae	42.7	2.6	7.9	128
Polygonum scandens L.	Polygonaceae	0.3	<0.1	0.1	1
Populus deltoides Marsh.	Salicaceae	1.3	0.1	0.2	4
Potentilla anserina L.	Rosaceae	5.7	0.5	1.4	17
Potentilla fruticosa L.	Rosaceae	2.0	0.2	0.6	6
Pycnanthemum virginianum (L.) B.L. Rob & Fernald	Lamiaceae	1.3	0.1	0.4	4
Rubus spp.	Rosaceae	0.3	<0.1	0.1	1
Rudbeckia hirta L.	Asteraceae	0.7	<0.1	0.1	2
Sagittaria latifolia Willd.	Alismataceae	1.0	0.1	0.2	3
Salix petiolaris J.E. Smith	Salicaceae	4.3	0.3	0.8	13
Scirpus acutus Bigelow	Cyperaceae	1.7	0.1	0.4	5
Scirpus americanus Pers.	Cyperaceae	0.7	0.1	0.2	2
Scirpus atrovirens Willd.	Cyperaceae	0.3	<0.1	0.1	1
Scirpus validus Vahl	Cyperaceae	1.0	0.1	0.3	3
Scutellaria galericulata L.	Lamiaceae	5.3	0.3	0.9	16
Scutellaria lateriflora L.	Lamiaceae	0.3	<0.1	0.1	1
Solanum dulcamara L.	Solanaceae	0.3	<0.1	0.1	1
Solidago uliginosa Nutt.	Asteracese	0.3	<0.1	0.1	1
Spartina pectinata Link	Poaceae	4.7	0.7	2.0	14
Spiraea alba Duroi	Rosaceae	1.7	0.1	0.3	5
Spiranthes lucida (H.H. Eaton) Ames	Orchidaceae	0.3	<0.1	0.1	1
Stachys tenuifolia Willd.	Lamiaceae	17.3	1.1	3.3	52
Taraxacum officiale Wiggers	Asteraceae	1.0	0.1	0.2	3
Teucrium canadense L.	Lamiaceae	2.7	0.2	0.5	8
Thelyptris palustris Schott	Polypodiaceae	0.3	0.1	0.4	1
Typha angustifolia L.	Typhaceae	19.0	2.2	6.5	57

Table 3-4 (cont'd).

Species	Family	Frequency of Occurrence (%)	Contribution to Total IV (%)	Species IV	N
Typha latifolia L.	Typhaceae	1.0	0.1	0.3	3
Unknown #1	unk.	0.3	<0.1	0.1	1
Unknown #2	unk.	<0.1	<0.1	<0.1	1
Verbena hastata L.	Verbenaceae	0.3	<0.1	0.1	1
Viola affinis Le Conte	Violaceae	0.3	<0.1	0.1	1
Vitis riparia Michaux	Vitaceae	0.3	<0.1	0.1	1

Table 3-5. Frequency of occurrence, contribution to total IV, life form/habit, and National Wetlands Inventory (NWI) classification of plant species contributing 1% or more of total Saginaw Bay coastal wet meadow (SBCWM) IV. The 15 species (5 sedges, 3 grasses, 1 cattail, and 6 forbs) contributed 84.0% of total SBCWM IV. A total of 300 0.25-m^2 sample plots were collected in 25 SBCWM. Percent frequency of occurrence was determined from the number of sample plots in which the species was found. N equals the number of plots in which a species occurred.

Species	N	Frequency of Occurrence (%)	Contribution to Total IV (%)	Life Form/ Habit[1]	NWI Region 3 Classification [2]
Calamagrostis canadensis	276	92.0	31.1	PNG	OBL
Carex aquatilis	150	50.0	14.6	PNEGL	OBL
Carex sartwellii	161	53.7	8.9	PNGL	FACW+
Carex stricta	70	23.3	5.5	PNEGL	OBL
Campanula aparinoides	141	47.0	4.5	PNF	OBL
Phalaris arundinacea	44	14.7	3.0	PNG	FACW+
Carex lacustris	57	19.0	2.9	PNEGL	OBL
Polygonum amphibium	128	42.7	2.6	PNEZF	OBL
Cladium mariscoides	103	34.3	2.5	PNEGL	OBL
Typha angustifolia	57	19.0	2.2	PNEF	OBL
Lythrum salicaria	37	12.3	1.4	PIF	OBL
Phragmites australis	20	6.7	1.3	PNEG	FACW+
Calystegia sepium	60	20.0	1.2	PIF	FAC
Galium obtusum	38	12.7	1.2	PNF	OBL
Stachys tenuifolia	52	17.3	1.1	PNF	OBL

(1) - E = Emergent, F = Forb, G = Grass, GL = Grass-like (sedges and rushes), I = Introduced, N = Native, P = Perennial, Z = Submerged (Reed, 1988).

(2) - OBL = obligate wetland species, with >99% probability of occurrence in wetlands; FACW+ = facultative wetland species, with 67%-99% probability of occurrence in wetlands, '+' indicates that the probability is closer to the higher rather than the lower end of the range; FAC = facultative species, with 34%-66% probability of occurrence in wetlands, are considered equally likely to occur in wetlands or non-wetlands (Reed, 1988).

Table 3-6. Species richness, Leaf-area index (LAI), Shannon-Wiener diversity index (H'), Evenness (J), and Dominance (1-J) by site of Saginaw Bay coastal wet meadow vegetation.

Site	Species richness [1] (species/m^2)	N [2]	LAI [1] (m^2/m^2)	H'	Evenness (J) [3]	Dominance (1-J)
1	20.0(0.7)	47	5.3(0.4)	1.59	0.80	0.20
2	13.8(0.8)	39	5.2(0.5)	1.50	0.75	0.25
3	14.8(1.0)	48	5.5(0.4)	1.57	0.79	0.21
4	17.5(2.8)	44	4.1(0.4)	1.52	0.77	0.23
5	21.8(1.9)	47	5.4(0.4)	1.64	0.83	0.17
6	21.6(0.9)	48	4.8(0.4)	1.63	0.82	0.18
8	9.8(1.0)	44	4.6(0.5)	1.31	0.66	0.34
9	14.4(0.9)	45	7.7(0.8)	1.54	0.78	0.22
10	16.4(1.8)	46	6.1(0.6)	1.66	0.84	0.16
11	13.0(0.8)	43	4.7(0.4)	1.59	0.80	0.20
13	13.8(0.6)	39	4.5(0.5)	1.53	0.77	0.23
14	17.2(1.1)	42	4.6(0.4)	1.66	0.84	0.16
15	16.8(0.4)	47	4.1(0.4)	1.57	0.79	0.21
18	27.2(1.7)	43	5.0(0.5)	1.71	0.86	0.14
19	11.6(0.7)	44	5.0(0.6)	1.32	0.67	0.33
20	18.6(0.4)	44	3.7(0.4)	1.65	0.83	0.17
21	10.2(1.6)	43	4.4(0.4)	1.47	0.74	0.26
22	9.0(0.8)	38	3.1(0.3)	1.17	0.59	0.41
24	10.2(1.1)	41	5.3(0.6)	1.38	0.69	0.31
25	10.8(0.8)	45	5.0(0.6)	1.40	0.71	0.29
26	17.6(0.9)	48	6.0(0.4)	1.64	0.83	0.17
27	11.4(0.5)	46	4.9(0.5)	1.43	0.72	0.28
28	11.2(0.4)	46	5.1(0.3)	1.70	0.86	0.14
30	22.8(1.6)	39	4.1(0.4)	1.62	0.82	0.18
31	13.8(1.8)	48	5.5(0.5)	1.39	0.70	0.30
All Sites	15.4(0.5)	1104	5.0(0.1)	1.53(0.03)	0.77	0.23

(1) - Mean(±1SEM)

(2) - N = the number of samples in which leaf contact occurred. Inflorescence and stem contacts were excluded

(3) - J = H'/H'max (H'max = 1.98)

Table 3-7. Comparison of species richness and leaf-area index (LAI) for various wet meadow sites.

A. Species richness

Wetland type	Location	Species richness	Reference
Wet meadow	Michigan, USA	15.4spp./m^2	This study
Wet grassland	Netherlands	20spp./m^2	Fliervoet and Werger, 1984(1)
Wet meadow	Spain	14.2spp./m^2	Rey Benayas and Scheiner, 1993
Wet meadow	Spain	23.9spp./m^2	Rey Benayas et al., 1999
Wet meadow	Kwa-Zulu Natal	20spp./100m^2	Eckhardt et al., 1996
Wet meadow	Switzerland	12-36spp./4m^2	Gusewell and Klotzli, 1998(2)

(1) - Species richness was the same for both vegetation types examined
(2) - Species richness varied depending on dominant species

B. Leaf-area index

Wetland type	Location	LAI	Reference
Wet meadow	Michigan, USA	5.0	This study
Wet grassland(1)	Netherlands	11.7	Fliervoet and Werger, 1984
Wet grassland(2)	Netherlands	8.4	Fliervoet and Werger, 1984
Ungrazed tall grass prairie	Kansas, USA	3.1	Conant and Risser, 1974
Grass meadow	Central Europe	2.1	Gloser, 1993
Savanna grassland	Kenya	3.1	Kinyamarino and Imbamba, 1991
Saline grassland	Mexico	1.6	Garcia-Moya and Montanez Castro, 1991
Floodplain grassland	Central Amazon	4.75	Piedade et al., 1991

(1) - *Circium-Molinia* grassland (Cirsio-Molinietum)
(2) - *Agrostis-Calamagrostis-Carex* grassland (Senecioni-Bromentum)

Table 3-8. Pearson product-moment correlation of plant species contributing 1% or more of total Saginaw Bay coastal wet meadow importance value. Correlation values significant at $P<0.05$ ($r_{cv\,(0.05,23)} = \pm0.398$; Snedecor and Cochran, 1980, Table A11) are indicated in boldface and with asterisks.

	CALCAN	CAMAPA	CARAQU	CARLAC	CARSTR	CARSAR	CLAMAR	CALSEP	GALOBT	LYTSAL	PHAARU	PHRAUS	POLAMP	STATEN	TYPANG
CALCAN	1.000														
CAMAPA	0.331	1.000													
CARAQU	-0.262	0.052	1.000												
CARLAC	0.083	-0.111	0.062	1.000											
CARSTR	**-0.596***	-0.172	-0.201	-0.166	1.000										
CARSAR	**-0.482***	-0.209	0.033	**-0.452***	0.291	1.000									
CLAMAR	**-0.459***	-0.280	0.071	-0.387	0.329	**0.840***	1.000								
CALSEP	-0.026	0.086	0.224	0.258	-0.094	-0.307	-0.348	1.000							
GALOBT	**-0.571***	0.147	0.235	-0.155	**0.505***	0.196	0.047	0.148	1.000						
LYTSAL	0.003	-0.114	-0.181	**-0.495***	-0.204	0.041	0.103	-0.248	-0.266	1.000					
PHAARU	-0.217	**-0.436***	-0.284	0.300	0.020	0.068	0.084	0.137	-0.018	0.004	1.000				
PHRAUS	0.078	0.112	-0.194	-0.061	-0.147	-0.213	-0.163	-0.113	-0.249	0.368	0.167	1.000			
POLAMP	0.301	-0.252	-0.251	0.362	-0.237	-0.284	-0.204	-0.037	**-0.502***	-0.024	0.028	0.139	1.000		
STATEN	-0.178	0.365	0.180	-0.310	0.342	0.317	0.296	0.035	**0.434***	-0.197	-0.274	-0.313	**-0.398***	1.000	
TYPANG	-0.091	-0.346	-0.092	-0.175	0.203	0.276	0.155	-0.168	0.097	-0.025	0.213	-0.390	-0.322	0.179	1.000

CALCAN = *Calamagrostis canadensis*; CAMAPA = *Campanula aparinoides*; CARAQU = *Carex aquatilis*; CARLAC = *Carex lacustris*; CARSTR = *Carex stricta*; CARSAR = *Carex sartwellii*; CLAMAR = *Cladium mariscoides*; CALSEP = *Calystegia sepium*; GALOBT = *Galium obtusum*; LYTSAL = *Lythrum salicaria*; PHAARU = *Phalaris arundinacea*; PHRAUS = *Phragmites australis*; POLAMP = *Polygonum amphibium*; STATEN = *Stachys tenuifolia*; TYPANG = *Typha angustifolia*.

Table 3-9. Median height and maximum/minimum height range of common plant species occurring in Saginaw Bay coastal wet meadows. Canopy Emergent species were those with median heights >90cm, Canopy Species were those with median heights between 50-90cm, and Understory Species were those with median heights <40cm. Clingers/Climbers were species utilizing other plants for support. N is the total number of leaf contacts observed during sampling. Species with N<5 were excluded from the analysis.

Species	N	Median Height (cm)	Height Range (cm)
"Canopy Emergents"			
Typha angustifolia	80	138.5	223-38
Phragmites australis	49	128	223-41
"Canopy Species"			
Spartina pectinata	29	84	129-28
Carex lacustris	292	79	145-22
Carex aquatilis	1278	73	159-11
Lythrum salicaria	94	70	146-28
Juncus balticus	26	67.5	107-30
Phalaris arundinacea	236	67	188-6
Carex bebbii	73	66	104-16
Cladium mariscoides	21	65	88-18
Calamagrostis canadensis	2707	63	208-7
Carex buxbaumii	15	62	93-30
Iris versicolor	7	58	75-25
Carex sartwellii	871	58	140-9
Poa palustris	8	57	99-27
Circium arvense	8	55.5	64-25
Carex stricta	354	49.5	109-7
Aster dumosus	48	44	96-16
Polygonum amphibium	50	42	91-11
Eupatorium perfoliatum	7	40	62-16
"Clingers/Climbers"			
Calystegia sepium	27	54	78-17
Campanula aparinoides	194	27	73-7
Galium obtusum	40	20.5	50-3
"Understory Species"			
Cornus stolonifera (seedlings)	10	39	54-20
Eleocharis rostellata	10	37.5	46-21
Mentha arvensis	7	37	47-11
Lathyrus palustris	20	32.5	51-8
Juncus brevicaudatus	12	32.5	41-23
Stachys tenuifolia	10	27.5	50-15
Anemone canadensis	15	25	52-4
Eleocharis smallii	6	25	32-13
Lysmachia quadriflora	13	23	59-10
Thelyptris palustris	10	22.5	30-14
Potentilla anserina	8	19	23-14

Table 3-10. Pearson product-moment correlation among Saginaw Bay coastal wet meadow major plant species IV and abiotic factors measured in 1997. Litter depth and peat depth were square-root transformed to achieve normal distribution. Plots in which litter depth was not determined were excluded from the analysis. Soil texture increased from fine- to coarse-textured substrates. Values indicated with boldface and an asterisk were significant at $P<0.05$ ($r_{cv(0.05,\,215)} = \pm 0.134$; Snedecor and Cochran, 1980, Table A11).

	Plot Elevation	Peat Depth	Litter Depth	Soil Texture
Calamagrostis canadensis	**-0.158***	**0.155***	**0.221***	-0.091
Campanula aparinoides	**0.367***	**-0.191***	**-0.366***	**0.275***
Carex aquatilis	**-0.309***	**0.235***	**0.346***	-0.025
Carex lacustris	**-0.281***	**0.189***	**0.394***	**-0.194***
Carex stricta	**0.475***	**-0.340***	**-0.556***	0.119
Carex sartwellii	**-0.225***	**0.268***	0.080	0.120
Cladium mariscoides	-0.103	**0.200***	0.009	**0.253***
Calystegia sepium	**0.306***	**-0.312***	-0.089	**-0.148***
Galium obtusum	**0.458***	**-0.183***	**-0.438***	**0.269***
Lythrum salicaria	-0.132	0.006	-0.035	-0.013
Phalaris arundinacea	0.042	-0.102	0.097	**-0.166***
Phragmites australis	**-0.184***	**0.172***	**0.165***	-0.119
Polygonum amphibium	**-0.299***	**0.267***	**0.241***	**-0.226***
Stachys tenuifolia	**0.302***	-0.076	**-0.289***	**0.203***
Typha angustifolia	-0.105	**0.156***	0.100	**0.156***

Table 3-11. Change in importance value across the elevation gradient for species found in Saginaw Bay coastal wet meadows. Data were collected in 288 sample plots at 24 study sites. Site #1 was isolated from Saginaw Bay by a dike, and so was excluded from the analysis. Sites became wetter as elevation decreased. Mean annual high water mark for Saginaw Bay (1918-1996) equaled 176.67 m AMSL.

Species	Elevation interval (m AMSL)							
	177.25	177.15	177.05	176.95	176.85	176.75	176.65	176.55
Phalaris arundinacea	84.2	15.9	6.0	10.9	4.1	0.8		
Carex bebbii	50.5	1.1	2.7	4.4	0.6			
Carex stricta	42.2	33.6	26.9	8.9	1.8	3.3		
Calamagrostis canadensis	23.2	86.8	96.0	107.2	98.5	64.2	69.5	25.2
Lathyrus palustris	13.9	4.9	3.6	2.7	0.7			
Stachys tenuifolia	13.3	4.7	5.1	2.4	0.8	0.7		
Potentilla anserina	12.9	3.3	2.3					
Anemone canadensis	10.0	4.5	2.5	0.2	0.6			
Campanula aparinoides	8.7	21.2	17.9	13.0	4.9	1.6	16.7	
Galium obtusum	8.3	11.1	4.1	0.3				18.0
Taraxacum officinale	6.9	0.5						
Agropyron repens	6.6	2.3	0.2					
Cerastium vulgatum	6.5							
Spiraea alba	6.4		0.4	0.3		0.8		
Calystegia sepium	6.4	6.8	3.2	4.6	1.1			
Carex sartwellii		14.4	17.3	31.6	35.7	55.3	14.6	
Aster dumosus		8.7	2.5	1.3				
Spartina pectinata		6.0	3.3					
Circium arvense		4.7	3.0					
Cornus stolonifera		2.9	2.5	0.2				
Poa palustris		2.3	0.2					
Impatiens capensis		2.3	1.0	2.5	0.4			
Eupatorium maculatum		2.2						
Cornus amomum		2.1	0.4					
Thelypteris palustris		1.9						
Apocynum canabinum		1.7	1.3	0.9				
Mentha arvensis		1.6	1.9	0.9				
Lycopus americanus		1.6	1.8	0.4				
Juncus brevicaudatus		1.4	4.2	1.1				
Eleocharis smallii		1.3	7.6	1.5	2.3			
Scutellaria galericulata		1.2	1.1	1.1	0.3			
Leerzia oryzoides		1.0	1.8	0.5				
Aster borealis		0.9	3.0	1.1	0.3			

Table 3-11 (cont'd)

Species	Elevation interval (m AMSL)							
	177.25	177.15	177.05	176.95	176.85	176.75	176.65	176.55
Lysmachia thrysiflora		0.8	0.6	1.3				
Lysmachia terrestris		0.7	0.3					
Iris versicolor		0.6	1.8	0.7				
Populus deltoides		0.5	0.2		0.4			
Eupatorium perfoliatum		0.5	1.0					
Lobelia kalmii		0.5						
Epilobium hirsutum		0.4		0.4				
Teucrium canadense		0.4	0.8	0.8				
Fragaria virginiana		0.3	0.2					
Rudbeckia hirta		0.3	0.2					
Vitis riparia		0.3						
Geum laciniatum		0.3						
Helenium autumnale		0.3	0.5					
Lythrum alatum		0.2	0.2					
Circium maculatum		0.2	0.6	0.4				
Spiranthes lucida		0.2						
Hypericum kalmianum		0.2	0.7					
Fraxinus pennsylvanica*								
Potentilla fruticosa			2.4					
Pycnanthemum virginianum			1.5					
Panicum spp.			1.2					
Poa spp.*								
Asclepias incarnata			0.9	0.2				
Solidago uliginosa			0.3					
Verbena hastata			0.3					
Viola affinis			0.2					
Equisetum hyemale			0.2					
Alisma plantago-aquatica			0.2					
Unknown #1			0.2					
Rubus spp.			0.2					
Panicum virgatum*								
Unknown #2*								
Scirpus americanus				0.7				
Onoclea sensibilus				0.2				
Carex hystericina				0.2				
Scutellaria lateriflora				0.2				
Acorus calamus				0.2				
Typha latifolia				0.8	0.4			
Equisetum arvense					0.4			
Polygonum scandens					0.4			
Juncus effusus					0.5			

Table 3-11 (cont'd)

Species	Elevation interval (m AMSL)							
	177.25	177.15	177.05	176.95	176.85	176.75	176.65	176.55
Solanum dulcamara					0.5			
Cicuta bulbifera				0.4	0.7			
Eleocharis rostellata				0.5		1.2		
Scirpus validus				0.5		2.2		
Carex comosa				0.3		0.8		
Carex buxbaumii				0.4	12.2	5.2		
Scirpus acutus		0.4	0.2	0.3	0.6	0.8		
Salix petiolaris		0.5	0.8	0.2	1.4	2.4		
Phragmites australis		0.7	0.6	4.9	9.5	3.4		
Juncus balticus		1.1	1.7	2.8	5.1	3.5		
Lythrum salicaria		1.8	6.5	1.9	9.6	4.7		
Cladium mariscoides		3.7	6.4	8.5	10.9	14.3		
Typha angustifolia		2.9	3.7	5.4	10.7	20.0		
Polygonum amphibium		4.2	4.7	10.2	12.2	14.6	7.4	
Sagittaria latifolia					0.5	0.7	7.7	
Scirpus atrovirens								20.9
Lysmachia quadriflora		2.5	2.9					18.1
Carex lacustris		2.0	2.7	11.8	15.6	14.7	34.3	36.6
Carex aquatilis		18.6	31.3	47.8	56.3	84.8	149.8	181.2
Totals		300	300	300	300	300	300	300

* - IV <0.1 at all elevation intervals.

Table 3-12. Change in importance value across the elevation gradient for species found at Site #1, a wet meadow isolated from Saginaw Bay by a dike. Data was collected in 12 sample plots, three plots at each of four elevations, in 1997. Sites became wetter as elevation decreased. Mean annual high water mark for Saginaw Bay (1918-1996) equaled 176.67 m AMSL. Species distribution patterns were similar for this site and 24 study sites not isolated from Saginaw Bay.

Species	Elevation interval (m AMSL)			
	177.15	177.05	176.95	176.85
Carex stricta	72.7		56.4	38.7
Phalaris arundinacea	41.9	19.4	81.9	31.0
Spartina pectinata	36.1			
Aster dumosus	33.3	14.6		
Calystegia sepium	29.0	20.9	3.2	
Galium obtusum	21.3			
Carex sartwellii	11.6	25.4	22.7	12.7
Calamagrostis canadensis	10.3	63.7	15.7	15.4
Mentha arvensis	8.8		4.0	
Polygonum amphibium	8.1		20.8	
Potentilla anserina	7.2	12.4		
Anemone canadensis	6.3			
Agropyron repens	3.2			
Cladium mariscoides	3.5	14.1	4.4	
Lathyrus palustris	3.5	11.3	3.2	
Scutellaria galericulata	3.1		3.3	
Carex aquatilis		118.3	16.1	
Apocynum canabinum			3.3	
Salix petiolaris*				
Stachys tenuifolia*				
Iris versicolor			6.9	
Scirpus validus			8.6	
Teucrium canadense			3.5	
Acorus calamus			3.8	
Typha angustifolia			15.7	
Cicuta bulbifera			4.0	12.4
Solanum dulcamara				16.8
Carex lacustris			22.5	173.0
Totals	300	300	300	300

* - IV<0.1 at all elevation intervals.

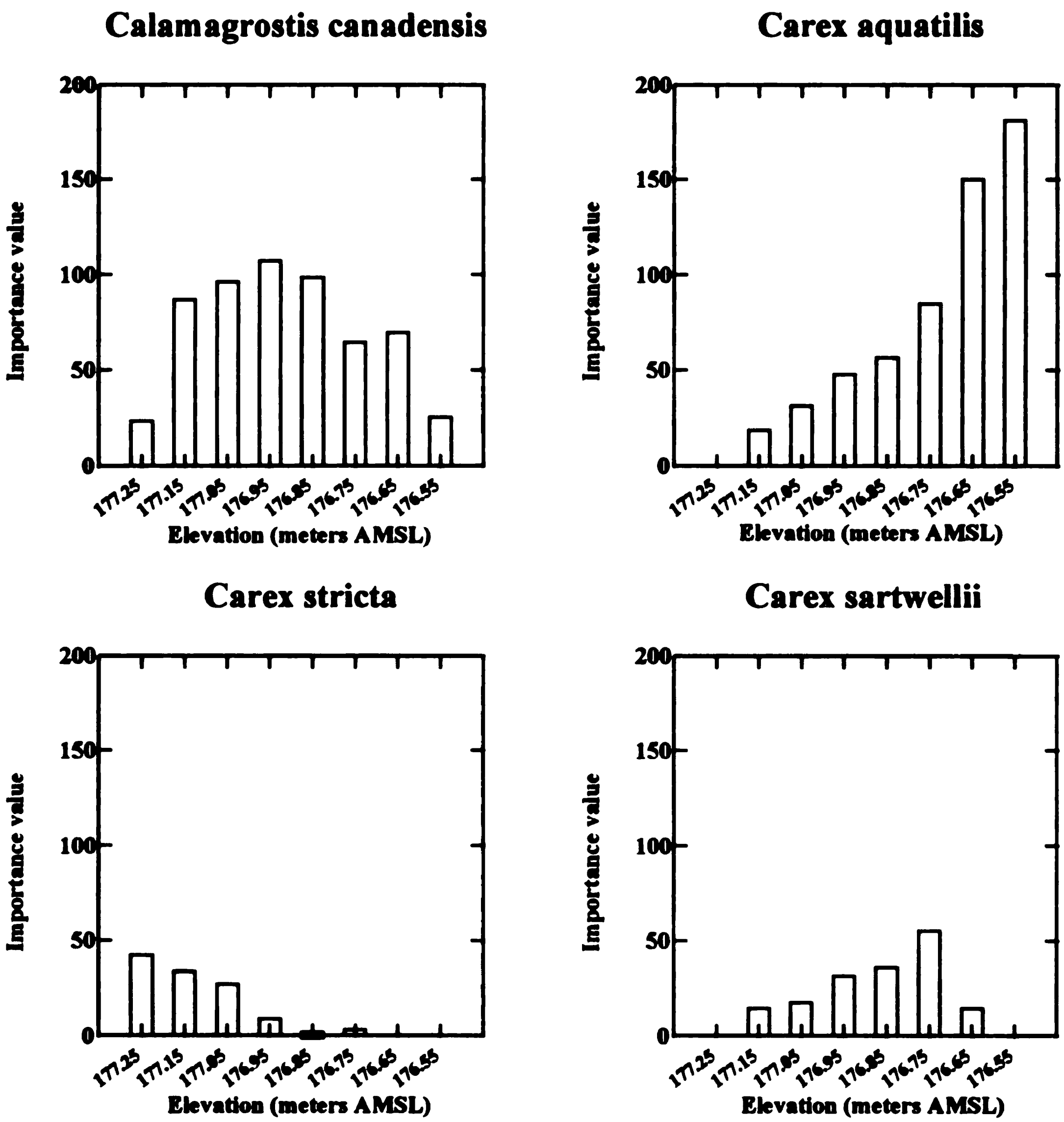

Figure 3-12. Importance value of *Calamagrostis canadensis*, *Carex aquatilis*, *Carex stricta*, and *Carex sartwellii* at different elevations within Saginaw Bay coastal wet meadows. Maximum possible IV = 300. The mean Saginaw Bay high water mark (1918-1996) equaled 176.67 m AMSL.

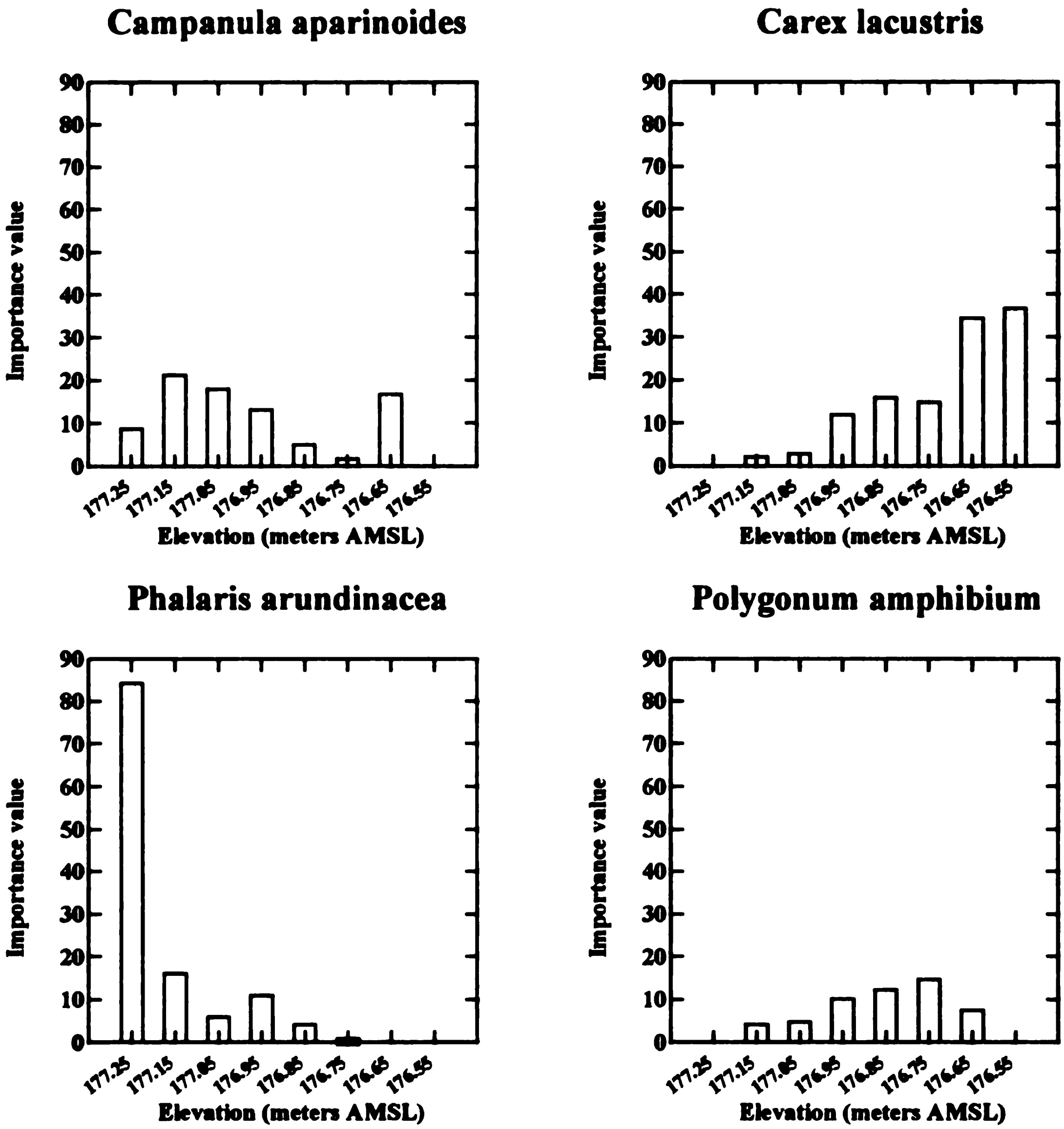

Figure 3-13. Importance value of *Campanula aparinoides*, *Carex lacustris*, *Phalaris arundinacea*, and *Polygonum amphibium* at different elevations within Saginaw Bay coastal wet meadows. Maximum possible IV = 300. The mean Saginaw Bay high water mark (1918-1996) equaled 176.67 m AMSL.

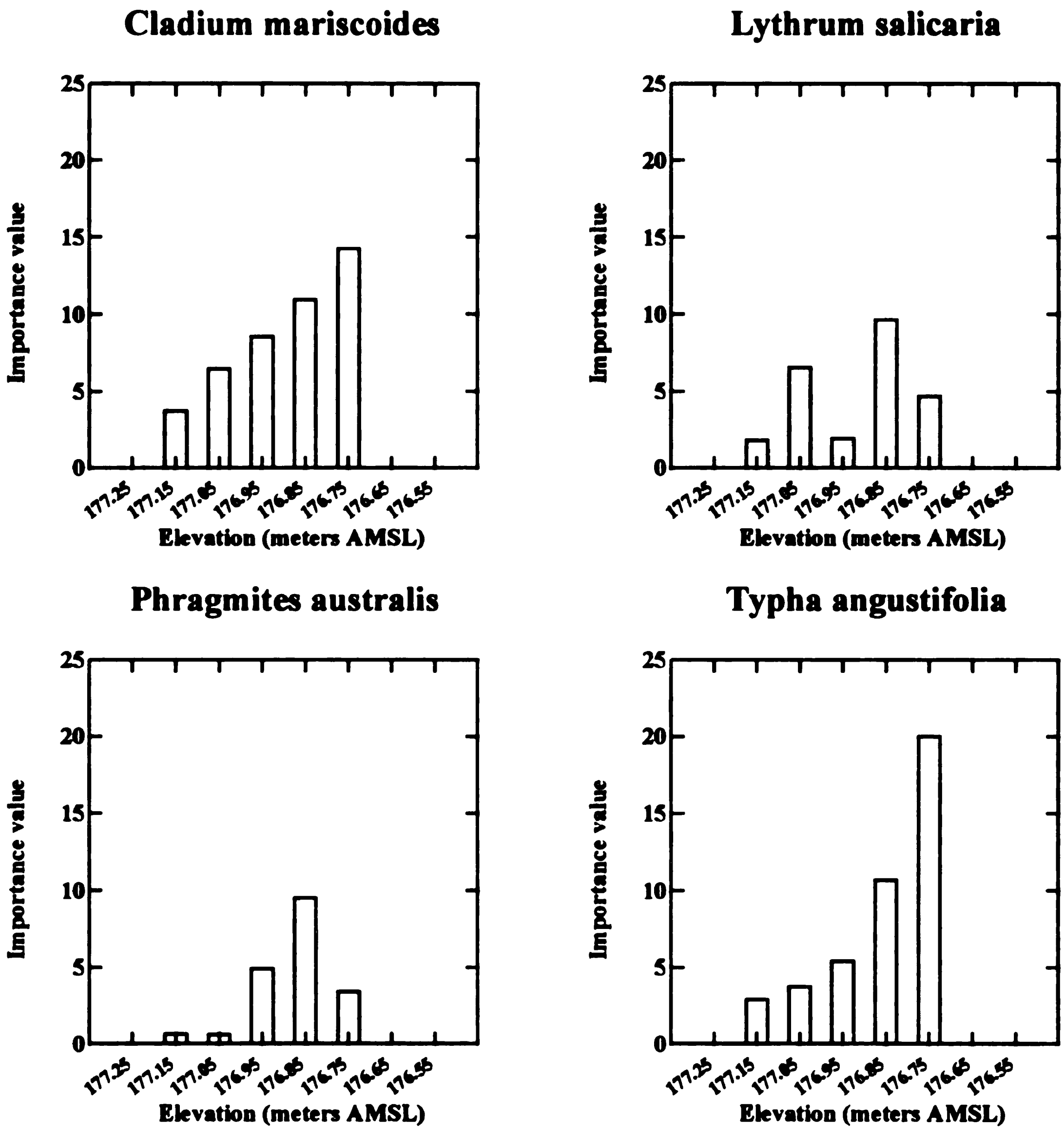

Figure 3-14. Importance value of *Cladium mariscoides*, *Lythrum salicaria*, *Phragmites australis*, and *Typha angustifolia* at different elevations within Saginaw Bay coastal wet meadows. Maximum possible IV = 300. The mean Saginaw Bay high water mark (1918-1996) equaled 176.67 m AMSL.

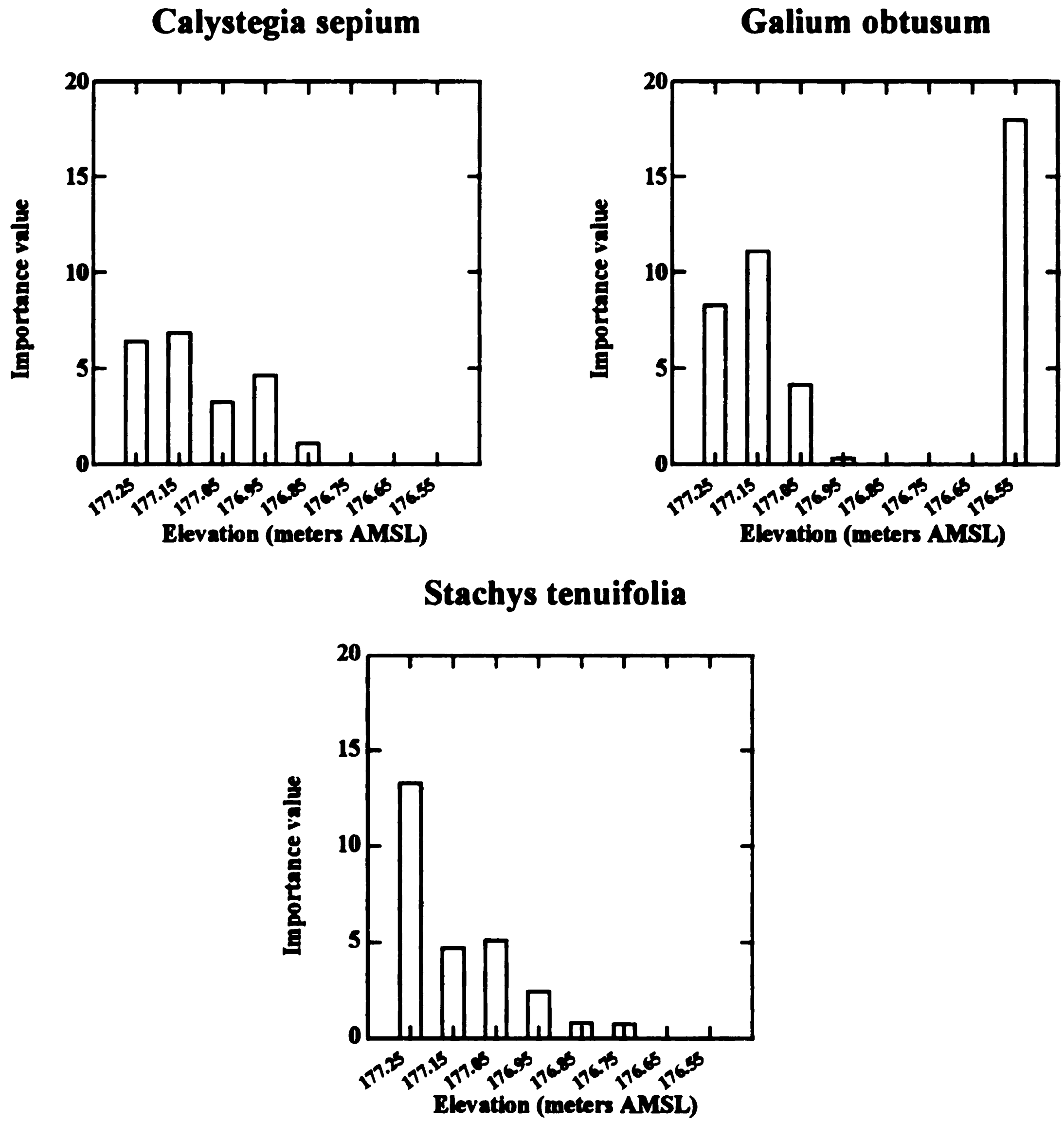

Figure 3-15. Mean importance value of *Calystegia sepium, Galium obtusum,* and *Stachys tenuifolia* at different elevations within Saginaw Bay coastal wet meadows. Maximum possible IV = 300. The mean Saginaw Bay high water mark (1918-1996) equaled 176.67 m AMSL.

Table 3-13. Pearson product-moment correlation between Saginaw Bay coastal wet meadow major plant species IV and hummock heights measured during 1997 vegetation sampling. Plots in which hummocks were not present or measured were excluded from the analysis. Values indicated with boldface and an asterisk were significant ($r_{cv(0.05, 49)} = \pm 0.273$; Snedecor and Cochran, 1980, Table A11(i)).

Species	Hummock Height
Calamagrostis canadensis	-0.048
Campanula aparinoides	0.099
Carex aquatilis	0.206
Carex lacustris	0.020
Carex sartwellii	-0.006
Carex stricta	-0.220
Cladium mariscoides	-0.255
Calystegia sepium	0.222
Galium obtusum	**-0.293***
Lythrum salicaria	**-0.326***
Phalaris arundinacea	-0.170
Phragmites australis	0.132
Polygonum amphibium	0.020
Stachys tenuifolia	-0.160
Typha angustifolia	-0.093

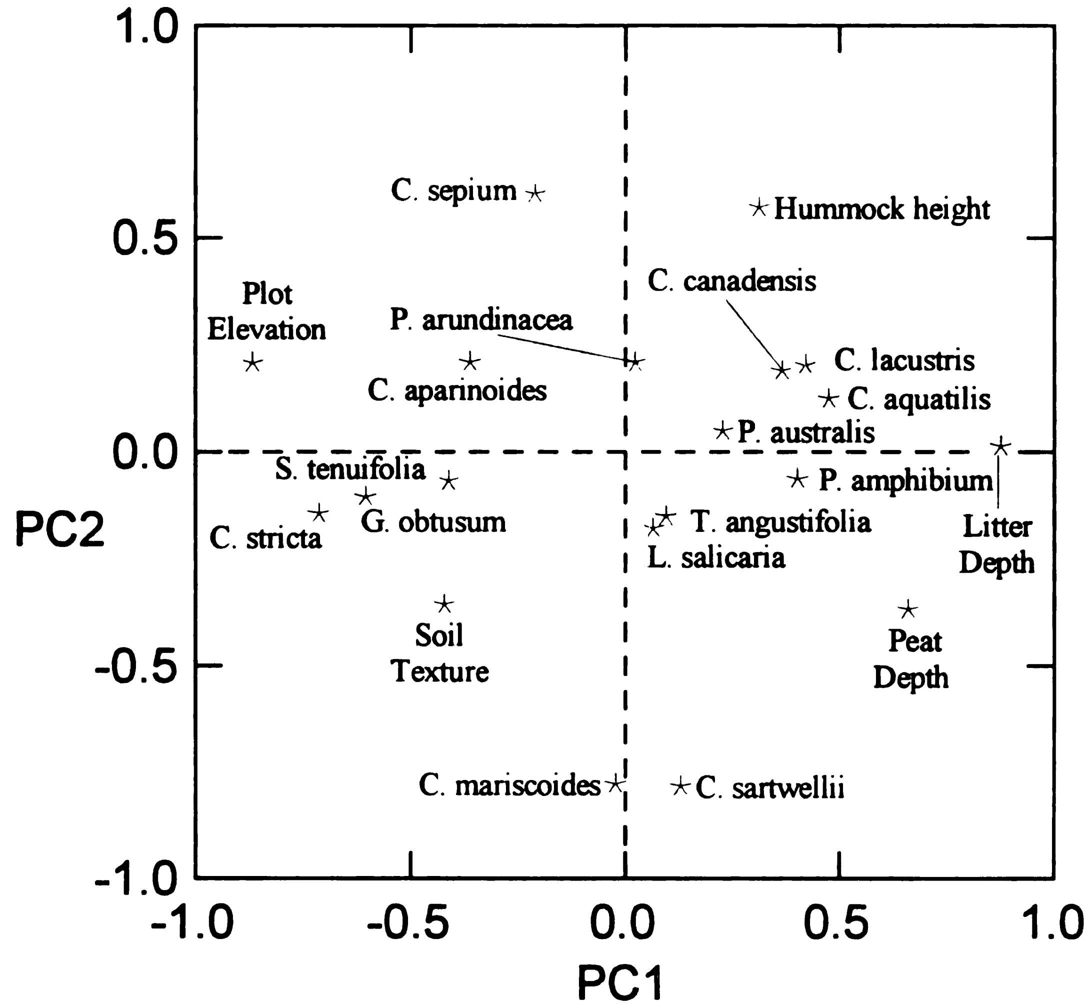

Figure 3-16. Principal component analysis bi-plot of major plant species importance values and abiotic factors in Saginaw Bay coastal wet meadows. PC1 was the best-fit line describing the association among the abiotic factors. The small angular offset of the elevation interval, soil texture, peat depth, and litter depth factors from PC1 indicated the strong linkage of these factors with PC1. Species located close to the negative end of PC1 (*C. stricta, G. obtusum*) were most strongly linked with higher elevation wet meadow plots containing thinner peat and litter mats and coarse-textured substrates. Those located close to the positive end of PC1 (*C. aquatilis, C. lacustris*) were most strongly linked with lower elevation wet meadow plots containing deeper litter mats and thicker peat.

Table 3-14. Physical and vegetation attributes that define the upper and lower Saginaw Bay coastal wet meadow sub-zones. Upper wet meadow vegetation occurred above 177.0m AMSL, lower wet meadow vegetation below that elevation. Data was collected in 300- 0.25m^2 plots in 25 wet meadows. N is the number of 0.25m^2 plots, except as indicated. All means were significantly different at P<0.05.

Variable	Upper wet meadow		Lower wet meadow	
	N	Mean(±1SEM)	N	Mean(±1SEM)
Species per 0.25m^2 plot	122	7.3(0.1)	178	4.9(0.1)
Vegetation height$^{(a)}$ (cm)	2591	50.1(0.3)	4116	69.3(0.2)
Hummock height$^{(b)}$ (cm)	15	23.4(3.1)	36	33.2(1.7)
Plot elevation (m AMSL)	122	177.09(0.01)	178	176.88(0.01)
Peat depth (cm)	122	1.1(0.1)	178	5.4(0.1)
Litter depth$^{(c)}$ (cm)	78	8.9(0.2)	137	18.4(0.2)

(a) - N equals number of vegetation contacts.
(b) - Plots in which hummocks were not present were excluded. N = 51.
(c) - Plots for which litter depths were not measured were excluded. N = 215.

Chapter 4 - Above-ground biomass and productivity of the vegetation in coastal wet meadows bordering Saginaw Bay[1]

Introduction

Wet meadows are an important component of the coastal wetland complex fringing Lake Huron's Saginaw Bay. Structural aspects of the macrophyte community, such as biomass production, govern the habitat value of these wetlands, and influence their ability to mitigate the impacts of flooding, erosion, pollution and sedimentation in the region (BURTON, 1985; WILCOX, 1995).

Biomass production estimates are available for certain Great Lakes wet meadow plant species (TILTON ET AL., 1978; JAWORSKI ET AL., 1979; KELLEY, 1985; KELLEY ET AL., 1985), for inland sedge and grass wet meadows in Wisconsin (STOUT, 1914; COSTELLO, 1936; KLOPATEK & STEARNS, 1978), Minnesota (BERNARD, 1974), and North America (BERNARD & GORHAM, 1978; RICHARDSON, 1978; BRINSON ET AL., 1981), and for wet meadow vegetation growing in prairie potholes (VAN DER VALK & DAVIS, 1978), English and Welsh rich fens (WHEELER & SHAW, 1991), Lake Okeechobee wetlands (HARRIS ET AL., 1995), and boreal lacustrine sedge fens (SZUMIGALSKI & BAYLEY, 1996). However, no studies have previously examined above-ground biomass production in Great Lakes coastal wet meadows.

Wet meadows are the sedge and/or grass dominated vegetation of wet or saturated soils (CURTIS, 1959; AUCLAIR ET AL., 1973; NIERING, 1985; KEDDY &

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[1] The chapter has been accepted in this form for publication in the Proceeding of the XXVII Congress of the *Societas Internationalis Limnologiae*.

REZNICEK, 1986; MNFI, 1989). While monocots dominate wet meadow vegetation, herbaceous dicots are important secondary community constituents (CURTIS, 1959; NIERING, 1986). Trees and shrubs are generally absent.

CURTIS (1959) provided the basic definition of wet meadows and wet prairies, describing sedge wet meadows as open communities found on wet soils, located low on the regional soil catena, with sedges supplying more than 50% of the vegetation dominance. Wet prairies differed from sedge meadows principally in that grasses, rather than sedges, were the dominant species (CURTIS, 1959). While intolerant of continuous inundation, wet meadow plants must be adapted to growing in more or less saturated conditions (CURTIS, 1959; AUCLAIR ET AL., 1973).

KEDDY & REZNICEK (1986) defined Great Lakes coastal wet meadows as the grass- and sedge- dominated herbaceous vegetation assemblage found between the yearly mean high water level and yearly maximum high water level in Great Lakes wetlands. They included wet meadows in a lake-margin wetland continuum composed of a series of discrete zones. These zones, from open water to uplands, were the submerged aquatic community, emergent cattail and bulrush marshes, the beach strand, wet meadows, and forest and shrub thickets. Keddy and Reznicek believed that the maximum high water level determined the lower limit of successful shrub invasion, and the mean high water level determined the lower limit of successful wet meadow growth.

Several factors are involved in Great Lakes coastal wet meadow development and maintenance. The most important include intra- and inter-specific competition (AUCLAIR ET AL., 1973; KEDDY, 1989), soil fertility (KEDDY, 1989), and water-level fluctuations (HARRIS ET AL., 1981; KELLEY ET AL., 1985; KEDDY & REZNICEK,

1986; KEOUGH, 1990; BATTERSON ET AL., 1991; WILCOX, 1995). These factors interact to define the composition and zonation of coastal wet meadow vegetation.

Our objectives were to determine the live biomass, standing dead biomass, and litter production of Saginaw Bay coastal wet meadow (SBCWM) vegetation, and to use these data to estimate SBCWM net above-ground primary productivity (NAPP).

Study area

Saginaw Bay, the southwestern lobe of Lake Huron (Figure 1-1), was formed and reshaped by Pleistocene glaciation and post-glacial Great Lakes water-level fluctuations (DORR & ESCHMAN, 1970). Covering 2960km^2, Saginaw Bay has maintained its current 622km shoreline for about the last 2500 years (DORR & ESCHMAN, 1970; SBNWI, 1998).

Saginaw Bay coastal wetlands may have covered more than 28000ha prior to European settlement (PRINCE & BURTON, 1995). Historically, wet meadow vegetation extended up to 5km inland along the Saginaw Bay shore line (DAVIS, 1900; ALBERT ET AL., 1988), but agricultural development has limited the present wet meadow zone to a narrow strip along the coast. Easily drained and very fertile, coastal wet meadows were among the first wetlands utilized after European settlement began in the 19th century. Development pressure has since resulted in the destruction of more than 99% of the region's original wet meadows (PRINCE & BURTON, 1995). Recent estimates of extant Saginaw Bay wetlands range between 6000-7300ha (JAWORSKI & RAPHAEL, 1978; USGS, 1996; SBNWI, 1998).

Methods

Biomass

Study sites were established throughout the Saginaw Bay coastal zone between Caseville, MI (43.93° N, 83.29° W) and Standish, MI (43.98° N, 83.96° W; Figure 4-1). Sites were contiguous with Saginaw Bay and subject to natural bay water level fluctuations.

Biomass samples were collected from 19 sites in July-August 1997, the period corresponding to maximum above-ground biomass ("peak standing crop") in Great Lakes wetlands (BARKO ET AL., 1977; KELLEY, 1985). At each site, the standing biomass contained in 12- 0.25m^2 sample plots was clipped at the substrate and then sorted, live biomass by species and dead material grouped as standing dead material. Plot placement was stratified within each site to capture potential biomass variability resulting from differences in inundation depth and frequency (see Chapter 3). Dry weights were determined for each species and for standing dead material (±0.1g) after oven-drying 48h at 60°C.

Biomass data were summed by plots, then pooled within sites to determine mean plot biomass for each site. Biomass data were pooled across sites by species to determine mean species biomass. Species frequency of occurrence was determined from the number of plots in which the species was found. Contributions to total wet meadow biomass were determined by dividing the pooled species biomass by the grand total of all biomass collected at all sites.

To aid interpretation of our results, we grouped species into eight categories: forbs, grasses, sedges, woody, dead, seedless vascular, rushes, and vines, classifying as forbs all herbaceous plants that were not grasses, sedges, or rushes. Woody vegetation included shrubs and trees; seedless vascular vegetation ferns and horsetails. Biomass data for each category were pooled across sites to determine mean category biomass and the contribution each category made to total SBCWM biomass.

Litter

Growing-season litter production was measured at two study sites in 1-m^2 by 0.9m tall open-topped enclosures. Fifteen enclosures, constructed of 1.5mm mesh aluminum screening material, were installed in groups of five, 3-5 meters from one another approximately two weeks after visible plant growth commenced in the spring. The bottom 5cm of screening was buried to prevent introduction of litter into the enclosures under the screening. All dead plant material was removed from the enclosures at the beginning of the experiment, while disturbing living plants as little as possible. Monthly thereafter, all vegetation located outside but within 2m of each enclosure was clipped to minimize introduction of material from outside the enclosures.

After 94 days, the period from the start of the growing season to peak standing crop (PSC), all standing material in the enclosures were clipped at the substrate, then all accumulated litter was raked from the enclosures. Any plant material lying on the substrate and not obviously fresh and green was considered litter. The standing plant material and litter were separately bagged and transported to the laboratory, where the standing plant material was sorted into living and dead material, and all samples were weighed after oven-drying 48h at 60°C.

Seasonal litter loss attributable to in-place decomposition was estimated at the two sites by loss from 20cm by 20cm litter bags. Forty-five bags, constructed from 1.5mm mesh black fiberglass screening material, received 10.0gm dry weight mixed living and standing dead plant material cut into 15 cm lengths. The mixture of living and dead plants simulated the decomposition of a natural mixture of fresh, unleached and old, leached material. Three bags were placed in contact with the substrate at each biomass enclosure. We chose 1.5mm mesh because it could contain herbaceous litter with minimal fragmentation loss, and was the mesh size most commonly used in decomposition studies of similar vegetation (BRINSON ET AL., 1981). Black screening matched the natural substrate color, minimizing differences in solar heating between the bags and substrate.

All litter bags were recovered after 87 days, packed in ice, and returned to the laboratory. The bags were gently washed to remove loose external debris, oven-dried 48h at 60°C, then opened and the contents weighed (±0.1g). Decomposition loss was determined by subtracting the litter mass remaining from the 10.0g initial weight of each bag.

Results and Discussion

Distribution of above-ground biomass

Mean PSC was 669g/m^2, live plants contributing 575g/m^2 and standing dead material 94g/m^2 to the total. Grasses and sedges constituted 75.3%, dead material 14.3%, and forbs 9.3% of total PSC. Woody and other plant types contributed <1% each to PSC (Figure 4-2).

Of 81 plant species encountered during sampling, five species, the grass *Calamagrostis canadensis*, and the sedges *Carex aquatilis, C. lacustris, C. sartwellii,* and *C. stricta,* contributed >32% of total PSC (Table 4-1). Nine forbs (*Campanula aparinoides, Circium arvense, Calystegia sepium, Galium obtusum, Impatiens capensis, Lathyrus palustris, Polygonum amphibium, Stachys tenuifolia,* and *Typha angustifolia*) each exhibited frequencies of occurrence >10%, and these collectively constituted almost 27% of total PSC. The 15 species together contributed 59% of total PSC.

Twenty species, representing 24.7% of species encountered, occurred in only one of the 228 sample plots. These species were either wetland plants uncommon to SBCWM or upland plants opportunistically occupying suitable micro-habitats within the wet meadow.

Mean PSC ranged between 323-933g/m^2 among sites, and between 113-2501g/m^2 among all sample plots (Table 4-2). The highest PSC occurred in plots containing *Typha angustifolia, Phragmities australis,* or *Lythrum salicaria*. The lowest PSC occurred in plots located near the maximum elevation of Saginaw Bay and dominated by *Eleocharis* spp. and short-stature wet meadow forbs.

SBCWM PSC fell within the range of values published for similar lacustrine and palustrine wetlands (Table 4-3). TILTON ET AL. (1978) estimated that PSC of *Carex*-dominated Great Lakes shoreline communities ranged between 200-1400g/m^2. KELLEY (1985) reported a PSC of 468g/m^2 for a Lake Michigan river-mouth *Carex/Calamagrostis* wet meadow. HARRIS ET AL. (1981) observed increasing annual PSC (from 337g/m^2 to

$1216g/m^2$) for *Calamagrostis canadensis* in Green Bay wet meadows as Lake Michigan water levels declined after a cyclic high (see Chapter 2). They attributed the increase to colonization of newly exposed mudflats.

Terrestrial grasslands exhibit lower PSC than SBCWM. Precipitation and soil moisture deficits limit grassland production (LAUENROTH, 1979), and soil moisture extremes reduce biomass production and NAPP in Canadian grasslands (HARCOMBE ET AL., 1993). However, even grasslands experiencing no significant annual drought period exhibit lower biomass production than SBCWM (LAUENROTH, 1979). Other factors, such as grazing intensity (WILLMS ET AL., 1996) and fire frequency (BRIGGS & KNAPP, 1995; BLAIR, 1997) also influence grassland production.

Our PSC value may underestimate SBCWM peak standing crop. During 1997, Lake Huron water levels were among the highest recorded since 1918. Many study sites were inundated for part of the growing season. Changes in vegetation zonation were observed, and signs of anoxic stress, including chlorosis, increased inter-node length, and adventitious root production, were noted in some wet meadow species (K. STANLEY, pers. obs.). Long periods of inundation negatively impact respiration and photosynthesis in the less inundation-tolerant wetland plants, reducing photosynthesis and diverting energy from production to survival (KOZLOWSKI, 1984; ERNST, 1990). Biomass production lags.

The mean litter biomass generated during the litter production experiment was $152g/m^2$, not including decomposition losses. The mean decomposition loss measured in the litter bag experiment was 5.46g/10.0g litter, suggesting that the $152g/m^2$ measured litter production represented approximately 45% of total seasonal litter production, and that an additional 186g/m^2 of litter was produced and decomposed in the 94 days between the start of the growing season and PSC.

The decomposition rate we observed (55% in 94 days) was 3-4 times higher than other reported values (DAVIS & VAN DER VALK, 1978; BRINSON ET AL., 1981). The comparatively low levels of refractory compounds found in herbaceous plant tissues, and rapid leaching of labile compound in the early stages of litter decay probably accounted for the high observed loss rate (DAVIS & VAN DER VALK, 1978; GODSHALK & WETZEL, 1978).

The litter production (152g/m^2) and litter decomposition (186g/m^2) values suggested that total growing-season litter production up to PSC was 338g/m^2. This value fell within the range of values published for similar wetlands (Table 4-4).

We measured new biomass production in September, October, and November 1998. New biomass production (plants with stem length <15cm) contributed only 5-10g/m^2/month (0.5-1.5%) to total plot biomass during that period. KELLEY (1985) demonstrated that peak live *Calamagrostis canadensis, Carex aquatilis,* and *Carex stricta* biomass occurred during July-August in a Lake Michigan wet meadow, after which it rapidly declined. By November, live *C. canadensis and* C. aquatilis biomass was nearly zero, and live *C. stricta* biomass was 30% of PSC and decreasing. Litter biomass increased rapidly following PSC, and essentially all live biomass was converted to litter by late fall (KELLEY, 1985).

Net above-ground primary productivity (NAPP)

Based on our PSC value (669g/m^2), and adding growing season litter production (152g/m^2) and litter decomposition losses (186g/m^2), we estimated SBCWM NAPP to be 1007g/m^2/yr. Our value was similar to those published for North American (RICHARDSON, 1978) and Taiwanese (HWANG, 1996) sedge-dominated wetlands (Table 4-3). The lower values reported for boreal lacustrine sedge fens were probably due to the cool, continental climate and northern latitude of the fen study site (SZUMIGALSKI & BAYLEY, 1996).

SBCWM NAPP was higher than that reported for terrestrial grasslands. As with PSC, precipitation and soil moisture availability are important factors in determining grassland productivity (LAUENROTH, 1979; HARCOMBE ET AL., 1993; BRIGGS & KNAPP, 1995), as are grazing intensity (WILLMS ET AL., 1996), and fire frequency (BRIGGS & KNAPP, 1995; BLAIR, 1997). Grazing and fire do not appear to be major factors in SBCWM, but hydrologic regime is (see Chapters 2 and 3), and unlike most grasslands, water deficits rarely, if ever, occur in SBCWM. The reliable water supply in SBCWM probably explains their greater NAPP (BERNARD, 1974).

PSC can underestimate NAPP for several reasons, including phenological differences in the occurrence of PSC and maximum shoot weight, losses due to shoot turnover during the growing season, herbivory losses, translocation of materials from shoots to roots during the growing season, and the assumption of zero herbaceous growth outside the growing season (VAN DER VALK & DAVIS, 1978; RICHARDSON, 1978; BRINSON ET AL., 1981; WHEELER & SHAW, 1991; SZUMIGALSKI & BAYLEY, 1996). Accounting for these differences, where necessary, increases the accuracy of NAPP estimates.

Differences in the timing of PSC and maximum shoot weight under-estimated sedge NAPP by 16-22% in prairie potholes (VAN DER VALK & DAVIS, 1978). However, peak *Calamagrostis canadensis, Carex aquatilis,* and *Carex stricta* biomass occurred between late-July and mid-August in a Lake Michigan wet meadow, and living shoot biomass did not differ significantly between July, August, and September (KELLEY, 1985). This suggested there was a minimal time differential between the occurrence of maximum shoot weight and PSC in these species. We believe a similar pattern also occurred in SBCWM, and that no correction for this difference was needed.

There is disagreement about the impact of herbivory on freshwater macrophytes (CARPENTER & LODGE, 1986; LODGE, 1991; CYR & PACE, 1993; FRANCE, 1995). Herbivory estimates ranging from 1-10% for grasses, sedges, and aquatic macrophytes (CRAWLEY, 1983; WETZEL, 1983) may accurately reflect vertebrate consumption, but may not accurately reflect losses to invertebrate grazers (LODGE, 1991). Muskrat herbivory was apparent in some SBCWM, and extensive insect damage to the plant *Polygonum amphibium* was commonly observed. However, we made no measurements of herbivory, and so can make no quantitative statements regarding its level. We made no correction for herbivory.

Translocation of materials from shoots to roots has been reported in alpine (MOONEY & BILLINGS, 1960; FONDA & BLISS, 1966) and wetland plants (GORHAM & SOMERS, 1973; BERNARD, 1974), and may involve 20-30% of summer and fall production in some wetland sedges (BERNARD, 1974). However, it is difficult to measure the volume of materials being translocated, or to determine whether translocated materials represent existing plant reserves or new photosynthetic products (KLOPATEK & STEARNS, 1978). Given these uncertainties, and given that we collected no translocation data for SBCWM vegetation, we made no adjustment of SBCWM NAPP for translocation losses.

Carex aquatilis reportedly produced winter growth of 40-50 g/m^2 (GORHAM & SOMERS, 1973). However, Lake Michigan wet meadow vegetation began growing from "near zero" in May (KELLEY, 1985), and our casual observations revealed no significant winter growth in SBCWM, so we made no correction for extra-growing season growth.

Summary and Conclusions

The peak standing crop biomass of Saginaw Bay coastal wet meadows was 669g/m^2, live plants contributing 575g/m^2 and standing dead material 94g/m^2 to the total. Mean PSC ranged between 323-933g/m^2 among 19 study sites. Seasonal mean litter production was 152g/m^2, with an additional 186 g/m^2 of litter being produced and decomposed between the start of the growing season and PSC. From adjusted PSC biomass, we estimated SBCWM NAPP to be 1007$g/m^2/yr$.

Research into the magnitude of losses attributable to herbivory, translocation of materials from shoot to root after PSC, and extra-growing season production in SBCWM would help refine this estimate. Studies of below-ground plant production would permit the estimation of total SBCWM primary productivity.

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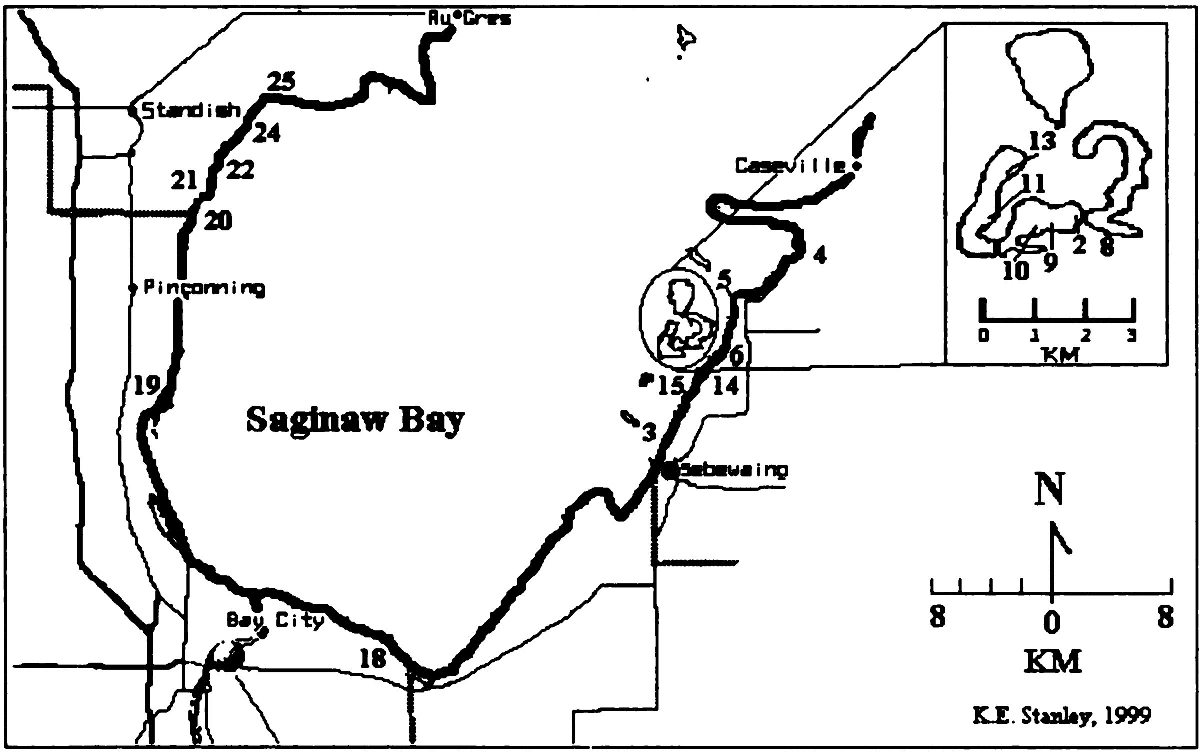

Figure 4-1. Saginaw Bay region, with study sites used in the biomass study. Map data from US Census Bureau TIGER database and Michigan Department of Natural Resources.

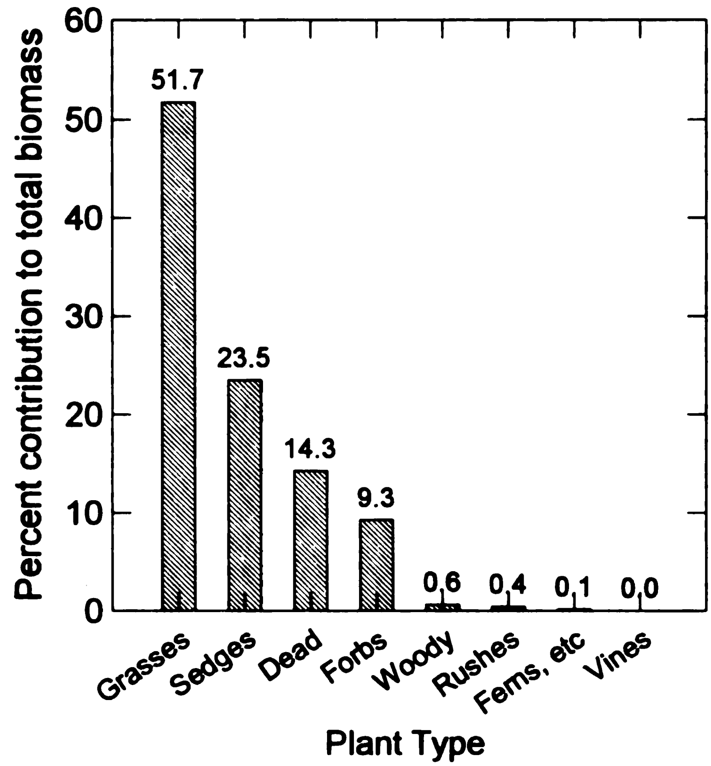

Figure 4-2. Percent contribution of plant types to the total oven-dry plant biomass of Saginaw Bay coastal wet meadows (SBCWM). Biomass collected from 228- 0.25m^2 sample plots in 19 wet meadows.

Table 4-1. Frequency of occurrence, determined from the number of sample plots in which a species occurred, percentage biomass contribution of a species to total Saginaw Bay coastal wet meadow (SBCWM) biomass, and mean above-ground biomass of plant species encountered during SBCWM biomass sampling. A total of 228 0.25-m^2 sample plots in 19 sites were collected in July-August 1997. Samples were oven-dried at 60° C for 48 hours before weighing. N equals the number of plots in which a species occurred.

Species	Frequency of occurrence (%)	Contribution to total wet meadow biomass (%)	Mean above-ground biomass (g/m^2, ±1 SEM)	N
Anemone canadensis	7.0	0.9	13.7(4.8)	16
Apocynum intermedium	6.6	0.9	13.0(3.7)	15
Asclepias incarnata	1.8	0.2	11.0(6.2)	4
Aster borealis	5.3	0.7	3.9(1.4)	12
Aster dumosus	9.2	1.2	35.4(17.9)	21
Calamagrostis canadensis	96.5	12.4	318.5(17.7)	220
Calystegia sepium	20.2	2.6	4.3(0.7)	46
Campanula aparinoides	51.8	6.7	11.4(1.5)	118
Carex aquatilis	51.3	6.6	158.9(13.8)	117
Carex bebbii	10.1	1.3	29.4(9.8)	23
Carex buxbaumii	0.9	0.1	11.2(11.2)	2
Carex hystericina	0.4	0.1	1.2(N/A)	1
Carex lacustris	20.2	2.6	98.5(17.4)	46
Carex sartwellii	58.8	7.6	61.5(6.0)	134
Carex stricta	23.2	3.0	54.5(7.3)	53
Cicuta bulbifera	0.9	0.1	<0.1	2
Cicuta maculata	1.8	0.2	0.5(0.5)	4
Circium arvense	11.8	1.5	13.8(3.4)	27
Cladium mariscoides	31.1	4.0	8.3(1.7)	71
Cornus amomum	3.9	0.5	10.9(5.2)	9
Cornus stolonifera	9.2	1.2	17.6(5.5)	21
Eleocharis rostellata	0.4	0.1	6.0(N/A)	1
Eleocharis smallii	6.6	0.9	1.0(0.3)	15
Eleocharis spp.	2.2	0.3	3.5(2.0)	5
Epilobium hirustum	1.3	0.2	26.0(14.8)	3
Equisetum arvense	0.4	0.1	2.0(N/A)	1
Eupatorium maculatum	0.9	0.1	60.0(47.2)	2
Eupatorium perfoliatum	1.8	0.2	7.9(5.1)	4
Fragaria virginiana	0.4	0.1	1.6(N/A)	1
Fraxinus pennsylvanica	0.9	0.1	<0.1	2
Galium obtusum	11.0	1.4	13.6(4.3)	25
Glyceria striata	1.8	0.2	7.8(6.3)	4
Helenium autumnale	0.9	0.1	11.8(10.6)	2
Hypericum kalmianum	1.8	0.2	23.9(23.4)	4
Impatiens capensis	11.0	1.4	1.8(0.4)	25
Iris versicolor	2.2	0.3	70.2(31.0)	5
Juncus balticus	7.9	1.0	25.1(6.9)	18
Juncus brevicaudatus	4.4	0.6	17.8(6.4)	10
Juncus effusus	0.4	0.1	19.6(N/A)	1

Table 4-1 (cont'd.)

Species	Frequency of occurrence (%)	Contribution to total wet meadow biomass (%)	Mean above-ground biomass (g/m^2, ±1 SEM)	N
Lathyrus palustris	19.7	2.5	5.4(0.9)	45
Leersia oryzoides	3.9	0.5	4.3(0.9)	9
Lobelia kalmii	0.4	0.1	<0.1	1
Lycopus americanus	6.6	0.9	3.5(1.3)	15
Lysmachia quadriflora	4.8	0.6	17.2(7.8)	11
Lysmachia terrestris	0.4	0.1	20.0(N/A)	1
Lysmachia thrysiflora	4.4	0.6	7.7(2.8)	10
Lythrum alatum	1.3	0.2	0.5(0.3)	3
Lythrum salicaria	7.9	1.0	128.6(31.4)	18
Mentha arvensis	5.7	0.7	6.6(2.1)	13
Phalaris arundinacea	13.6	1.8	129.4(46.3)	31
Phragmites australis	7.0	0.9	258.8(67.8)	16
Polygonum amphibium	40.8	5.3	9.5(1.0)	93
Polygonum scandens	0.4	0.1	4.0(N/A)	1
Populus deltoides	1.8	0.2	3.1(1.5)	4
Potentilla anserina	5.3	0.7	6.3(2.6)	12
Potentilla fruticosa	2.2	0.3	53.2(13.7)	5
Pycnantheum virginianum	1.8	0.2	54.8(26.5)	4
Rubus spp.	0.4	0.1	0.8(N/A)	1
Rudbeckia hirta	0.9	0.1	5.6(2.8)	2
Sagittaria latifolia	0.9	0.1	14.0(13.6)	2
Salix petiolaris	0.9	0.1	50.4(42.8)	2
Salix spp.	1.8	0.2	5.0(3.6)	4
Scirpus acutus	1.3	0.2	21.3(10.6)	3
Scirpus americanus	1.3	0.2	23.9(13.9)	3
Scirpus validus	0.9	0.1	41.4(24.6)	2
Scutellaria galericulata	5.7	0.7	2.8(1.0)	13
Scutellaria lateriflora	0.4	0.1	2.8(N/A)	1
Solidago uliginosa	0.4	0.1	8.4(N/A)	1
Spartina pectinata	4.4	0.6	62.8(23.0)	10
Spiraea alba	0.9	0.1	25.8(20.2)	2
Spiranthes lucida	0.4	0.1	0.8(N/A)	1
Stachys tenuifolia	19.7	2.5	5.8(1.1)	45
Teucrium canadense	2.6	0.3	5.4(3.4)	6
Thelyptris palustris	0.4	0.1	188.0(N/A)	1
Typha angustifolia	21.5	2.8	105.5(13.1)	49
Typha latifolia	1.3	0.2	71.3(48.4)	3
Unknown #1	0.4	0.1	1.2(N/A)	1
Viola affinis	0.4	0.1	0.4(N/A)	1
Vitis riparia	0.4	0.1	8.4(N/A)	1

Table 4-2. Mean peak standing crop (PSC) biomass and range of sample values among 19 Saginaw Bay coastal wet meadows based on 12- 0.25m^2 sample plots per site. Weights determined after oven-drying at 60° C for 48 hours.

Site	Mean PSC biomass (g/m^2, ±1SEM)	Range of sample plot biomass values (g/m^2)
2	724(70.7)	467 - 1214
3	741(69.8)	366 - 1274
4	433(94.7)	146 - 1328
5	746(173.0)	166 - 2501
6	596(50.5)	338 - 860
8	814(61.6)	368 - 1100
9	862(82.5)	553 - 1440
10	746(83.5)	391 - 1272
11	600(64.0)	311 - 970
13	785(70.9)	404 - 1300
14	372(76.4)	113 - 813
15	514(72.5)	172 - 921
18	933(110.1)	362 - 1558
19	699(79.3)	322 - 1208
20	323(42.6)	138 - 563
21	657(59.8)	429 - 1188
22	839(87.8)	365 - 1264
24	711(91.8)	210 - 1200
25	616(53.7)	349 - 1006
All	669(21.2)	113 - 2501

Table 4-3. Peak standing crop (PSC) biomass, net biomass production, and net above-ground primary productivity (NAPP) values for grass/sedge dominated ecosystems. Net biomass production includes live biomass produced during the growing season. NAPP includes net biomass production, with corrections for growing-season litter production and decomposition losses.

Species/Ecosystem Type	Latitude	Location	PSC (g/m^2)	Net Biomass production (g/m^2/yr)	NAPP (g/m^2/yr)	Reference
Type						
Wetland						
Rich Fen	various	England	810	...	...	Wheeler and Shaw, 1991
Lacustrine Sedge Fen	54° N	Canada	...	163[1]	...	Szumigalski and Bayley, 1996
Carex-dominated marsh	various	various	...	...	870	Richardson, 1978
Calamagrostis-Caricetum meadow	43° N	Wisconsin	...	794[2]	...	Stout, 1914
Coastal wet meadow	43° N	Michigan	468	...	...	Kelley ET AL., 1985
Coastal wet meadow	43° N	Michigan	669	...	1007	This study
Terrestrial						
Grassland	various	various	...	525[3]	...	Lauenroth, 1979
Grassland	29° N	Texas	340-372[4]	379-393[4]	462	Harcombe ET AL., 1993
Grassland	39° N	Kansas	...	506[5], 404[6]	...	Briggs and Knapp, 1995
Grassland	39° N	Kansas	...	450-520[4]	...	Blair, 1997
Rough Fescue Grassland	49° N	Alberta, Canada	683	...	316-447[4]	Willms ET AL., 1996

1 - Herbaceous stratum only.
2 - Originally 7078 pounds/acre/year.
3 - Value for Lauenroth's Group 6 grasslands, characterized by lack of significant annual drought.
4 - Range of annual PSC values observed during multi-year study.
5 - Annually burned lowland grasslands.
6 - Long-term unburned lowland grasslands.

Table 4-4. Distribution of peak above-ground biomass among biomass components for grass/sedge dominated ecosystems.

Ecosystem Type	Standing Live Biomass (g/m^2)	Standing Dead Biomass (g/m^2)	Litter (g/m^2)	Reference
Type				
Wetland				
Coastal wet meadow	575	94	338(1)	This study
Coastal wet meadow	468(2)	...	488(2)	Kelley ET AL., 1985
Rich Fen	810	...	37-2115(3)	Wheeler and Shaw, 1991
Lacustrine sedge fen	...	...	15.3(4)	Szumigalski and Bayley, 1996
Terrestrial				
Grassland	340-372(3)	903-1113(3,5)	(5)	Harcombe et al., 1993
Grassland	398	398	1190	Willms ET AL., 1996

1 - Includes $152 g/m^2$ litter produced plus $186 g/m^2$ litter produced and decomposed prior to measurement. Production measured over 94 day period from beginning of growing season to collection of peak standing crop biomass. No correction made for herbivory.
2 - Weighted mean based on areal extent of community type and percent cover of dominant species.
3 - Range for community type.
4 - $g/m^2/yr$.
5 - Combined standing dead and litter.

Chapter 5 - The impact of anthropogenic disturbance and Purple Loosestrife on Saginaw Bay coastal wet meadow vegetation

Introduction

Natural disturbances, such as herbivory, fire, or fluctuating water levels, govern the development and maintenance of wet meadow vegetation (Curtis, 1959; Keddy and Reznicek, 1986; see Chapters 2 and 3). Saginaw Bay is in constant flux, alternately inundating and exposing the coastal wet meadow zone (see Chapter 2). Most plants are not adapted to this hydrologic regime (Keough et al., 1999), and are excluded from wet meadows. However, certain grasses and sedges have successfully adapted to the variable Saginaw Bay hydroperiod, allowing them to dominate wet meadow vegetation (see Chapter 3).

European settlement introduced a new set of disturbance factors to the Saginaw Bay region. Timber harvesting, diking, ditching, draining, plowing, filling, and paving impacted the coastal landscape, while sediment, fertilizer, pesticide, and sewage runoff impacted the water quality of Saginaw Bay. Exotic species introductions have increased competitive stresses faced by native taxa. These anthropogenic, or human-induced, disturbances represent relatively new threats to the stability of coastal wet meadow vegetation, and little study of the problem has been undertaken to date. It is important to understand how anthropogenic disturbance impacts coastal wet meadow vegetation if we are to protect and maintain the integrity of this wetland plant community.

Goals and objectives

The goal of this chapter was to examine the impacts of anthropogenic disturbance, and of the introduction of *Lythrum salicaria* L. (Purple Loosestrife), on Saginaw Bay coastal wet meadow vegetation, and to determine in what ways, if any, that wet meadow vegetation suffering anthropogenic disturbance or *L. salicaria* invasion differed from that subject only to natural hydrologic disturbance. The specific objectives were:

1. to determine the hydrologic, edaphic, and vegetation characteristics of anthropogenically-impacted, and *L. salicaria*-impacted, Saginaw Bay coastal wet meadow vegetation; and
2. to compare and contrast the hydrologic, edaphic, and vegetation characteristics of anthropogenically-impacted, and *L. salicaria*-impacted, wet meadows with those lacking disturbance or *L. salicaria*.

Disturbance

Disturbance is any event that destroys biomass (Grime, 1979). Disturbance can be natural or anthropogenic. Natural wet meadow disturbances include climatic and hydrologic fluctuation, herbivory, and fire (Curtis, 1959; Foote et al., 1988; Thompson and Shay, 1989; Bowles et al., 1996). Natural disturbance regimes often enhance community spatial and temporal heterogeneity (White, 1979; Sousa, 1984; Pickett and White, 1985). Great Lakes water-level fluctuations enhance the spatial and temporal heterogeneity of Great Lakes coastal wetland vegetation, and are a good example of the influence natural disturbance can have on community structure and composition (Harris et al., 1981; Keddy and Reznicek, 1986; Keough, 1990; see Chapter 3).

Anthropogenic wet meadow disturbances include alterations of natural hydrology such as ditching, diking, tiling, draining, and pumping to facilitate drainage, and grazing, mowing, burning, cultivation, clearing of native vegetation, filling, and paving (Curtis, 1959; Moran, 1981, Mitsch and Gosselink, 1993; Bowles et al., 1996).

Anthropogenic wet meadow alteration is often, but not always, detrimental to native vegetation. Deliberate burning was once used to improve the quality of marsh hay harvested from Saginaw Bay coastal wet meadows (H. Davis, pers. comm.). Occasional fires increased fen species diversity, reduced exotic species diversity, and suppressed shrub growth in Michigan and Illinois prairie fens (Kohring, 1982; Bowles et al., 1996). Similarly, mowing increased species diversity in Czech wet meadow plots (Leps, 1999). Mowing removed the tall plants, allowing greater light penetration to occur. Mowing also decreased litter accumulation, increased spring soil temperatures, and promoted seed germination in the mown plots (Ibid., 1999).

Disturbance varies in scale, sometimes impacting individual plants, sometimes entire communities (Collins and Glenn, 1988). Disturbance frequency decreases as scale increases from the individual to the ecosystem, creating a landscape mosaic of vegetation patch sizes and seral stages (Ibid., 1988).

Disturbance also varies in severity. Filling generally has a greater impact on a wet meadow than does grazing. Filling permanently alters wet meadow elevation, influencing site hydrology, soil and seed bank composition, and future land use options. Grazing impacts, which include soil compaction, changes in plant species composition via selective grazing, and eutrophication via urine and feces deposition, can often be reversed once grazing ceases (Jensen, 1985; Kiehl et al., 1996). On the other hand, heavy grazing pressure can severely impact wetland soil and vegetation composition, whereas small-scale, localized changes in wet meadow elevation can result in greater habitat and species diversity.

Purple Loosestrife

Disturbance creates opportunities for aggressive species to increase their presence on the landscape (Collins and Glenn, 1988). Many non-native plants compete extremely effectively when first introduced into new phyto-geographic regions. When an ecologically plastic exotic species is introduced into a disturbed landscape, the result is often explosive growth and rapid dominance of the vegetation by the introduced exotic.

Lythrum salicaria, introduced from Europe in the 1800's in ships ballast (Thompson et al., 1987) as an escaped ornamental, and by deliberate introduction into wetlands (Stuckey, 1980) is now widely established in eastern North America. Its lightweight seeds are the primary dispersal mechanism. Seeds float to new sites, or are carried on the feathers or fur of wetland vertebrates (Mullin, 1998). Wind is of minor importance as a dispersal mode (Ibid., 1998). Purple Loosestrife is considered a problematic wetland weed in the northeastern US and Canada because it lacks natural enemies in North America, is thought to threaten wetland plant species diversity, and provides relatively poor feeding and breeding habitat for native wetland fauna (Anderson, 1995).

Wetland scientists and natural resource managers are concerned about the potential impact of *L. salicaria* on the biodiversity and habitat quality of Great Lakes and other wetlands (Thompson et al., 1987; Mal, et al., 1992). Given these concerns, its presence in Saginaw Bay coastal wet meadows, and its potential as an indicator of wet meadow disturbance, the impact of *L. salicaria* on coastal wet meadow vegetation was examined in the study.

Methods

Site selection

The study took place in Saginaw Bay, the southwestern lobe of Lake Huron (Figure 1-1). Vegetation data were collected in 25 wet meadow study sites during 1997 (see Chapter 1 text, and Figure 1-2, for details of site selection). However, only 12 of the 25 sites could be reasonably classified as either disturbed or undisturbed, so only these 12 sites were included in the disturbance portion of the study.

The undisturbed sites were in fact reference sites (*sensu* Brinson, 1993) because, while representative of existing Saginaw Bay coastal wet meadows, none were truly undisturbed. All wet meadows in the Saginaw Bay coastal zone have experienced varying degrees of human impact. Sites were accepted as reference sites if they were exposed to the natural water level fluctuations of Saginaw Bay, and aerial photos, historical documents, or anecdotal evidence indicated that anthropogenic disturbance had only minimally-impacted native wet meadow vegetation and soils at the site. Sites were accepted as disturbed if aerial photos, historical documents, or anecdotal evidence indicated that anthropogenic activities had resulted in disturbance of the native wet meadow hydrology, vegetation, or soils at the site.

The six reference sites were all located on Middle Ground Island or Maisou Island in the Wildfowl Bay State Game area (Figure 5-1). The Wildfowl Bay SGA is a group of low sand barrier islands located approximately 2km off the eastern shore of Saginaw Bay near Sebewaing, MI. The island vegetation was a mix of emergent marsh, wet meadow, shrub-scrub and forested wetlands, and upland oak-hickory forests (Albert et al., 1988). Upland forests abutted three of the six reference sites, forested or shrub-scrub wetland the other three. The nearest agricultural activity was 2km distant on the main land. Anecdotal evidence and aerial photographs indicated that these sites have never been cultivated, drained, or diked, and had not been permanently inhabited since European settlement. One site (Site #2) was located near an artificial boat channel. Aerial photographs indicated that the channel was excavated prior to 1938, and it was a stable feature on the landscape. On inspection, no lingering signs of excavation-related disturbance could be found at the site (see Chapter 2). The islands were used as cattle pastures during the 1930's, but all grazing activity was discontinued by 1940 (T.J. Jahr, Jr, pers. comm.). The islands have been maintained as public hunting land in recent years. Land use during that period has been limited to hunting and a few temporary camps during the hunting season.

The disturbed sites were located throughout the Saginaw Bay coastal zone and had suffered various anthropogenic impacts (Table 5-1). Two sites (Sites #1 and #21) were located behind levees. Site #1 had been cultivated and cropped in the 1930's, grazed from the early 1940's to the mid-1980's, and mechanically drained from the 1940's to the late-1980's. A levee-ditch system was installed between 1941-1949, breaking surface hydrologic contact between the site and Saginaw Bay. Agricultural utilization was discontinued and the land abandoned in the late 1980's, but the fields immediately adjacent to the site were under active agricultural management before and during the study. Site #21 had had *Phalaris arundinacea* L. (Reed Canary grass) seeds broadcast on un-tilled substrates in the 1950's, and then been grazed throughout the 1960's. The levee protecting Site #21 was breached in the late 1970's or early 1980's, reestablishing the natural hydrologic regime and terminating agricultural utilization of the site. There were cultivated fields within 100m of the site.

Three sites (Sites #18, #19, and #31) backed up to flood-control levees. Extensive excavation and fill deposition had occurred at these sites during levee construction, disrupting natural vegetation assemblages, soil structures and elevation contours. They were, however, exposed to the natural hydrologic fluctuations of Saginaw Bay. Sites #18 and #31 bordered levees constructed between 1950-1963. These sites were immediately adjacent to cultivated fields. Site #19 bordered the outer levee of a waterfowl management impoundment constructed between 1963-1969. This site was >1km from uplands or agricultural fields. It appears to have formed on sediments washed out of the impoundment area.

The sixth site (Site #26) had no history of hydrologic or edaphic alteration, but a greater or lesser portion of this wet meadow had been mowed approximately yearly since the early 1960's to suppress shrub growth. It was immediately adjacent to upland woods and active pasture lands.

Only two of the disturbed sites had been anthropogenically disturbed in the 10-15 years before the study commenced. The levee at Site #1 continued to interrupt natural surface hydrology until after the study was completed in 1997, and Site #26 was mowed at least yearly throughout the study period. Otherwise, there had been no significant soil disturbance, topographic or hydrologic alteration, or vegetation management of these sites since the mid-1980's.

Vegetation data from all 25 wet meadow study sites were utilized in the Purple Loosestrife portion of the study. Six of the sites contained *L. salicaria*, 19 did not (Figure 5-2).

Vegetation sampling

Vegetation data for this study were collected at the 25 wet meadow study sites during 1997. Details of the sampling protocol can be found in Chapter 3.

Statistical analysis

To examine disturbance impacts on wet meadow vegetation, the 12 disturbance sites were grouped into two categories: six reference and six disturbed sites. To examine the impact of *L. salicaria* on wet meadow vegetation, 300 sample plots from 25 wet meadow sites were divided into two categories: 37 plots that contained Loosestrife ("Loosestrife" plots) and 263 plots that did not contain Loosestrife ("non-Loosestrife" plots).

The 37 Loosestrife plots were also examined to determine if an increase in the relative dominance of Purple Loosestrife impacted the other species found in these plots. To do this, the Loosestrife plots were divided into two categories: 23 plots in which the percent IV of Purple Loosestrife was less than the mean percentage IV (7.2±1.2%) of Purple Loosestrife for all the Loosestrife plots ("low-Loosestrife" plots), and 14 plots in which the percent IV of Purple Loosestrife was greater than the mean percentage IV of

Purple Loosestrife for all Loosestrife plots ("high-Loosestrife" plots). Plot above-ground biomass, stem density, species richness, and Shannon-Wiener diversity were compared between low- and high-Loosestrife plots for evidence of significant differences between the categories. As the goal of the analysis was to estimate the impact of *L. salicaria* on other species in the plots, Purple Loosestrife was excluded from these analyses.

The data sets were examined to determine if the variables met parametric statistical assumptions. Species importance values (IV), biomass, stem densities, soil texture data, and peat and litter depths were non-normally distributed or heteroscedastic. IV and species biomass were $\log_{10}(X+1)$ transformed, and peat and litter depths were square-root transformed to meet parametric assumptions for the disturbance site and non-Loosestrife/Loosestrife plot contrasts. Stem density and soil texture data could not be transformed to meet parametric assumptions for either site or plot contrasts, and peat and litter depth, hummock height, and plot elevation could not be transformed for plot contrasts. None of the data could be transformed to meet parametric statistical assumptions for the low-Loosestrife/high-Loosestrife plot contrasts. Data that could not be transformed were analyzed using non-parametric statistical techniques.

For variables meeting parametric assumptions, two-sample t-tests were used to compare differences between category means. Statistical power analysis (Cohen, 1988) was performed *post-hoc* to determine the power of the test (ranging between 0.0-1.0) whenever a t-test failed to falsify the null hypothesis. The Mann-Whitney U test was used to compare differences between variables failing to meet parametric assumptions. For all tests, the critical value for rejection of the null hypothesis was established at $P<0.05$ before testing. SYSTAT (v.7.0.1) was used to perform the statistical analyses.

Differences between reference and disturbed sites were also examined using the Michigan Floristic Quality Assessment (Herman et al., 1996). The Michigan FQA was designed to assess the fidelity with which the plant species composition of a parcel of land reflected the pre-settlement flora of the state. The purpose of the measure is to provide a consistent and practical tool for identifying, comparing, and monitoring changes in the floristic quality, and by extension the natural significance, of elements of Michigan's landscape (Ibid., 1996).

Briefly, to apply the FQA, a mean coefficient of conservatism and floristic quality must be determined for the site. To do this, each native species found at the site is assigned a coefficient of conservatism (CC_i) ranging from 0-10. The CC_i represents the estimated probability that the species occurs in a landscape relatively unaltered from its pre-settlement condition. The higher a species' CC_i, the greater its fidelity to a high quality remnant natural community. Exotic species ("adventive", *sensu* Herman et al., 1996) are not a part of the pre-settlement flora, and so are not assigned a CC_i. The mean coefficient of conservatism ($\overline{CC}$) for the site is calculated ($\overline{CC} = \frac{\sum CCi}{n}$; n = the number of native species), and $\overline{CC}$ is multiplied by the square root of the total number of native species present at the site to determine the floristic quality index (FQI) for that site ($FQI = \overline{CC} \times \sqrt{n}$). The FQI standardizes the $\overline{CC}$ for different size sites (for a detailed exposition of the method, see Herman et al., 1996, or Herman et al., 1997).

The $\overline{CC}$ and FQI were compared for the reference/disturbed sites using two sample t-tests. ($\overline{CC}$ and FQI comparisons are only appropriate for site-by-site data, and so were not applied to the non-Loosestrife/Loosestrife plot data). For both the disturbance and Loosestrife data sets, the relative number of native and adventive species were compared using Fisher's Exact test, and the relative numbers of forbs, grasses, sedges, rushes, ferns, shrubs, and trees were compared using the Likelihood Ratio Chi-square test.

T-tests were also used to determine which of 15 major species plot importance values might differ significantly between reference/disturbed and non-Loosestrife/Loosestrife categories (see Chapter 3 for the definition of major species). Additional statistical tests of differences in species biomass and stem density were performed on those individual species showing an overall significant t-test result on species IV. This procedure was used to maintain the nominal $\alpha = 0.05$ significance level throughout the analysis in a manner analogous to a protected-F procedure (Wilkinson et al., 1996).

Results

Disturbance effects

Thirty-nine species were encountered in 36 plots at the six reference sites, compared to 61 species encountered in 36 plots at the six disturbed sites. Ten species, or 27.1% of those encountered in the reference sites, occurred only in the reference sites, whereas 32 species, or 52.6% of those encountered in the disturbed sites, occurred only in the disturbed sites (Table 5-2). A total of 7.9% of species found in the reference sites were adventive species, whereas 11.9% of species found in disturbed sites were adventive species, a statistically non-significant difference (two-tailed Fisher's Exact test, $P = 0.736$).

Similarly, the relative contribution of forbs, grasses, sedges, ferns, rushes, shrubs, and trees to wet meadow vegetation composition did not differ significantly between the reference and disturbed sites (Likelihood Ratio Chi-square, $\chi^2 = 2.572$, df = 6, P = 0.860).

The mean($\pm$1SEM) FQI for reference sites was 21.0(0.8), ranging between 23.5-19.0, whereas the mean($\pm$1SEM) FQI for disturbed sites was 21.6(2.1), ranging between 29.5-16.6 (Table 5-3). The mean FQI values were not significantly different (t-test, $t_{(.05,10)} = 0.092$, P = 0.928, Power = 0.05).

Species with either a high or low coefficient of conservatism were found in both reference and disturbed sites, so a species' coefficient of conservatism could not be used by itself to identify potential disturbance indicator species. However, several weedy species (USDA-ARS, 1971) uncommon in Michigan's wetlands (*Agropyron repens* (L.) Beauv., *Cerastium fontanum* Baumg., *Circium arvense* (L.) Scop., *Equisetum arvense* L., and *Taraxicum officinale* Wiggers), were encountered only in disturbed sites. All except *E. arvense* were adventive species with no assigned coefficient of conservatism, and *E. arvense* had a coefficient of conservatism of zero. *Lythrum salicaria* and *Solanum dulcamara* L., adventive wetland species, were encountered only in disturbed sites. *L. salicaria* occurred in three of six disturbed sites.

There were no statistically detectable differences (statistical power: 0.55-<0.05) between reference and disturbed sites with respect to mean plot above-ground biomass, stem density, litter depth, hummock height, and elevation, or mean site species richness, Shannon-Wiener diversity, coefficient of conservatism, and FQI (Table 5-4). Statistically significant differences (P<0.05) were detected for mean plot peat depth and soil texture.

Peat depth was greater in plots at disturbed sites, and plots in reference sites collectively exhibited finer-textured soils than did disturbed site plots.

Six of the 15 major wet meadow species, *Calamagrostis canadensis* (Michaux) Beauv., *Calystegia sepium* (L.) R.Br., *Campanula aparinoides* Pursh, *Carex stricta* Lam., *Phragmites australis* (Cav.) Steudel, and *Stachys tenuifolia* Willd. exhibited statistically significant differences in mean plot IV between reference and disturbed sites (Table 5-5). Closer examination of these species indicated that *C. stricta* produced significantly greater plot IV, above-ground biomass, and stem density in the disturbed sites, *P. australis* produced significantly greater plot IV and above-ground biomass in disturbed sites, and *C. sepium* produced significantly greater plot IV in disturbed sites (Table 5-6). By contrast, *S.* tenuifolia exhibited significantly greater plot IV, above-ground biomass, and stem density in reference sites, *C. canadensis* exhibited significantly greater plot IV and above-ground biomass in reference sites, and C. *aparinoides* exhibited significantly greater plot IV and stem density in reference sites.

Purple Loosestrife effects

Lythrum salicaria was not commonly found in Saginaw Bay coastal wet meadows, and was not a dominant species where it was found. Purple Loosestrife occurred in only 37 (12.3%) of 300 sample quadrats. In these 37 plots, the mean(±1SEM) percentage IV of *L. salicaria* was 7.2(1.2)% and the maximum percentage IV of *L. salicaria* in any sample plot was 28.5%. Mean(±1SEM) plot stem densities differed by a non-significant 9.4% between non-Loosestrife and Loosestrife plots (271±7.9 stems/0.25m^2 in non-Loosestrife plots versus 299±18.7 stems/0.25m^2 in Loosestrife plots; $t_{(.05, 298)} = -0.917$, P =

0.360, Power = 0.15). *L. salicaria* had the greatest individual species IV in only two (5.4%) of 37 plots containing Loosestrife.

Three Michigan adventive species were found in non-Loosestrife plots, whereas six were found in Loosestrife plots, a statistically non-significant difference (two tailed Fisher's Exact, P = 1.000). Similarly, there was no significant difference between non-Loosestrife and Loosestrife plots in the relative contribution of forbs, grasses, sedges, ferns, rushes, shrubs, and trees to wet meadow vegetation composition (Likelihood Ratio Chi-square, $\chi^2 = 3.717$, df = 7, P = 0.812).

There were no statistically detectable differences (statistical power: 0.38-0.14) between non-Loosestrife and Loosestrife plots with respect to mean plot above-ground biomass, stem density, species richness, Shannon-Wiener diversity, or soil texture (Table 5-7). Statistically significant differences ($P<0.05$) between plots were detected for mean plot peat depth, litter depth, hummock height, and elevation. Peat depth was significantly greater in Loosestrife plots (mean difference = 2.8cm). Similarly, litter depth was significantly greater in Loosestrife plots, (mean difference = 2.3cm), and plot elevation was significantly greater in non-Loosestrife plots, (mean difference = 6cm). Hummock heights was significantly greater in non-Loosestrife plots (mean difference = 11cm).

Four of the 15 major wet meadow species, *Calystegia sepium* (L.) R. Br., Carex *aquatilis* Wahl., *Polygonum amphibium* L., and *Stachys tenuifolia* Willd., exhibited statistically significant differences in mean plot IV between non-Loosestrife and Loosestrife plots (Table 5-8). Closer examination of these four species indicated that *C. aquatilis* exhibited significantly greater IV, above-ground biomass, and stem density in non-Loosestrife plots. *C. sepium, P. amphibium,* and *S. tenuifolia* also exhibited significantly greater IV in non-Loosestrife plots, but no statistically significant differences between non-Loosestrife and Loosestrife plots in above-ground biomass or stem density were detected for these three species (Table 5-9).

The mean percentage IV of Purple Loosestrife was significantly greater (t-test, $t_{(0.05,35)} = 8.015$, $P<0.001$, Power > 0.98) in high-Loosestrife plots (mean ±1SEM = 14.6±1.8%) compared to low-Loosestrife plots (2.7±0.35%). Plot stem densities of species other than Purple Loosestrife were significantly greater in low-Loosestrife plots, but there were no statistically significant differences in plot above-ground biomass of the other species, or in species richness or Shannon-Wiener diversity between the low-Loosestrife and high-Loosestrife plots (Table 5-10). However, while the difference was not statistically significant, both above-ground biomass and species richness did exhibit lower mean plot values in the high-Loosestrife plots.

Six of the 15 major species (*Calamagrostis canadensis, Campanula aparinoides, Carex aquatilis, Carex sartwellii, Cladium mariscoides,* and *Polygonum amphibium*) exhibited significantly lower stem densities in high-Loosestrife plots, whereas none of the major species had significantly greater stem densities in high-Loosestrife plots. However, the above-ground biomass of these species did not differ significantly between the categories.

Lower stem densities did not translate into taller stems. *Calamagrostis canadensis, Carex aquatilis,* and *Carex sartwellii* had lower maximum, median, and mean stem height in high-Loosestrife plots, and *Campanula aparinoides* had greater maximum, median, and mean stem height in high-Loosestrife plots, but these differences were not statistically significant. There were no significant differences between low-Loosestrife and high-Loosestrife plots in median, mean, or maximum stem heights among any of the major species.

Discussion

Disturbance effects

The lack of statistically significant differences between reference and disturbed sites suggests that Saginaw Bay coastal wet meadow vegetation was resistant to disturbance impacts and resilient once anthropogenic disturbance ended. Resistance, the ability of a vegetation assemblage to remain relatively unchanged during a stressful period, and resilience, the ability of a vegetation assemblage to recover after a disturbance has occurred, are important measures of plant community stability (Barbour et al., 1987).

More species occurred in disturbed sites than in reference sites. The reference sites were all located on islands approximately 2km from the mainland, whereas the disturbed sites were all on the mainland itself, suggesting that proximity to upland and agricultural propagule sources might account for the greater species richness observed at the disturbed sites. However, three of the six reference sites were immediately adjacent to upland forest vegetation, and all six were adjacent to at least some upland or wetland forest or shrub-scrub vegetation. Nonetheless, there were no agricultural fields within 2km of the reference sites, whereas all the disturbed sites were in close proximity to pastures or cultivated fields. The presence of certain agricultural weeds (e.g., *Agropyron repens* = Quackgrass) only in the disturbed sites may reflect unavoidable differences in propagule proximity between reference and disturbed sites.

Studies have demonstrated that disturbing grassland vegetation creates opportunities for less competitive species to infiltrate and survive within the established grassland community, increasing the overall abundance of the less competitive community members (Collins and Uno, 1983; Platt and Weis, 1985; Collins and Glenn, 1988). Anthropogenic wet meadow disturbance similarly created opportunities for less competitive native wetland species, adventive wetland species, and ruderal upland species to gain a foothold in the wet meadow vegetation matrix. Tillage, trampling, and construction activity disrupted the rhizomatous root matrix and exposed bare soil, increasing colonization opportunities for other species. Topographic alteration increased habitat diversity within the wet meadow, allowing greater plant diversity to develop. Dikes, ditches, and drains disrupted the natural hydrologic regime, allowing scrub-shrub and forested wetland succession to occur. The net result was a greater number of plant species growing in disturbed wet meadow sites.

The native wet meadow species *Aster borealis* (T. & G.) Prov., *Hypericum kalmianum* L., *Juncus brevicaudatus* (Englem.) Fern., *Lysmachia quadriflora* Sims, and *Potentilla fruticosa* L. occurred only in disturbed sites. These species, all with high coefficients of conservatism, persisted despite anthropogenic disturbance, as did the 15 major species constituting the bulk of the vegetation. This was further evidence of the vegetation's resistance to anthropogenic impacts.

Wet meadow vegetation is a disclimax ecosystem, dependent upon periodic fire or flooding to eliminate taller, more robust competitors and suppress succeeding seral stages (Costello, 1936; Curtis, 1959; Keddy and Reznicek, 1986; and see Chapter 3). This vegetation has successfully adapted to these disturbance regimes, and in doing so may have become "pre-adapted" to other types of disturbance as well. Pre-adaptation may enhance both wet meadow vegetation stability and its resistance to anthropogenic disturbance impacts.

The statistical power of the t-tests ranged between 0.55-<0.05. Low statistical power can be the result of small effect or sample sizes, rather than a lack of difference between categories (Cohen, 1988). Effect sizes are often fairly low in observational studies because extraneous variables introduce uncontrollable noise to the system, masking the effect under study. In such cases, improving statistical power relies on increasing the sample size, which increases the signal-to-noise ratio, or on increasing the critical α level used in statistical tests (Ibid., 1988).

It was not possible to increase sample sizes in this study. There were only 25 wet meadows to study. Only 37 plots had been colonized by *L. salicaria*. The disturbance status of only 12 sites could be positively determined. These facts could not be changed. However, adjustments in experimental design, such as pairing reference and disturbed sites, or increasing the critical α level used during data analysis would improved statistical power in future studies (Ibid., 1988).

Significant differences in peat depth and soil texture were noted between reference and disturbed sites. Soil texture was coarser and peat depth was deeper in disturbed sites compared to reference sites. In all but one of the disturbed sites (Site #26), anthropogenic disturbance involved cultivation or construction-related earth-moving activity. The coarser soils found at disturbed sites may have been imported for levee construction, may have resulted from the mixing of mucks and sandy mineral substrates during cultivation, or may have resulted from the loss of organic matter via oxidation after substrates were disturbed.

Thicker peat mats were not consistent with this soil disturbance hypothesis. Soil disruption should have reduced peat thickness by exposing peat to the effects of oxidation and erosion, yet this did not seem to be the case. The mean difference in peat bed thickness between reference and disturbed sites was 1.3cm. This difference was statistically significant, but perhaps too small to have any biological significance.

Seven major wet meadow species may act as indicators of disturbance, or lack of disturbance, in Saginaw Bay coastal wet meadows. *Calamagrostis canadensis, Campanula aparinoides* and *Stachys tenuifolia* exhibited significantly lower IV, biomass, or stem density in the disturbed sites, whereas *Calystegia sepium, Carex stricta,* and *Phragmites australis* exhibited significantly higher IV, biomass, or stem density in disturbed sites. The presence of *C. aparinoides* (Marsh Bellflower) and *S. tenuifolia* (Smooth Hedge Nettle) as major species appear to be good indicators of relatively undisturbed wet meadow vegetation. On the other hand, the presence of *C. sepium* (Hedge Bindweed) and *P. australis* (Giant Reed) may be good indicators of anthropogenic disturbance in these wetlands. *C. canadensis* and *C. stricta* exhibited significantly greater IV, biomass, and in the case of *C. stricta*, stem density in reference and disturbed sites, respectively. However, these species, being two of the four dominant species of these coastal wet meadow, were present in large quantities in all wet meadows studied, and so would not make good disturbance indicator species.

The seventh potential disturbance indicator among the major species was *Lythrum salicaria*. Significantly, it occurred only in disturbed sites. However, Purple Loosestrife was not always found in disturbed wet meadows, occurring in only three of the six disturbed sites. Nonetheless, Purple Loosestrife is widely accepted as an indicator of disturbance in North American wetlands, and its impacts on wet meadow vegetation will be discussed in the following section.

Several other species, with relatively low wet meadow IVs, were also good anthropogenic wet meadow disturbance indicators. *Agropyron repens*, *Cerastium fontanum*, *Circium arvense*, *Equisetum arvense*, *Solanum dulcamara*, and *Taraxicum officinale* occurred at low frequency in Saginaw Bay coastal wet meadows, and then almost exclusively in disturbed sites. All were non-native species except *E. arvense* (Herman et al., 1996), and all were as much upland as wetland species. *E. arvense* and *S. dulcamara*, facultative wetland (FAC) species, were about equally likely to occur in wetlands and non-wetlands, and the others were facultative upland (FACU) species, with a 1-33% frequency of occurrence in wetlands (Reed, 1988). The presence of one or more of these species in a wet meadow was a good indication that the site had experienced some form of anthropogenic disturbance.

Purple Loosestrife effects

Most Saginaw Bay coastal wet meadows were not heavily impacted by *Lythrum salicaria*. Purple Loosestrife occurred in only six of 25 wet meadow study sites, and in only 37 of 300 sample plots examined. *L. salicaria* was not a dominant species in these wetlands, exhibiting the greatest individual species IV in just two sample plots.

There were few statistically significant differences between non-Loosestrife and Loosestrife plots among the variable examined. The mean plot biomass, stem density, species richness, Shannon-Wiener diversity, soil texture, the number of native and adventive species, and the relative contribution of forbs, grasses, sedges, ferns, rushes, shrubs, and trees to vegetation composition did not differ significantly between non-Loosestrife and Loosestrife plots. Similarly, in the low-Loosestrife and high-Loosestrife plot comparisons, *Lythrum salicaria* had no significant impact on plot above-ground biomass, species richness or the Shannon-Wiener diversity of the other species in the Loosestrife plots.

These results suggest that Purple Loosestrife was not altering the native vegetation structure and composition of Saginaw Bay coastal wet meadows. Anderson (1995) concluded after reviewing 71 *L. salicaria*-related papers that there was no evidence supporting the idea that Purple Loosestrife was responsible for a decline in species diversity in North American wetlands. Treberg and Husband (1999) noted no significant difference in species richness between non-Loosestrife and Loosestrife plots in the Bar River, Ontario, and no correlation between the percent cover of *L. salicaria* and species richness. The results of the present study support these conclusions.

Treberg and Husband (1999) also reported that no species were more likely to be found in plots lacking Loosestrife than they were to be found in plots with Loosestrife. While this study agreed for the most part with Treberg and Husband's findings, the two studies differed on that point. The present study found that *Carex aquatilis* exhibited greater IV, above-ground biomass, and stem density in non-Loosestrife sites than in Loosestrife sites, and *Calystegia sepium, Polygonum amphibium,* and *Stachys tenuifolia* had greater IV in non-Loosestrife sites. The cause of the difference in results may involve differences in sampling methodology, or Treberg and Husband may have had low power to detect statistically significant differences in their sample plots.

Previous investigators (Rawinski and Malecki, 1984; Thompson, et al., 1987; Thompson, 1991; Mal, et al., 1992) have concluded that *L. salicaria* has negative impacts on both wetland flora and fauna. However, while not denying that Purple Loosestrife may be a problem, Anderson (1995) and Hager and McCoy (1998) reject these claims as unsupported by the scientific evidence. Hager and McCoy state that much of the evidence cited to support the hypothesis that Purple Loosestrife is detrimental to North American wetlands is based on either personal observation rather that quantifiable measurements, or faulty experimental design and execution. Both Anderson (1995) and Hager and McCoy (1998) argue that the reliable scientific evidence on the topic is inconclusive.

The difference between the findings reported in Rawinski and Malecki (1984) and Thompson, et al. (1987) and the present study may lie in the degree to which Purple Loosestrife dominated the vegetation being examined. Rawinski and Malecki (1984) and Thompson, et al. (1987) studied wetlands in which Purple Loosestrife was the dominant species. In the present study, Purple Loosestrife was not a dominant species, even in most of the Loosestrife plots. The mean percent plot IV of *Lythrum salicaria* in the 37 Loosestrife plots examined in this study was 7.2%, and Purple Loosestrife IV never exceeded 28.5% in any of the 300 sample plots examined. Purple Loosestrife was not a significant problem in Saginaw Bay coastal wet meadows at the level at which it was present during the study. However, this is not to say that Purple Loosestrife might not become a problem in these wetlands in the future.

Thompson, et al. (1987) suggested that *L. salicaria* could be present in wetlands for years as a minor vegetation constituent before rapidly becoming the dominant species, and there were signs that Purple Loosestrife was having a small, but measurable impact on the vegetation at some study sites. Comparison of low-Loosestrife and high-Loosestrife plots indicated that the plot stem density of species other than Purple Loosestrife was significantly lower in high-Loosestrife plots, and even though differences in above-ground biomass and species richness were not statistically significant, there was lower plot biomass and species richness in the high-Loosestrife plots as well. Further, three of the four dominant Saginaw Bay coastal wet meadow species (*Calamagrostis canadensis, Carex aquatilis,* and *Carex sartwellii*) exhibited significantly lower stem densities in high-Loosestrife plots, and while not statistically significant, these three dominant species also exhibited lower maximum, median, and mean stem heights in high-Loosestrife plots. These data suggest that while Purple Loosestrife was not yet significantly impacting these wetlands as a whole, it might already be negatively influencing vegetation structure and composition in portions of these sites. These data also suggest that Purple Loosestrife may have negative impacts on wet meadow vegetation, even at low levels of relative dominance.

There were statistically significant differences in peat depth, plot elevation and hummock height between non-Loosestrife and Loosestrife plots. Soil texture did not differ significantly between non-Loosestrife and Loosestrife plots. Soil disturbance (e.g., cultivation, levee, ditch, and drain construction, sedimentation) seemed to be a major factor in *L. salicaria* establishment in the Loosestrife sites. Loosestrife IV was highest at Sites #18, 19, and 31, where levee construction had removed native vegetation and disrupted native soil structures and elevation contours, and at Site #28, which occasionally received river sediments. By contrast, Purple Loosestrife did not occur at Site #26, which was regularly mowed, or at Site #21, which was seeded with Reed Canary grass in the 1950's and grazed, but never cultivated. Significantly, neither of these sites had ever experienced major disruption of the native soil profile.

Observation of other Saginaw Bay wetlands also implicated soil disturbance as a factor in the spread of Purple Loosestrife. High *L. salicaria* stem densities were noted in constructed waterfowl impoundments at the Nayanquing Point and Wigwam Bay State Game areas on Saginaw Bay, near flood-control levees bordering southern Saginaw Bay, along the dredged and sediment-laden Quanicassee River, which empties into southern Saginaw Bay, and in farm and roadside drainage ditches throughout the region. These sites were closely associated with past or present dredging or excavation.

There is evidence to suggest that some sort of disturbance may be a necessary prerequisite to successful Purple Loosestrife establishment. Rachich and Reader (1999) demonstrated that removal of above-ground vegetation and litter in a *Phalaris arundinacea* stand in Ontario resulted in a significantly greater establishment rate for *L. salicaria*. In fact, they reported that no Purple Loosestrife seedlings became established in their vegetated control plots (Ibid., 1999). Rachich and Reader concluded that their findings supported the view (Thompson et al., 1987; Wilcox, 1989) that Purple Loosestrife cannot become established in intact wetland vegetation assemblages.

Purple Loosestrife was rarely encountered in relatively undisturbed Saginaw Bay coastal wet meadows. However, certain natural events did create opportunities for *L. salicaria* establishment. Rafts of dead cattail culms or blue-green algae occasionally collected in flooded wet meadows and smothered the underlying vegetation. When floodwaters receded, *L. salicaria* could become established in the resulting bare patches (K. Stanley, pers. obs.). Rarely did more than a few Loosestrife plants become established in this way at any site, and in the 3-5 years such sites were observed, Purple Loosestrife rarely spread beyond these small patches to other parts of the wet meadow.

In some cases, the high aspect dominance of *L. salicaria* may result in a misperception of the severity of a Purple Loosestrife outbreak. Purple Loosestrife is highly visible when flowering, sometimes appearing to be the only plant present in a wetland. However, if these sites were sampled, other, less apparent species might be found to contribute substantially to vegetation composition (Hager and McCoy, 1998). Hager and McCoy reported that much of the original data used to established the existence of a Purple Loosestrife problem came from the study of herbarium sheets, and personal observations in the field, rather than quantifiable data. The problem may simply have looked worse than it actually was because Purple Loosestrife is so very visible. They also believed that misperception due to "observer-expectancy bias" was part of the problem; researchers saw a problem because they expected to see a problem (Hager and McCoy, 1998).

Another factor contributing to the perception of Purple Loosestrife infestation may be that because it benefits from anthropogenic soil disturbance, Purple Loosestrife thrives where it can readily be observed, and so seems to be increasingly present. Large Purple Loosestrife populations were visible near constructed waterfowl impoundments, flood-control levees, and drainage ditches throughout the Saginaw Bay coastal zone. These managed sites were regularly viewed by resource managers and readily accessible to the general public. The more remote Saginaw Bay coastal wetlands, which did not support large Loosestrife populations, were less often disturbed, and less often observed. This may bias the common perception of the impact Purple Loosestrife is having on regional wetlands.

Implications for management and restoration

Saginaw Bay coastal wet meadows are stable vegetation assemblages, resistant to disturbance impacts, and resilient once disturbance is ended. *Lythrum salicaria*, though present at some sites, has not yet significantly impacted wet meadow vegetation. Under the influence of the natural hydrologic regime, this vegetation association resists exotic introductions and recovers from anthropogenic disturbance without intervention.

This bodes well for future Saginaw Bay coastal wet meadow restoration. Restoration can probably be accomplished in most cases by restoring natural hydrology at the restoration site, because wet meadow plant propagule sources are available throughout the region. However, wet meadow restoration should be undertaken with minimal soil disturbance, as large-scale dredging, excavation, contouring, or other soil disturbances encourage the establishment of *L. salicaria* and other wetland weeds (Mal et al., 1992). Levees can be breached to restore natural hydrology, but they should be left to erode naturally. Similarly, drainage ditches can be plugged at their ends, but then they should be left to fill naturally. Slow erosion of these structures will allow natural successional processes to occur and native vegetation assemblages to develop, while minimizing opportunities for Loosestrife to become established as the wetland recovers.

Where restoration involves bare ground, such as cultivated fields, the site could be contoured and allowed to naturally re-vegetate with upland species before restoring hydrology to minimize the bare soil available to *L. salicaria* after flooding. Such actions might facilitate a more natural wet meadow successional trajectory and minimize the impact of adventive plants on wet meadow recovery.

Summary and Conclusions

There were few statistically significant differences in vegetation and physical variables between reference and disturbed Saginaw Bay coastal wet meadows. Saginaw Bay coastal wet meadows exhibited resistant to anthropogenic disturbance impacts, and resilience once released from anthropogenic disturbance.

Lythrum salicaria was not present in most Saginaw Bay coastal wet meadows, and had not severely impacted those wet meadows in which it was found. There were few statistically significant differences in vegetation and physical variables between sites that contained Purple Loosestrife and those that did not contain Purple Loosestrife. Similar results were obtained when comparing non-Loosestrife and Loosestrife plots, and when analyzing the impact of Purple Loosestrife on other plant species within Loosestrife plots. Soil disturbances, such as tillage or excavation for drainage or construction, appeared to be the anthropogenic disturbance most likely to facilitate *L. salicaria* success in wet meadows.

The presence of *Campanula aparinoides* or *Stachys tenuifolia* as major species ($\geq$1% of total vegetation IV) were good indicators of relatively undisturbed Saginaw Bay coastal wet meadow vegetation. The presence of *Calystegia sepium, Lythrum salicaria,* or *Phragmites australis* as a major species, or low frequency occurrences of *Agropyron repens*, *Cerastium fontanum*, *Circium arvense*, *Equisetum arvense*, *Solanum dulcamara*, or *Taraxicum officinale* were good indicators of prior anthropogenic disturbance.

Additional studies should be undertaken to investigate the impact of *L. salicaria* on Saginaw Bay wetlands, with emphasis placed on comparing Loosestrife-free and Loosestrife-dominated wetlands. Statistical power analysis should be used to determine the power of the test when testing fails to falsify the null hypothesis. Low power suggests that small sample sizes, small effect sizes, or incorrect experimental design may be responsible for the failure to falsify the null hypothesis, and that further investigation is warranted. A better understanding of the impacts of *L. salicaria* in these wetlands could be obtained through the proper use of power analysis, and by careful experimental design.

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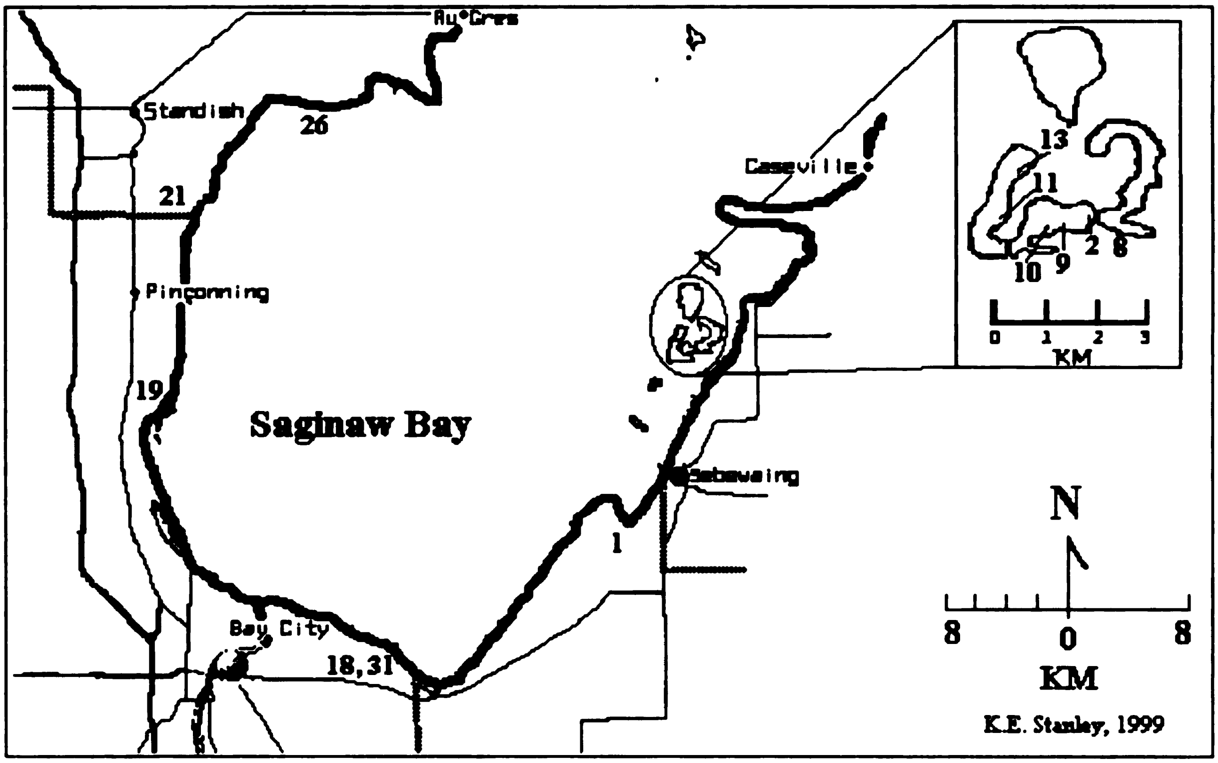

Figure 5-1. Map of reference and disturbed Saginaw Bay wet meadow study sites. The reference sites, Sites 2, 8, 9, 10,11, and 13, were all located on Middle Ground Island and Maisou Island in the Wildfowl Bay State Game area (inset). The disturbed sites, Sites 1, 18, 19, 21, 26, and 31, were located on the main land. Map data from US Census Bureau TIGER database and Michigan Department of Natural Resources.

Table 5-1. Sites used to study the impact of anthropogenic disturbance on Saginaw Bay coastal wet meadow vegetation.

Site	Location	Disturbed (Y/N)	Anthropogenic disturbance type
1	"Sheep Farm" - North side of Kindler Rd., 1300m east of the intersection of Clark and Kindler Rds, Akron Twp., Tuscola Co, MI	Y	Behind levee, ditching, cultivation, grazing
2	Middle Ground Island at Dynamite Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
8	Middle Ground Island - on the south shore 300m east of Dynamite Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
9	Middle Ground Island - on the south shore 500m west of Dynamite Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
10	Middle Ground Island - on the south shore 1000m west of Dynamite Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
11	Maisou Island - on the east shore 500m north of Boxcar Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
13	Maisou Island - 800m southeast of the northern tip of island on the east shore, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI	N	Natural regime only
18	Coryeon Point, 50m northwest of the north end of Cotter Rd, Hampton Twp, Bay Co., MI	Y	Levee construction, soil disturbance, topographic alteration
19	Nayanquing Point Wildlife Management area, 800m south, and 800m east of the south end of Tower-Beach Rd, Fraser Twp, Bay Co., MI	Y	Levee construction, soil disturbance, topographic alteration
21	East end of Bordeau Rd. at LaClair Rd, Standish Twp, Arenac Co., MI	Y	Behind levee, grazing
26	South end of Hale Rd at Saginaw Bay, Arenac Twp, Arenac Co., MI	Y	Mowing
31	Coryeon Point, 350m south of the east end of Nebobish Rd at Saginaw Bay, Hampton Twp, Bay Co., MI	Y	Levee construction, soil disturbance, topographic alteration

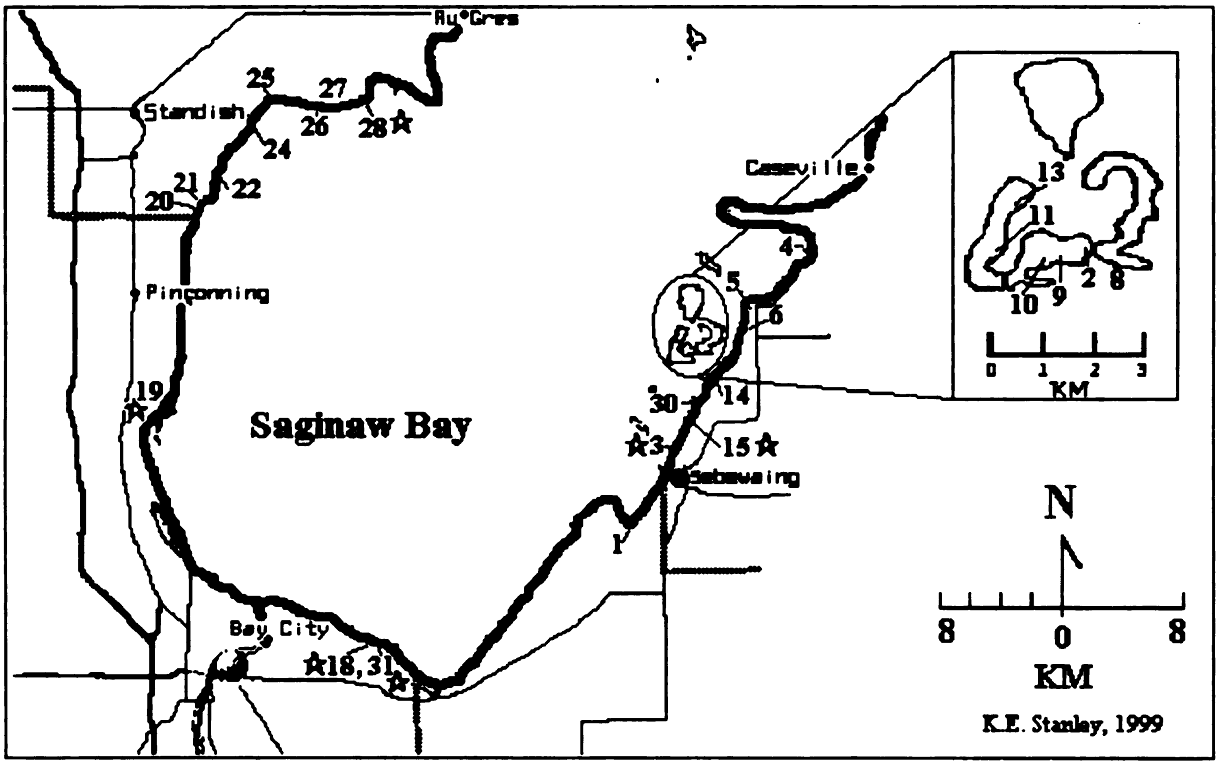

Figure 5-2. Map of the 25 study sites used in the Purple Loosestrife portion of the study. Sites #3, 15, 18, 19, 28, and 31 (indicated with stars) were Purple Loosestrife sites. The other 19 sites contained no Purple Loosestrife. Map data from US Census Bureau TIGER database and Michigan Department of Natural Resources.

Table 5-2. Plant species that occurred only in reference or only in disturbed Saginaw Bay coastal wet meadow study sites. Ten species occurred only in reference sites, 32 species occurred only in disturbed sites. The coefficient of conservatism reflects the probability that the species will be found in a landscape relatively unaltered from it's pre-settlement condition (Herman et al., 1996). Asterisks indicate that the species was adventive. Coefficients of conservatism are not assigned to adventive species.

Species occurring only in disturbed sites	Coefficient of conservatism	Species occurring only in reference sites	Coefficient of conservatism
Acorus calamus	6	*Epilobium hirsutum*	*
Agropyron repens	*	*Leerzia oryzoides*	3
Aster borealis	9	*Lysmachia terrestris*	6
Aster dumosus	7	*Lysmachia thrysiflora*	6
Cerastium fontanum	*	*Rubus* spp.	N/A
Cornus amomum	2	*Rudbeckia hirta*	1
Eleocharis smallii	5	*Scirpus acutus*	5
Equisetum arvense	0	*Scirpus americanus*	5
Eupatorium maculatum	4	*Spiranthes lucida*	7
Fraxinus pennsylvanicus	2	*Thelypteris palustris*	2
Fragaria virginiana	2		
Geum laciniatum	2		
Hypericum kalmianum	10		
Iris versicolor	5		
Juncus brevicaudatus	8		
Juncus effusus	3		
Lysmachia quadriflora	8		
Lythrum salicaria	*		
Mentha arvensis	3		
Unknown Grass	N/A		
Panicum virgatum	4		
Polygonum scandens	2		
Potentilla anserina	5		
Potentilla fruticosa	10		
Pycnanthemum virginianum	5		
Scirpus validus	4		
Solanum dulcamara	*		
Spartina pectinata	5		
Spiraea alba	4		
Taraxicum officinale	*		
Unknown #1	N/A		
Viola affinis	2		

Table 5-3. Mean coefficient of conservatism ($\overline{CC}$) and Floristic Quality Index (FQI) for reference and disturbed Saginaw Bay wet meadow sites. Number of species used to calculate the FQI was the number of species occurring only in sampling plots, not the total number of species observed during sampling at a site.

Site	Site disturbed? (Y/N)	Site $\overline{CC}$	Number of species	Site FQI
1	Y	4.3	29	23.0
2	N	4.7	23	22.7
8	N	4.4	19	19.0
9	N	4.4	21	20.0
10	N	4.5	27	23.5
11	N	5.0	19	22.0
13	N	4.2	20	19.0
18	Y	4.7	39	29.5
19	Y	4.3	18	18.2
21	Y	4.2	17	17.2
26	Y	4.7	29	25.1
31	Y	3.7	20	16.6

Table 5-4. Results of statistical tests comparing the means of various plant and abiotic wet meadow attributes for reference and disturbed Saginaw Bay coastal wet meadow sites. Significant differences (P<0.05) are indicated in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

A. T-tests of variables meeting parametric assumptions.

Measure	Reference sites (mean, ±1SEM)	N	Disturbed sites (mean, ±1SEM)	N	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test[(1)]
Plot above-ground biomass (g/m^2)	624.9(25.4)	72	674.7(29.9)	72	-1.374	142	0.172	0.20	0.22
Site species richness (species /site)	18.7(1.5)	6	22.5(2.6)	6	-1.285	10	0.228	0.74	0.19
Site Shannon-Wiener diversity (H')	1.52(0.05)	6	1.52(0.06)	6	0.038	10	0.970	<0.05	<0.05
Site Coefficient of Conservatism	4.5(0.1)	6	4.3(0.1)	6	1.246	10	0.241	0.66	<0.23
Site Floristic Quality Index (FQI)	21.0(0.8)	6	21.6(2.1)	6	0.092	10	0.928	0.05	0.05
Plot peat depth (cm)	3.4(0.4)	72	4.7(0.5)	72	-2.095	142	**0.038***	0.35	0.55
Plot litter depth (cm)	15.3(0.9)	72	14.4(0.8)	36	0.977	106	0.331	0.18	0.14
Plot elevation (m AMSL)	176.97(0.01)	72	176.98(0.01)	72	0.448	142	0.655	0.08	<0.09
Plot hummock height (cm)	32.3(3.3)	16	24.9(3.2)	8	1.419	22	0.170	0.56	0.24

(1) - Power values falling outside the table (Cohen, 1988, Table 2.3.5) are listed as less than or greater than the nearest tabulated value for that sample size or effect size.

B. Mann-Whitney U test of variables failing to meet parametric assumptions.

Measure	Reference sites (mean, ±1SEM)	N	Disturbed sites (mean, ±1SEM)	N	U	N	Probability
Plot stem density ($stems/m^2$)	1011.7(41.1)	72	1183.0(79.6)	72	2457.0	144	0.590
Plot soil texture	Sandy loam	72	Sand	72	1789.0	144	**<0.001***

Table 5-5. Comparison of mean plot importance values of major Saginaw Bay coastal wet meadow species in reference and disturbed sites. Significant differences (P<0.05) are highlighted in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

Species	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test[1]
Calamagrostis canadensis	2.625	134	**0.010***	0.43	0.68
Calystegia sepium	-3.541	33	**0.001***	1.0	0.78
Campanula aparinoides	2.547	74	**0.013***	0.57	0.65
Carex aquatilis	-0.392	61	0.697	0.10	0.07
Carex lacustris	-2.433	29	0.095	0.65	0.40
Carex sartwellii	-0.351	75	0.727	0.08	<0.07
Carex stricta	-2.727	35	**0.010***	0.88	0.72
Cladium mariscoides	1.058	32	0.298	0.33	0.15
Galium obtusum	2.377	12	0.096	1.29	<0.65
Lythrum salicaria	(2)				
Phalaris arundinacea	-2.194	32	0.082	0.68	0.41
Phragmites australis	-2.036	13	**0.045***	0.92	<0.40
Polygonum amphibium	-0.073	67	0.942	0.33	0.27
Stachys tenuifolia	3.313	26	**0.003***	1.0	0.69
Typha angustifolia	-0.914	15	0.375	0.43	<0.13

(1) Power values falling outside the table (Cohen, 1988, Table 2.3.5) are listed as less than or greater than the nearest tabulated value for that sample size or effect size.
(2) Among the 12 reference and disturbed sites, *L. salicaria* only occurred in disturbed sites.

Table 5-6. Results of statistical tests comparing mean plot importance values, above-ground biomass, and stem densities of the six major species found to have significantly different (P<0.05) IV in reference and disturbed Saginaw Bay coastal wet meadows. Significant differences (P<0.05) are highlighted in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

A. T-test results for variables meeting parametric assumptions.

Species	Measure	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test[1]
Calamagrostis canadensis	IV	2.625	134	**0.010***	0.43	0.68
Calamagrostis canadensis	BM	3.593	134	**<0.001***	0.55	0.88
Calystegia sepium	IV	-3.541	33	**0.001***	1.0	0.78
Calystegia sepium	BM	-1.919	33	0.064	0.47	0.25
Campanula aparinoides	IV	2.547	74	**0.013***	0.57	0.65
Campanula aparinoides	BM	2.120	74	0.059	0.55	0.51
Carex stricta	IV	-2.727	35	**0.010***	0.88	0.72
Carex stricta	BM	-2.560	35	**0.015***	0.74	0.57
Phragmites australis	IV	-2.036	13	**0.045***	0.92	<0.40
Phragmites australis	BM	-2.239	13	**0.043***	1.09	<0.52
Stachys tenuifolia	IV	3.313	26	**0.003***	1.0	0.69
Stachys tenuifolia	BM	1.850	26	**0.046***	0.62	0.33

(1) - Power values falling outside the table (Cohen, 1988, Table 2.3.5) are listed as less than the smallest tabulated value for that sample size or effect size.

B. Mann-Whitney U results for stem density data, which did not meet parametric assumptions.

Species	Measure	U	N	Probability
Calamagrostis canadensis	Stem density	2285.5	136	0.936
Calystegia sepium	Stem density	120.0	35	0.424
Campanula aparinoides	Stem density	860.0	76	**0.043***
Carex stricta	Stem density	56.5	37	**0.001***
Phragmites australis	Stem density	12.0	15	0.071
Stachys tenuifolia	Stem density	134.5	28	**0.031***

Table 5-7. Results of statistical tests comparing the means of various plant and abiotic wet meadow attributes of non-Loosestrife and Loosestrife Saginaw Bay coastal wet meadow plots. A total of 300 sample plots were collected at 25 sites; 37 plots contained Loosestrife, 263 plots did not. Litter depths were determined in 215 plots. Hummocks occurred in 51 plots. Significant differences ($P<0.05$) are indicated in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

A. T-tests of variables meeting parametric assumptions.

Measure	Non-Loosestrife plots (mean,±1SEM)	Loosestrife plots (mean,±1SEM)	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test
Above-ground biomass (g/m^2)	563.2(16.0)	638.9(41.8)	-1.665	298	0.388	0.29	0.37
Species richness	6.5(0.2)	7.7(0.7)	-2.377	298	0.072	0.29	0.38
Shannon-Wiener diversity (H')	0.438(0.01)	0.472(0.04)	-0.968	298	0.334	0.14	0.14

B. Mann-Whitney U test of variables failing to meet parametric assumptions.

Measure	Non-Loosestrife plots (mean,±1SEM)	N	Loosestrife plots (mean,±1SEM)	N	U	Probability
Plot stem density ($stems/m^2$)	1084(31.6)	263	1196(74.8)	37	4050.0	0.099
Plot peat depth (cm)	4.0(0.2)	263	6.8(0.8)	37	3456.0	**0.004***
Plot litter depth (cm)	15.0(0.5)	180	17.3(1.4)	35	2402.0	**0.026***
Plot hummock height (cm)	31.4(1.7)	46	20.4(4.2)	5	180.0	**0.039***
Plot elevation (m AMSL)	176.98(0.01)	263	176.92(0.02)	37	6305.0	**0.003***
Plot soil texture	Sandy loam	263	Loamy sand	37	4521.0	0.455

Table 5-8. Comparison of mean plot importance value of major Saginaw Bay coastal wet meadow species in non-Loosestrife and Loosestrife plots. Significant differences ($P<0.05$) are highlighted in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

Species	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test[1]
Calamagrostis canadensis	0.958	278	0.339	0.15	0.13
Calystegia sepium	1.830	58	**0.044***	0.95	0.42
Campanula aparinoides	1.567	140	0.119	1.04	0.91
Carex aquatilis	3.871	157	**<0.001***	0.85	0.95
Carex lacustris	(2)				
Carex sartwellii	-1.298	175	0.196	0.24	0.20
Carex stricta	1.029	77	0.307	0.48	0.15
Cladium mariscoides	-0.012	102	0.991	<0.05	<0.05
Galium obtusum	-0.170	36	0.866	0.13	<0.05
Lythrum salicaria	(3)				
Phalaris arundinacea	1.010	48	0.317	0.44	0.16
Phragmites australis	0.418	18	0.681	0.18	0.07
Polygonum amphibium	2.053	128	**0.042***	0.52	0.56
Stachys tenuifolia	1.951	54	**0.040***	1.00	0.46
Typha angustifolia	-0.794	55	0.430	0.26	0.10

(1) Power values falling outside the table (Cohen, 1988, Table 2.3.5) are listed as less than the smallest tabulated value for that sample size or effect size.

(2) *C. lacustris* occurred only in non-Loosestrife plots.

(3) *L. salicaria*, by definition, only occurred in Loosestrife plots.

Table 5-9. Results of statistical tests comparing the mean importance value, aboveground biomass, and stem density of the four major species found to have significantly different ($P<0.05$) IV in non-Loosestrife and Loosestrife Saginaw Bay coastal wet meadow plots. Significant differences ($P<0.05$) are highlighted in boldface and marked with an asterisk. The effect size and power of the test provide measures of the sensitivity of individual t-tests.

A. T-test results for variables meeting parametric assumptions.

Species	Measure	t-value	Degrees of Freedom	Probability	Effect Size (d)	Power of the test[1]
Calystegia sepium	IV	1.830	58	**0.044***	0.95	0.42
Calystegia sepium	BM	0.981	58	0.330	0.50	0.15
Carex aquatilis	IV	3.871	157	**<0.001***	0.85	0.95
Carex aquatilis	BM	2.881	157	**0.005***	0.60	0.74
Polygonum amphibium	IV	2.053	128	**0.042***	0.52	0.56
Polygonum amphibium	BM	0.063	128	0.950	0.02	<0.07
Stachys tenuifolia	IV	1.951	54	**0.040***	1.00	0.46
Stachys tenuifolia	BM	0.340	54	0.735	0.10	0.05

(1) - Power values falling outside the table (Cohen, 1988, Table 2.3.5) are listed as less than the nearest tabulated value for that sample size or effect size.

B. Mann-Whitney U results for stem density data, which did not meet parametric assumptions.

Species	Measure	U	N	Probability
Calystegia sepium	Stem density	147.5	60	0.283
Carex aquatilis	Stem density	2134.5	159	**0.005***
Polygonum amphibium	Stem density	975.0	130	0.412
Stachys tenuifolia	Stem density	136.0	56	0.304

Table 5-10. Comparison of plot above-ground biomass, stem density, species richness, and Shannon-Wiener diversity (H') of species other than Purple Loosestrife in low-Loosestrife and high-Loosestrife plots. Stem density of the other species was significantly greater ($P<0.05$) in low-Loosestrife plots. Though not significantly different, above-ground biomass and species richness exhibited lower mean plot values in the high-Loosestrife plots. Shannon-Wiener diversity was the same for both categories. Probabilities determined using the Mann-Whitney U test.

Measure	Low-Loosestrife plots (mean, ±1SEM)	N	High-Loosestrife plots (mean, ±1SEM)	N	U	N	Probability
Plot above-ground biomass (g/m^2)	602.6(50.8)	23	448.5(57.0)	14	9496	266	0.062
Plot stem density ($stems/m^2$)	1376.3(76.7)	23	800.3(100.9)	14	3225	266	**<0.001***
Site species richness	7.0(0.9)	23	6.4(1.2)	14	138	37	0.470
Site Shannon-Wiener Diversity (H')	0.47(0.05)	23	0.48(0.07)	14	163	37	0.950

APPENDICES

Appendix A

Supplementary Data for Chapter 1

Appendix A1. Climatological Norms

Table A-1. Climatological norms for Bay City and Standish, Michigan.

	Average Temperature °C (°F)				Average First/Last Freeze Date		Growing Season	Average Annual Precipitation cm (in)	
	July		January						
Location	Max	Min	Max	Min	Spring	Fall	Days	Rain	Snow
Bay City	28(82)	16(61)	-2(29)	-9(15)	5/1	10/17	168	71(27.9)	98(38.7)
Standish	28(82)	13(56)	-2(28)	-12(11)	5/19	9/23	126	71(27.8)	115(45.3)

Adapted from Keen (1993).

Appendix A2. Saginaw Bay Coastal Wet Meadow Sites

Table A-2. Site number, site name (if any), site location, site ownership, and special site access information for coastal wet meadows bordering Saginaw Bay between Port Austin and Au Gres, MI. Sites marked with an asterisk were not included in the study.

Site #	Name - Location (Ownership, special site access information, if any)
1	Sheep Farm - 1300m east of the intersection of Clark and Kindler Rds, north side of Kindler Rd, Akron Twp., Tuscola Co., MI. (MDNR)
2	Middle Ground Island, 30m northwest of the south outlet to Dynamite Cut, Wildfowl Bay State Game area, Fairhaven Twp., Huron Co., MI. (MDNR)
3	Kilmanagh Road - 400m north of the intersection of Kilmanagh and Ross Rds., Fairhaven Twp., Huron Co., MI. (MDNR, via the Gibbs property)
4	On the west side of State Highway M-25, 800m south of the intersection of M-25 and Filion Rd, McKinley Twp., Huron Co., MI. (Doerfner property)
5	Finn-Feather Public Access - approximately 500m northwest of the intersection of M-25 and Pigeon Rd (M-142), Fairhaven Twp, Huron Co., MI. (MDNR, via the Cootes property)
6	Approximately 400m north of the west end of Weale Rd at Saginaw Bay, Fairhaven Twp., Huron Co., MI. (Abbott property)
*7	West end of Geiger Rd. at Saginaw Bay, on the north side, Fairhaven Twp., Huron Co., MI. (Klass property)
8	Middle Ground Island - on the south shore 300m east of Dynamite Cut, Wildfowl Bay State Game area. (MDNR)
9	Middle Ground Island - on the south shore 500m west of Dynamite Cut, Wildfowl Bay State Game area. (MDNR)
10	Middle Ground Island - on the south shore 1000m west of Dynamite Cut, Wildfowl Bay State Game area. (MDNR)
11	Maisou Island - on the east shore 500m north of Boxcar Cut, Wildfowl Bay State Game area. (MDNR)
*12	Maisou Island - on the east shore 1000m north of Boxcar Cut, Wildfowl Bay State Game area. (MDNR)
13	Maisou Island - 800m southeast of the northern tip of island on the east shore, Wildfowl Bay State Game area. (MDMR)
14	0.4mi east of the west end of Haist Rd. at Valley Island Rd, on the north side of Haist Rd, Fairhaven Twp., Huron Co., MI. (MDNR)
15	800m north of intersection of Kilmanagh Rd and Rose Island Rd on Rose Island Rd, Fairhaven Twp., Huron Co., MI. (MDNR)
*16	North end of Berger Rd at Saginaw Bay, Akron Twp., Tuscola Co., MI. (MDNR)
*17	West bank of the Quanicassee River, between M-25 and Old State Rd, Wisner Twp., Tuscola Co., MI. (MDNR)
18	Coryeon Point, 50m northwest of the north end of Cotter Rd, Hampton Twp., Bay Co., MI. (MDNR)
19	Nayanquing Point Wildlife Management area, 800m south, and 800m east of the south end of Tower-Beach Rd, Fraser Twp., Bay Co., MI. (MDNR)
20	East end of Worth Rd at the Saganing creek, Standish Twp, Arenac Co., MI (Saganing River Rod

Table A-2 (cont'd).

Site #	Name - Location (Ownership, special site access information, if any)
	and Gun Club property)
21	East end of Bordeau Rd. at LaClair Rd, Standish Twp., Arenac Co., MI. (Grobsky property)
22	East end of Irwin Rd at Saginaw Bay, Standish Twp., Arenac Co., MI. (Viola property)
*23	East end of Palmer Rd at Saginaw Bay, Standish Twp., Arenac Co., MI. (MDNR)
24	Mouth of the Pine River, near the east end of Pine River Rd. on the south side at the Public Access boat ramp, Standish Twp., Arenac Co., MI (MDNR)
25	300m south of the east end of Langdon Rd, Standish Twp., Arenac Co., MI. (Waldie property)
26	South end of Hale Rd at Saginaw Bay, Arenac Twp., Arenac Co., MI. (Lentz property)
27	700m south of the east end of Stover Rd, Au Gres Twp., Arenac Co., MI. (Green Point Farms property, via the Wigwam Bay State Game area - East Unit)
28	South end of Big Creek Rd, Au Gres Twp., Arenac Co., MI. (Horatio Davis property)
*29	South end of Dreyer Rd , Au Gres Twp., Arenac Co., MI. (Luberda property)
30	100m south of the west end of Dutcher Rd, Fairhaven Twp., Huron Co., MI. (Hines property, via Bayshore Dr.)
31	Coryeon Point, 350m south of the east end of Nebobish Rd at Saginaw Bay, Hampton Twp., Bay Co., MI. (MDNR, via USACOE levee)

Appendix B

Supplementary Data for Chapter 2

Appendix B1 - Precipitation data.

Table B-1. Mean monthly precipitation at the National Weather Service climatological reporting station in Sebewaing, MI: 1961-1990.

Month	Rainfall (cm)	Percent of annual total
January	2.9	4.3
February	2.7	4.0
March	4.3	6.4
April	5.9	8.7
May	6.1	8.9
June	7.1	10.4
July	6.1	9.1
August	7.7	11.4
September	9.0	13.2
October	6.0	8.8
November	5.6	8.2
December	4.4	6.5
Annual total	67.9	100.0

Appendix B2 - Well field installation

In August, 1994, five groundwater observation wells was installed at Site #1, the disturbed hydrologic study site (see Figure 2-3). These wells, labeled OW1 through OW5, were located 359, 259, 159, 59, and 9 meters, respectively, on a north-south line (6° magnetic) from the on-site drainage ditch bordering the site. These pilot wells verified the feasibility of using the groundwater monitoring equipment and techniques developed for the study, and provided some preliminary site groundwater data.

In April, 1995, 24 additional monitoring wells were installed at the site (see Figure 2-5). These wells were oriented in a grid parallel to the pilot well transect. Wells #11 through #16 comprised well transect #1, Wells #21 through #26 comprised well transect #2, and so on.

First, Well #41 was installed 15m west of the east site boundary and 10m south of the on-site ditch. Then, moving westward (276° magnetic), Wells #31, #21, and #11 were installed at 50m intervals. Each of these monitoring wells was positioned 10m south of the on-site drainage ditch, itself oriented east-west. Five additional observation wells were installed southward (186° magnetic) from these first wells at 50m intervals, placing groundwater monitoring wells at distances of 10m, 60m, 110m, 160m, 210m, and 260m south of the on-site ditch. Each transect extended 260m north to south, and 150m separated Transect #1 from Transect #4. The area enclosed by the disturbed site well field was 3.9 ha.

In May 1996, 18 groundwater monitoring wells were installed at Site #2, the reference hydrologic study site, on Middle Ground Island at Dynamite Cut (Figure 2-4).

Twelve wells (#201 through #206, comprising Transect #20, and #221 through #226, comprising Transect #22) were installed in May 1996, 30m either side of a well transect (Wells #211 through #216, comprising Transect #21) installed in July 1995. The groundwater wells were placed 30m apart along a north-south elevation gradient parallel to Dynamite Cut (4° magnetic), except for wells with numbers ending in 4 and 5, which were placed 33m apart. The 3m offset originated when Well #214 was displaced down-gradient (to the north) by 3m to permit groundwater monitoring at an apparent change in vegetation. The reference site well field encompassed an area 153m long by 60m wide (0.92 ha) arrayed on a long north-south axis and spanned a vegetation gradient ranging from cattail marsh at the north end to a *Calamagrostis/Carex* wet meadow at the south end.

Water bordered the site on three sides: Saginaw Bay on the south, Wildfowl Bay on the north, and Dynamite Cut on the east. The island, approximately 200m wide at this point, sloped from a distinct, elevated Saginaw Bay shoreline through wet meadow vegetation to cattail marsh in Wildfowl Bay. There was no distinct Wildfowl Bay shoreline. The site flooded from north to south according to annual variations in Saginaw Bay levels and local seiche activity.

The site was effectively a peninsula, making it hard to determine the distances separating various groundwater wells from permanent standing water. This was important because the distance between a well and standing water, the hydraulic head at that well, and site soil hydraulic conductivity determine groundwater recharge rates following groundwater draw-down.

Wells #201, #211, and #221, located at the north end of the well field, remained in standing water throughout the study and functioned as indicators of Saginaw Bay water level. Wells #206, #216, and #226, located at the south end of the well field, were only inundated during storm surges and in 1997, the peak of the most recent 11-year Saginaw Bay hydroperiod. The three latter wells were positioned approximately 33m north of the south shore of Middle Ground Island. However, Well #226 was also located approximately 20m from Dynamite Cut, as were all other wells in Transect #22. Wells in Transects #20 and #21 were positioned 80m and 50m, respectively, from Dynamite Cut. This meant, for example, that well #204 was located 93m from Saginaw Bay, but only 80m from Dynamite Cut. Similarly, well #224 was also located 93m from the Saginaw Bay, but only 20m from Dynamite Cut.

Distances from Wildfowl Bay to various groundwater monitoring wells varied by hour and day with local seiche activity, and by month and year with the annual and inter-annual Saginaw Bay hydroperiod. For example, the distance separating Well #204 and Wildfowl Bay varied from zero to more than 50m, while that separating Well #224 and Wildfowl Bay varied from zero to 12m, depending on local seiche activity, the time of the year, and the year in which observations were collected.

No fixed distances separated the reference site wells from surface water. However, no well in this well field was more than 95m from surface water, or more than 39cm above the surface of Saginaw Bay during the study.

In May 1997, 6 groundwater monitoring wells were installed in two transects of three wells each spanning the wet meadow zone at Site #3, the Kilmanagh Road site. Wells #301 through #303 comprised Transect #30, and Wells #311 through #313 comprised Transect #31. The transects started 5-10m from the tree line marking the upland boundary and ended 5-10m from the cattail marsh. The transects were 50m apart and perpendicular (304° magnetic) to the Saginaw Bay shore line (34° magnetic at this site). The wells in each transect were also 50m apart. The area contained within the well field was 100m long by 50m wide (0.5ha). This site was inundated by rising Saginaw Bay water levels approximately 30 days after the well field was installed. No useful groundwater data was obtained from this site.

Appendix B3 - Soil moisture sampling

Each sampling period, nine soil samples were collected at the disturbed hydrologic study site from randomly selected points in vegetation sampling zones 1, 4, 6, 9, 11, and 13, the 6 zones containing groundwater monitoring wells. (For vegetation sampling, the reference and disturbed hydrologic study sites were divided into sampling zones: 8 zones at the reference site and 13 zones at the disturbed site. These zones were 20m wide and oriented perpendicular to the well transects at the sites. While not originally intended to be part of the hydrologic and edaphic study, these zones provided a convenient method for organizing the soil moisture sampling into easily definable areas that were similar in elevation to the monitoring wells.) At the reference site, three samples were collected from randomly selected points in zones 1, 2, 4/5 (wells marked the boundary between zones 4 and 5), 7, and 8, the zones containing monitoring wells. In all, 72 soil samples, 18 from the reference site and 54 from the disturbed site, were collected each sampling period.

Samples were collected at sunrise to minimize evapotranspiration losses. Soil samples were not collected less than 48 hours after measurable precipitation, or in zones exhibiting complete soil saturation. Evidence of complete saturation included inundation, water pooling around boots when walking or standing in a sampling zone, or coring holes filling to the surface with water after a soil sample had been collected.

Appendix B4 - Detailed disturbed site groundwater hydrology

In early May 1995 at the disturbed hydrologic study site, many lower elevation monitoring wells were inundated to depths of 25cm, and groundwater was no more than 10cm below the ground surface anywhere at the site (Figure B1). As in the early growing season at the reference site, groundwater contours mirrored ground surface contours at all elevations.

Groundwater levels at the disturbed site gradually declined in the following six weeks, reaching depths of as much as 60cm below the ground surface by the end of June (Figure B2). Groundwater declines of more than 40cm were observed in wells located as little as 10m from the on-site drainage ditch.

Groundwater levels then remained static until late October (Figure B3), when they began to rebound towards the ground surface. By year's end, some groundwater recharge had occurred across the site, with the greatest changes occurring in wells closest to the on-site drainage ditch (Figure B4). Recharge was apparently occurring in response to late season rainfall and infiltration from the on-site drainage ditch, which had partially refilled after drying out in late October.

Groundwater recharge continued through the winter. By mid-February 1996, groundwater levels at all monitoring wells had increased by 25-30cm from December 1995 levels (Figure B5). Wells closest to the on-site ditch still exhibited greater groundwater increases than did wells further from the ditch. Groundwater levels had risen to the ground surface throughout the wetland by late March; the entire wet meadow was saturated to, or above, the ground surface (Figure B6). This condition persisted until the end of June.

By 7/1/96, groundwater decline had once again occurred in wells more than 60m from the on-site ditch (Figure B7), and by mid-July the summer groundwater pattern being observed at the reference site was evident at the disturbed site as well (Figure B8). This pattern did not change at the disturbed site until mid-September, when heavy rainfall apparently triggered groundwater rebound (Figure B9). As in 1995, the most rapid recharge occurred in those areas closest to the on-site drainage ditch. Groundwater recharge continued through late fall (Figure B10), with infiltration from the on-site ditch appearing to contribute most to raising groundwater levels.

By late January 1997, the entire disturbed site was saturated to the ground surface (Figure B11), and by 3/1/97, the entire site was inundated to 5-30cm depth (Figure B12). The site remained inundated until early June, when groundwater declines of 30-40cm were observed in wells more than 160m from the on-site ditch (Figure B13). However, this groundwater decline was short-lived. The entire disturbed site was inundated again by mid-July in response to late June precipitation (Figure B14) and remained so until early October, when surface water depths began a gradual decline to site-wide surface saturation by mid-December (Figure B15).

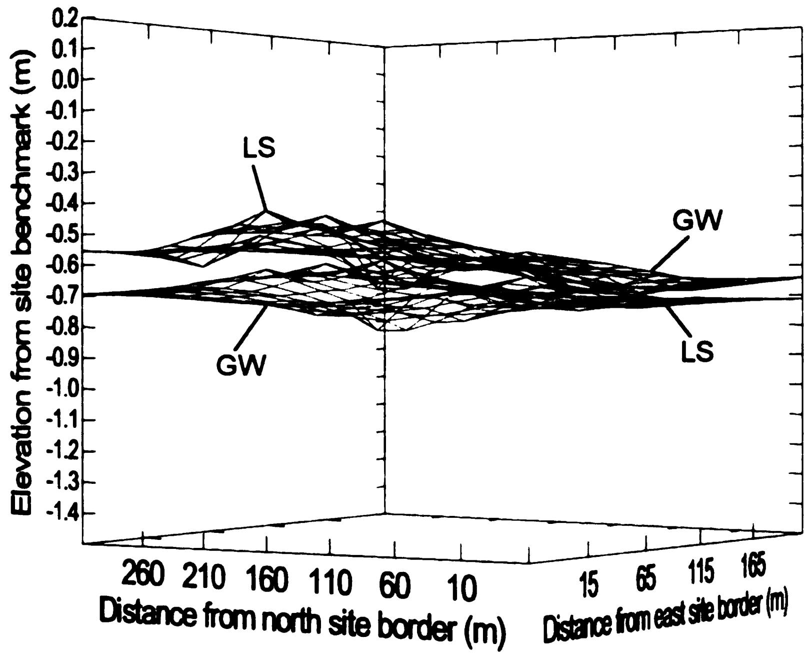

Figure B1. Groundwater condition on 5/9/95 at the disturbed hydrologic study site. Groundwater levels were within 10cm of the ground surface throughout the well field in the early growing season, with some of the lower elevation monitoring wells inundated to depths up to 25cm. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

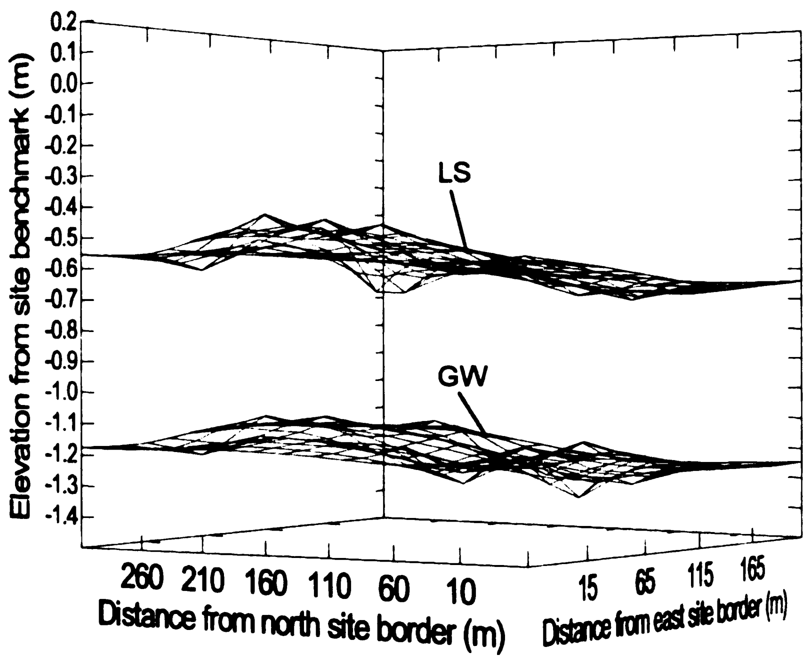

Figure B2. Groundwater condition on 6/29/95 at the disturbed hydrologic study site. Groundwater levels dropped between mid-May 1996 and late-June 1996 to as much as 60cm below the ground surface. This was true in wells located as little as 10m from the on-site drainage ditch. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

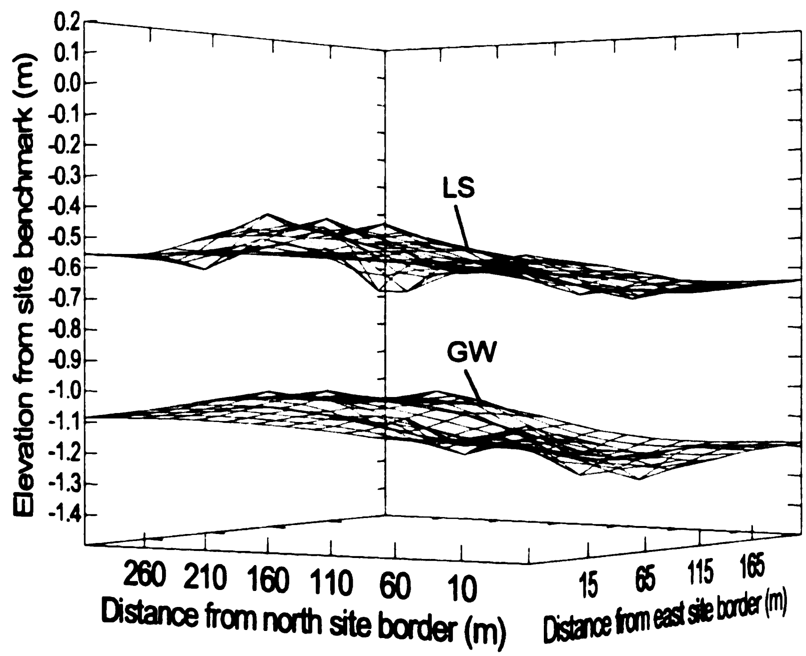

Figure B3. Groundwater condition on 10/20/95 at the disturbed hydrologic study site. Groundwater levels established in late June were unchanged until late October. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

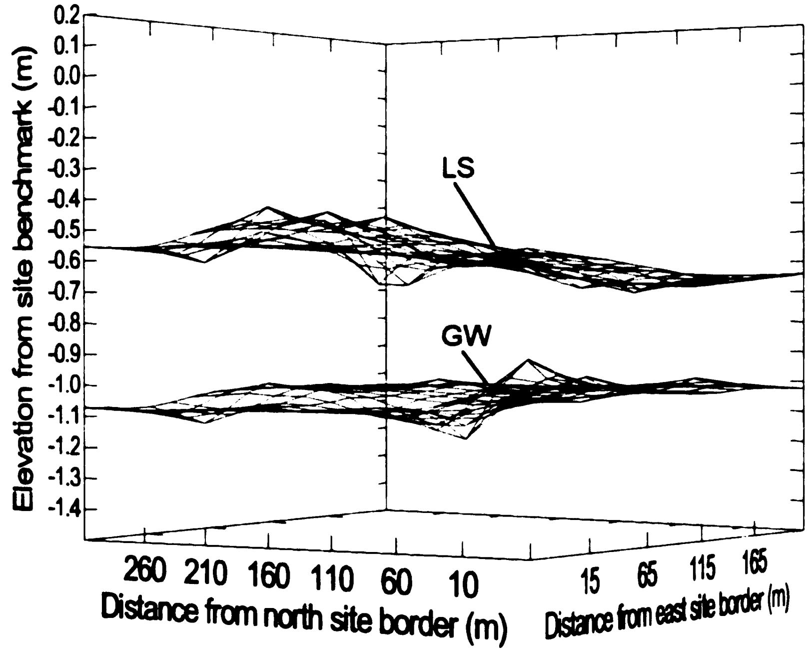

Figure B4. Groundwater condition on 12/26/95 at the disturbed hydrologic study site. Partial groundwater level rebound has occurred across the site, with the largest increases observed in the wells closest to the on-site drainage ditch. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

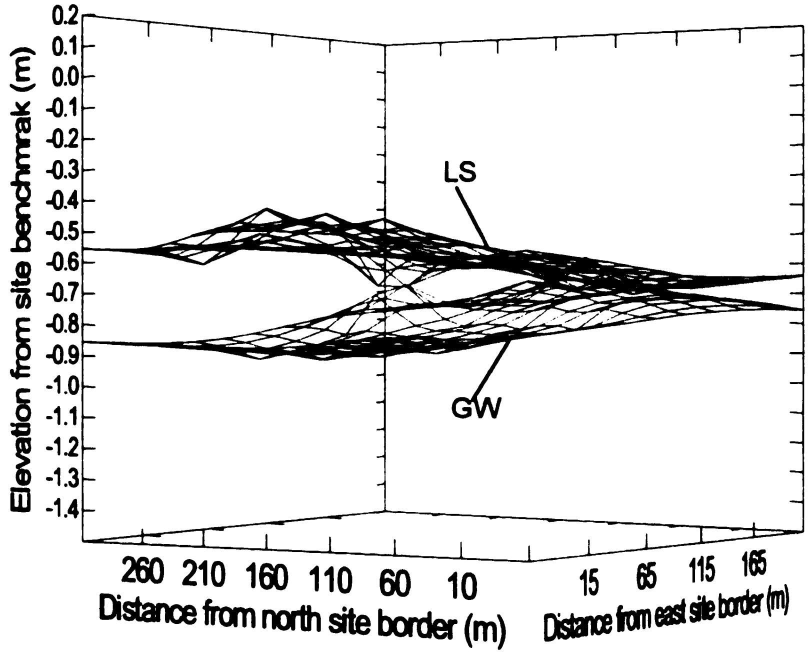

Figure B5. Groundwater condition on 2/14/96 at the disturbed hydrologic study site. Groundwater levels across the site had increased by 25-30cm since December 1995. Wells closest to the on-site ditch still showed greater groundwater increases than did wells further from the ditch, probably due to continued infiltration of surface water from the ditch into adjacent areas. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

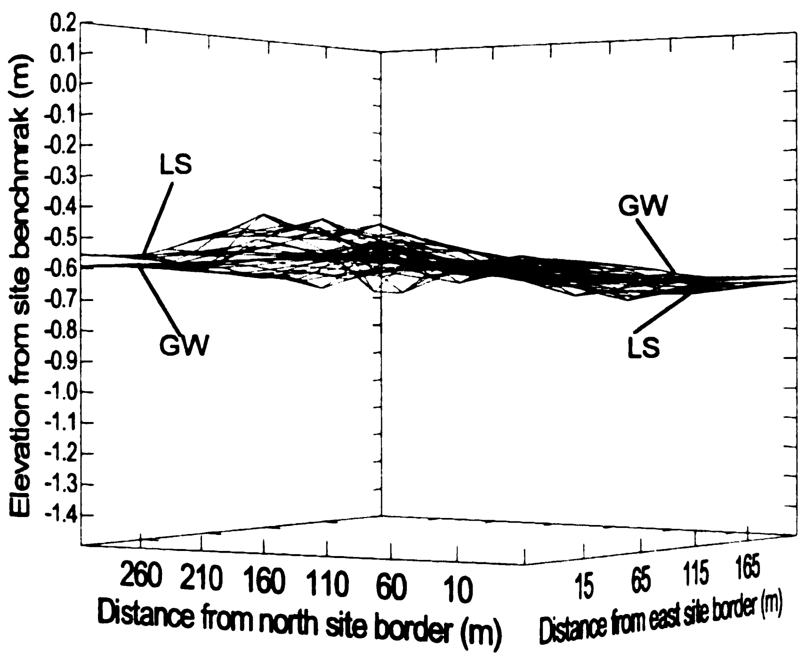

Figure B6. Groundwater condition on 3/21/96 at the disturbed hydrologic study site. On this date, groundwater levels had risen to the surface across the wetland and almost all the wet meadow was saturated to, or above, the ground surface. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

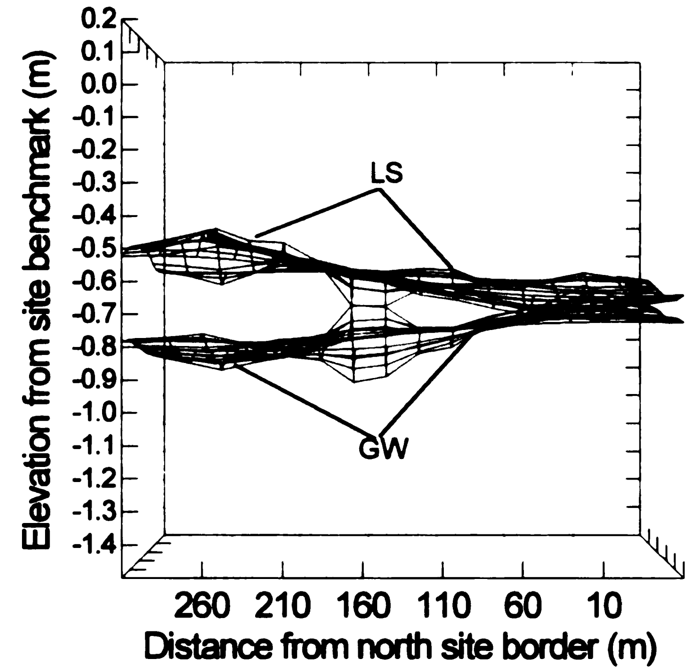

Figure B7. Groundwater condition on 7/1/96 at the disturbed hydrologic study site. Groundwater decline was once again observed at wells greater than 60m from the on-site ditch. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the east.

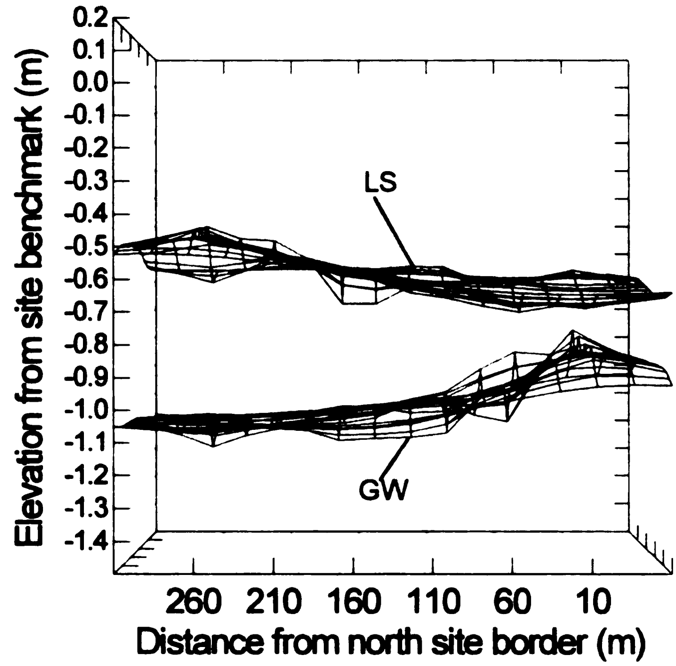

Figure B8. Groundwater condition on 7/15/96 at the disturbed hydrologic study site. The summer pattern of groundwater decline, observed previously at the disturbed site and concurrently at the reference site, was evident here. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the east.

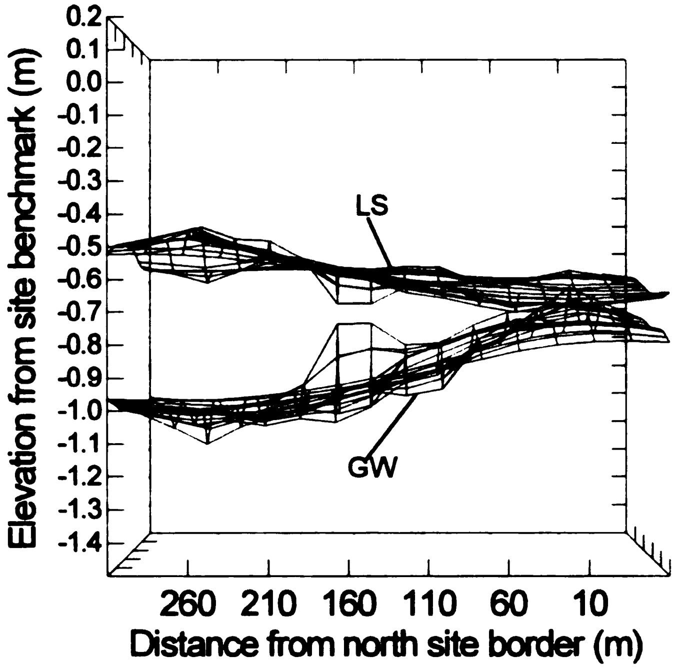

Figure B9. Groundwater condition on 9/16/96 at the disturbed hydrologic study site. Intense rainfall event triggered fall groundwater recharge. As in 1995, the most rapid recharge occurred closest to the on-site drainage ditch. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the east.

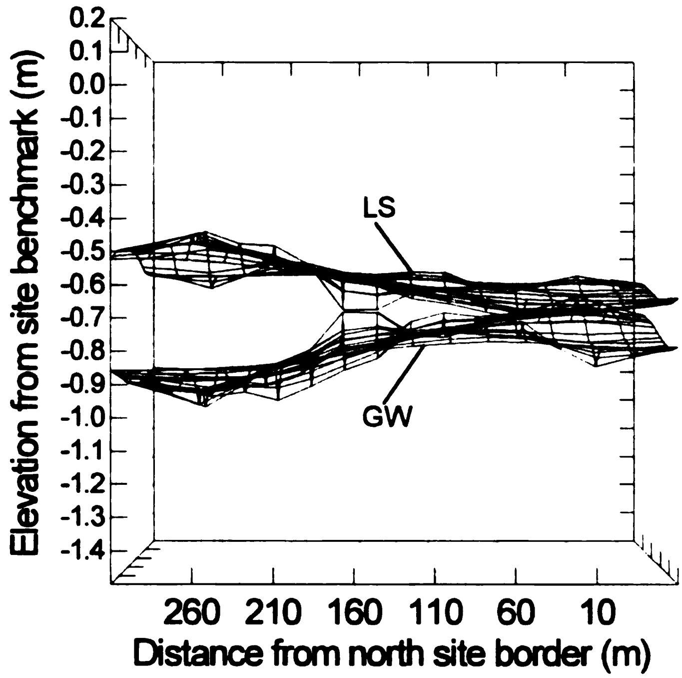

Figure B10. Groundwater condition on 12/10/96 at the disturbed hydrologic study site. As in 1995, infiltration of surface water into the wet meadow from the on-site ditch apparently constituted the major influence in raising groundwater levels in the wetland. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the east.

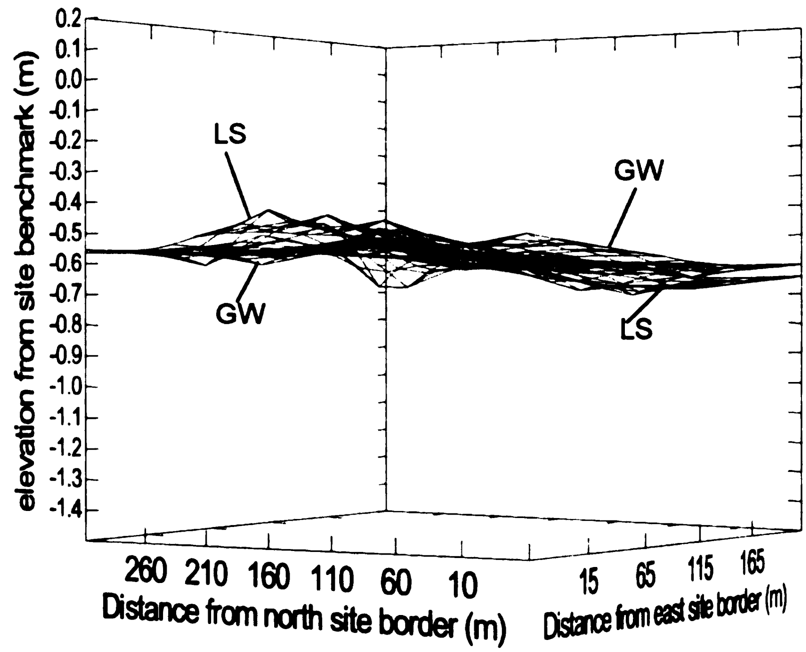

Figure B11. Groundwater condition on 1/26/97 at the disturbed hydrologic study site. Groundwater levels mirrored the land surface throughout the site. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

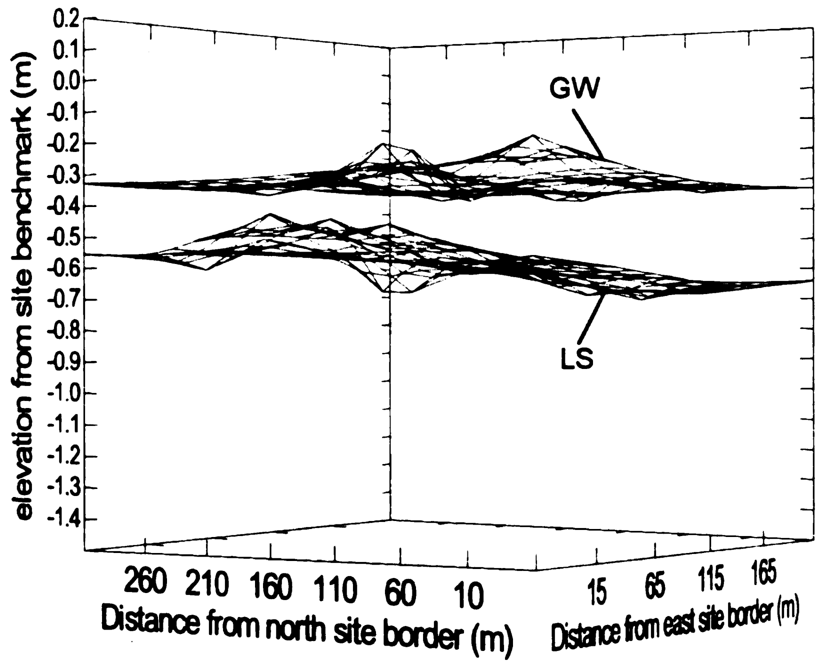

Figure B12. Groundwater condition on 3/1/97 at the disturbed hydrologic study site. The entire site was inundated to between 5-30cm depth. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

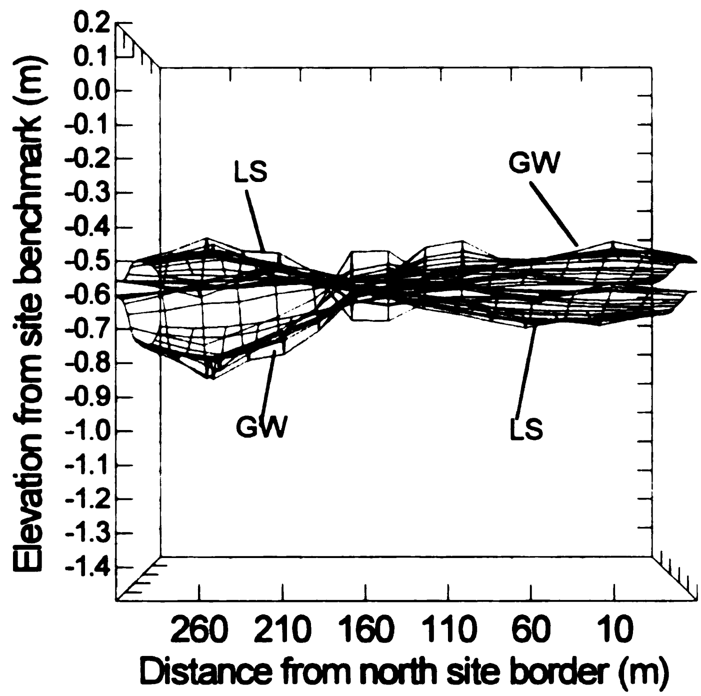

Figure B13. Groundwater condition on 6/11/97 at the disturbed hydrologic study site. Groundwater decline of 30-40cm was observed at wells more than 160m from the on-site ditch. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the east.

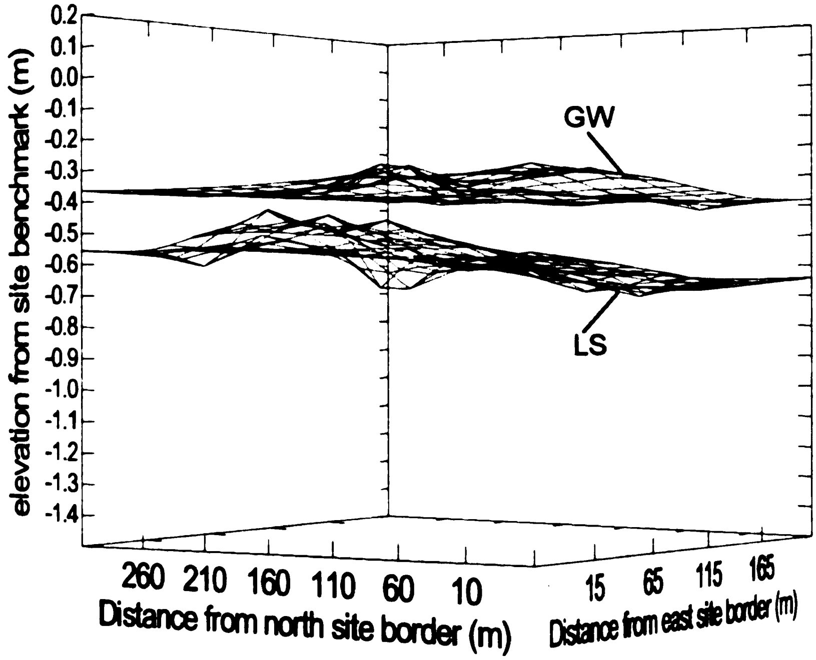

Figure B14. Groundwater condition on 7/10/97 at the disturbed hydrologic study site. Late June precipitation inundated the entire site. This condition was unchanged until early October 1997. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

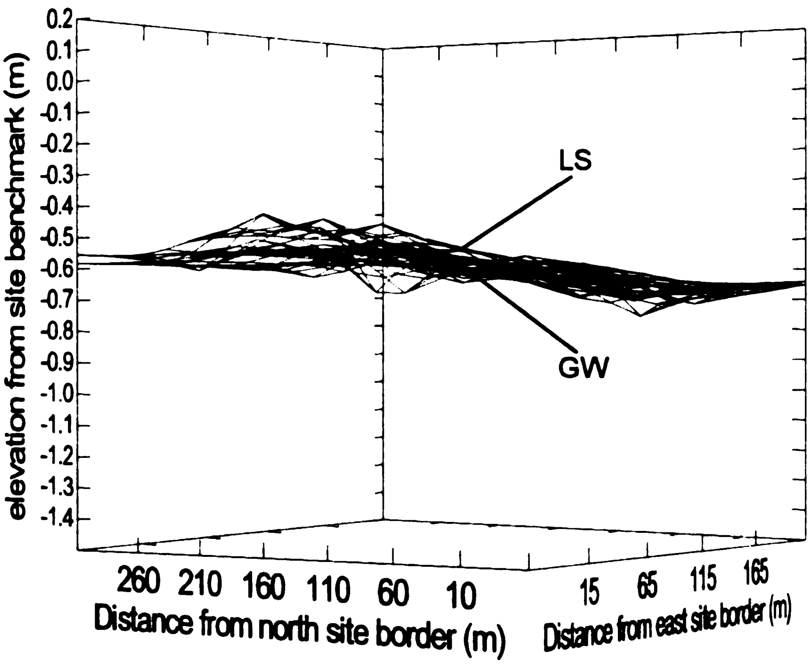

Figure B15. Groundwater condition on 12/18/97 at the disturbed hydrologic study site. Seasonal groundwater recharge was completed; the wetland was saturated to the land surface throughout the site. LS = land surface; GW = groundwater surface. Surface and groundwater elevations were measured at each monitoring well and determined with respect to a site benchmark. Surface and groundwater contour interpolation was performed using an inverse squared distance smoothing function (SPSS, Inc., 1996). Elevation increases with distance from north site border. View point is from the northeast.

Appendix C

Supplementary Data for Chapter 3

Appendix C1 - Soil physical and chemical data.

Table C-1. Soil physical and chemical analysis for wet meadow sites located in the Saginaw Bay coastal zone. Single sample numbers (e.g., 15, 27) indicate that one aliquot was collected and processed per site. For sample numbers containing a slash (e.g., 1/9, 6/1), the number left of the slash is the site number, and the number to the right of the slash is the number of the sample collected at that site.

Sample	pH	Bray-P (PPM)	Olsen-P (PPM)	K (PPM)	CA (PPM)	MG (PPM)	OM (%)	CA-CEC (meq/100g)	NO3-N (PPM)	NH4-N (PPM)	Sand (%)	Silt (%)	Clay (%)	Texture*	Mean BD (n=3)
1/1	7.1	3.5	16.5	42	5728	857	39.88	35.9	7.8	6.9	64.5	18.4	17.1	SL	0.36
1/4-5	7.3	4.5	30.5	42	5591	829	25.08	35	3.2	5.55	70.2	14.7	15.1	SL	0.44
1/9	6.9	11.5	23.5	89.5	6000	886	43.36	37.6	9.85	11.85	62.6	22.7	14.7	SL	0.47
1/13	6.8	8.5	32	58	5455	829	31.74	34.3	14.85	8.25	74.6	12.7	12.7	SL	0.49
2/2	7.7	1.5	13.5	47.5	3500	195	6.43	19.2	2.9	5.35	54.6	34	11.4	SL	0.38
2/5	7.2	2.5	6.5	10.5	1046	115	1.91	6.2	0.35	1.35	93.6	5	1.4	S	1.22
2/8	7.3	6	8.5	31.5	2000	419	6.43	13.6	4.15	3.25	76.4	22.7	0.9	LS	0.78
3	8.1	0.5	3.5	26.5	2476	110	1.31	13.4	0.15	1.4	92.7	2.4	4.9	S	1.44
4/1	7.1	3.5	7.5	16	2238	210	6.43	13	1.55	2.8	91.5	6.7	1.8	S	0.98

Table C-1 (cont'd).

Sample	pH	Bray-P (PPM)	Olsen-P (PPM)	K (PPM)	CA (PPM)	MG (PPM)	OM (%)	CA-CEC (meq/100g)	NO3-N (PPM)	NH4-N (PPM)	Sand (%)	Silt (%)	Clay (%)	Texture*	Mean BD (n=3)
4/2	8.4	3	6.5	21	2143	130	0.91	11.9	0.1	0.6	92.4	3.2	4.4	S	1.23
5/1	8.2	2.5	5.5	10.5	1409	84	0.91	7.8	0.65	1.9	98.4	1.2	0.4	S	1.34
5/2	8.3	0.5	5.5	52.5	2857	180	1.12	15.9	0.15	1.4	69.5	12.7	17.8	SL	1.55
6/1	8	0.5	23.5	47.5	2953	215	3.91	16.7	1.85	1.8	82.6	10	7.4	LS	0.99
6/2	7.9	1	5.5	26.5	2572	155	3.41	14.2	1.5	1.1	94.4	4.2	1.4	S	1.34
8	7.6	8	8.5	42	2715	238	6.1	15.7	3.15	4.05	73.9	20.7	5.4	SL	0.74
9	7.2	7.5	9.5	37	2191	400	10.17	14.4	2.65	3.4	71.1	25.1	3.8	SL	0.59
10	6.1	3.5	10.5	31.5	2334	424	12.21	20.1	1.25	3.95	63.8	26.4	9.8	SL	0.24
11	6.5	3	7.5	21	1818	286	5.22	11.5	1.1	2.35	71	21.6	7.4	SL	0.38
13	6.8	4	12.5	31.5	2524	457	12.03	16.5	2.95	3.25	62.6	28	9.4	SL	0.41
14	8.3	0.5	3.5	31.5	2857	200	1.22	16	0.65	1.2	77.3	9.3	13.4	SL	1.26
15	8.6	0.5	9.5	21	2429	63	0.72	12.7	0.15	0.45	95.6	1.2	3.2	S	1.57
18	7.6	3	5.5	16	1500	170	2.83	9	0	1.7	94.5	4.4	1.1	S	0.89
19	6.7	3.5	30.5	10.5	1182	190	4.12	7.5	10.1	1.5	91.6	5.2	3.2	S	0.71
20	7.7	3.5	16.5	73.5	2500	448	6.31	16.4	1.7	2.7	61.5	14.7	23.8	SCL	1.19
21	7	3.5	16.5	47.5	3810	481	32.5	23.2	3.25	5.4	52.6	28	19.4	SL	0.63
22	7	3.5	22.5	16	1211	137	2.62	7.2	0.7	1.4	95.6	2.2	2.2	S	0.58
24	6.7	3	11.5	31.5	2300	329	9.24	14.3	2	2.75	78.6	10	11.4	SL	0.51
25	7.3	10	11.5	26.5	1632	280	3.62	10.6	0.7	2.25	85.2	6.4	8.4	LS	0.95
26	6	3	11.5	26.5	1895	235	10.93	15.1	1.3	3.3	88.6	6	5.4	S	1.3
27	6.8	3.5	7.5	26.5	2750	319	11.15	16.5	1.85	2.55	77.9	14.7	7.4	LS	0.58
28	7.4	2	9.5	37	2700	391	11.4	16.8	2.3	2.85	71.9	14.7	13.4	SL	0.5
30	8.5	2	14.5	16	1842	50	0.4	9.7	0.55	0.7	96.4	1.4	2.2	S	1.34
31	7.2	3	8.5	16	1579	205	2.83	9.6	0.95	1.7	95.2	3.4	1.4	S	0.55

* - Texture codes: SL = Sandy Loam, S = Sand, LS = Loamy Sand, SCL = Sandy Clay Loam.

Appendix C2 - Species stem density data

Table C-2. Stem densities of plant species encountered in Saginaw Bay coastal wet meadows in 1997. A total of 300-0.25m^2 sample plots were collected in 25 coastal wet meadows. Percent frequency of occurrence was determined from the number of sample plots in which the species was found. N equals the number of plots in which a species occurred.

Species	Frequency of Occurrence (%)	Contribution to Total Stem Density (%)	Mean Species Stem Density (stems/m^2, ±1SEM)	N
Acorus calamus	0.3	0.0	20.0(N/A)	1
Agropyron repens	2.7	0.1	29.0(11.7)	8
Alisma plantago-aquatica	0.3	0.0	16.0(N/A)	1
Anemone canadensis	8.3	0.4	57.8(13.6)	25
Apocynum canabinum	5.3	0.0	7.8(1.5)	16
Asclepius incarnata	1.7	0.0	4.0(0.0)	5
Aster borealis	7.7	0.1	5.2(1.4)	23
Aster dumosus	10.7	0.4	36.8(9.0)	32
Calamagrostis canadensis	93.3	32.4	382.5(17.0)	280
Calystegia sepium	20.0	0.5	25.0(5.8)	60
Campanula aparinoides	47.3	5.5	127.7(12.6)	142
Carex aquatilis	53.0	21.8	454.0(31.2)	159
Carex bebbii	8.7	1.2	158.5(49.2)	26
Carex buxbaumii	4.0	1.3	370.3(97.6)	12
Carex comosa	0.7	0.0	24.0(8.0)	2
Carex hystericina	0.3	0.0	8.0(N/A)	1
Carex lacustris	20.3	1.4	77.5(14.0)	61
Carex sartwellii	59.0	11.3	211.8(18.8)	177
Carex stricta	26.3	9.6	400.5(42.6)	79
Carex vulpinoidea	0.3	0.0	20.0(N/A)	1
Cicuta bulbifera	1.3	0.0	19.0(7.5)	4
Cicuta maculata	1.7	0.1	41.6(31.7)	5
Circium arvense	10.0	0.1	8.7(0.9)	30
Cladium mariscoides	34.7	1.8	58.1(5.3)	104
Cornus amomum	3.0	0.0	12.0(4.3)	9
Cornus stolonifera	7.0	0.1	9.9(1.9)	21
Eleocharis rostellata	0.7	0.1	43.0(15.0)	2
Eleocharis smallii	9.3	1.4	45.1(17.4)	28

Table C-2 (cont'd).

Species	Frequency of Occurrence (%)	Contribution to Total Stem Density (%)	Mean Species Stem Density (stems/m^2, ±1SEM)	N
Epilobium hirsutum	1.0	0.0	8.0(2.3)	3
Equisetum arvense	0.3	0.0	12.0(N/A)	1
Equisetum hyemale	0.3	0.0	16.0(N/A)	1
Eupatorium maculatum	1.7	0.0	15.2(6.2)	5
Eupatorium perfoliatum	2.3	0.0	6.9(2.3)	7
Fragaria virginiana	0.7	0.0	18.0(6.0)	2
Fraxinus pennsylvanica	0.7	0.0	0.0(0.0)	2
Galium boreale	12.7	1.4	118.8(24.1)	38
Geum spp.	0.3	0.0	16.0(N/A)	1
Helenium autumnale	0.7	0.1	94.0(82.0)	2
Hypericum kalmianum	1.7	0.0	16.8(12.2)	5
Impatiens capensis	8.7	0.2	19.2(3.4)	26
Iris versicolor	2.3	0.1	39.4(9.3)	7
Juncus balticus	9.7	0.7	81.9(17.8)	29
Juncus brevicaudatus	4.3	0.8	198.8(52.8)	13
Juncus effusus	0.3	0.0	56.0(N/A)	1
Lathyrus palustris	18.3	0.2	12.1(1.7)	55
Leerzia oryzoides	4.3	0.2	9.4(2.0)	13
Lobelia kalmii	0.7	0.0	4.0(0.0)	2
Lycopus americanus	5.7	0.1	12.9(3.2)	17
Lysmachia quadriflora	5.0	0.4	98.7(41.1)	15
Lysmachia terrestris	1.0	0.1	57.3(13.3)	3
Lysmachia thrysiflora	3.7	0.1	24.7(8.2)	11
Lythrum alatum	1.0	0.0	6.7(3.5)	3
Lythrum salicaria	12.3	0.4	38.2(6.1)	37
Mentha arvensis	6.3	0.1	23.4(5.6)	19
Onoclea sensibilus	0.3	0.0	4.0(N/A)	1
Panicum spp.	0.3	0.0	0.0(N/A)	1
Panicum virgatum	0.3	0.0	0.0(N/A)	1
Phalaris arundinacea	16.7	1.6	109.0(22.8)	50
Phragmites australis	6.7	0.2	31.2(7.7)	20
Poa palustris	1.7	0.2	123.2(69.6)	5
Poa spp.	1.3	0.1	88.0(70.8)	4
Polygonum amphibium	43.3	0.6	14.6(1.1)	130
Polygonum scandens	0.3	0.0	4.0(N/A)	1
Populus deltoides	1.7	0.0	9.6(3.2)	5
Potentilla anserina	7.0	0.4	68.2(18.0)	21
Potentilla fruiticosa	2.0	0.1	70.0(21.8)	6
Pycnanthemum virginianum	1.3	0.1	33.0(13.6)	4
Rubus spp.	0.3	0.0	4.0(N/A)	1
Rudbeckia hirta	0.7	0.0	16.0(12.0)	2

Table C-2 (cont'd).

Species	Frequency of Occurrence (%)	Contribution to Total Stem Density (%)	Mean Species Stem Density (stems/m^2, ±1SEM)	N
Sagittaria latifolia	1.0	0.0	28.0(8.3)	3
Salix petiolaris	4.7	0.0	1.6(0.3)	14
Scirpus acutus	1.7	0.0	17.6(7.3)	5
Scirpus americanus	1.0	0.0	42.7(23.2)	3
Scirpus atrovirens	0.3	0.0	4.0(N/A)	1
Scirpus validus	1.0	0.1	48.0(18.5)	3
Scutellaria galericulata	5.3	0.1	15.0(3.1)	16
Scutellaria lateriflora	0.3	0.0	8.0(N/A)	1
Solanum dulcamara	0.3	0.0	28.0(N/A)	1
Solidago uliginosa	0.3	0.0	80.0(N/A)	1
Spartina pectinata	4.7	0.3	61.1(31.0)	14
Spiraea alba	1.7	0.0	5.6(1.6)	5
Spiranthes lucida	0.3	0.0	4.0(N/A)	1
Stachys tenuifolia	18.7	0.5	29.2(5.0)	56
Taraxacum officiale	1.0	0.0	16.0(8.3)	3
Teucrium canadense	2.7	0.1	32.5(16.1)	8
Thelyptris palustris	0.3	0.2	656.0(N/A)	1
Typha angustifolia	19.0	0.2	10.0(1.3)	57
Typha latifolia	1.0	0.0	5.3(1.3)	3
Unknown #1	0.3	0.0	4.0(N/A)	1
Unknown #2	0.3	0.0	0.0(N/A)	1
Verbena hastata	0.3	0.0	4.0(N/A)	1
Viola affinis	0.3	0.0	32.0(N/A)	1
Vitis riparia	0.3	0.0	4.0(N/A)	1
Totals		100.0		2384

Appendix C3 - Vertical distribution of vegetation parts

Table C-3. Vertical distribution of leaf, stem, and inflorescence contacts in Saginaw Bay coastal wet meadows. Table data are expressed as percentages, with actual counts in parentheses.

Contact Type	Height Class				% of total contacts
	>90cm	40-90cm	<40cm	Total	
Leaf contacts	18.5(1015)	62.2(3409)	19.3(1060)	100.0(5484)	81.8
Stem contacts	10.2(100)	53.8(530)	36.0(354)	100.0(984)	14.7
Inflorescence contacts	73.5(175)	18.9(45)	7.6(18)	100.0(238)	3.5
All contacts	19.2(1290)	59.4(3984)	21.4(1432)	100.0(6706)	100.0