

**Long-Term Vegetation Dynamics Following
Water Level Stabilization in a
Prairie Marsh**

By

Richard E. Grosshans

A thesis presented to the University of Manitoba in partial fulfillment of the requirements
for the degree Master of Science in the Faculty of Graduate Studies

Department of Botany
University of Manitoba
Winnipeg, Manitoba, Canada
R3T 2N2

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**LONG-TERM VEGETATION DYNAMICS FOLLOWING WATER LEVEL STABILIZATION
IN A PRAIRIE MARSH**

BY

RICHARD E. GROSSHANS

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
of
MASTER OF SCIENCE**

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ABSTRACT

Within prairie marshes, flood-drought cycles produce fluctuating water levels that lead to cyclical changes in plant community structure and composition. These natural flood-drought cycles are recognized as essential to maintaining habitat diversity and productivity of prairie marshes. Indeed, annual waterfowl production is closely tied to the availability of suitable and diverse wetland habitat. It is also recognized that disruption of this cycle (usually human-induced water level stabilization) results in a reduction in habitat complexity, biodiversity and productivity of prairie marshes. The ecological processes driving such changes, however, are incompletely understood. The objective of this study is to examine the long-term vegetation dynamics of a prairie marsh following water level stabilization. We hypothesize that disruption of the natural disturbance regime (flood-drought cycles) in prairie marshes increases the influence of competition among macrophyte species. An increase in competitive interactions results in elimination of subordinate species, while consolidating the abundance of competitive dominants. We used colour infrared aerial photography, GPS and GIS, microtopographic maps, and ground-truthing surveys to examine the role of interspecific competition in structuring wetland communities in the Marsh Ecology Research Program (MERP) experimental marshes at Delta Marsh, Manitoba, Canada. The MERP complex consists of ten sand-diked and two "control" marshes, each between ca. 5-7 ha in area. Water level fluctuations in Delta Marsh were artificially stabilized in 1961, disrupting the natural flood-drought cycle. Since 1989, water levels in the twelve marshes have been left to equilibrate with the surrounding marsh. At present, six emergent plant zones characterize the twelve marshes: salt-tolerant species, annuals, reed grass, whitetop, cattail and bulrush. Our results indicate that long-term stabilization of water levels has led to increasingly distinct vegetation patterns, which we attribute to competitively dominant species "sorting themselves out" along an elevation gradient. Elevation is a complex environmental gradient that combines such factors as water depth, oxygen availability, salinity, deadfall accumulation and rhizome/seed bank composition. The influence of these factors increases with prolonged water level stabilization, with the result that interspecific competition becomes a major driving force in shaping vegetation patterns. With water level stabilization, there is a paradigm shift from a disturbance-driven ecosystem to a competition-driven one. This investigation provides important insight into the role of fluctuating water levels on the structure, composition and habitat diversity of prairie marshes.

ACKNOWLEDGMENTS

This study would not have been possible without the endless support of my numerous friends, family, colleagues and advisors who have accompanied me throughout the extent of this adventure. I could especially count on my wife and best friend, Christine, to listen, make me smile, and always keep the fire lit to burn away the procrastination. Next, I thank Dr. Frank Rohwer, Delta's former scientific director, for giving me the opportunity of a lifetime, to conduct research through the world renowned Delta Waterfowl and Wetlands Research Station. I also thank all the people at Delta for their support and expertise over the years, and for making two extremely long, grueling field seasons very memorable experiences. In particular I would like to thank Delta's "moms", Sandy, Alice, Brenda, and the rest of their crew, who kept a watchful eye over all of us and kept us fed and comfortable in our second home. I extend thanks to all my Delta colleagues and fellow students for their fantastic camaraderie, which made the Delta experience what it is. I must extend my deepest thanks to my field team, Megan Hodgson, Steve Kembel, Boyan Tracz and Jocelyn Chorney for putting up with chest waders in the scorching heat, *Phragmites* jungles, green aphid goop, and loon-poop filled marshes. This study also could not have been possible without the endless support of the original MERP team. I thank Dr. Arnold van der Valk, Dr. Henry Murkin and Lisette Ross for supplying me with mounds of historical maps, vegetation data, advice, useful tips and info regarding the whole MERP study site, history and pit-traps. I thank Dr. Gordon Goldsborough, Dr. Richard Staniforth and Dr. Rene van Acker, my committee members, for their advice and guidance. Lastly, and definitely not least, I thank my advisor, Dr. Norm Kenkel, for providing a place in his research team for an aspiring young wetland biologist. I thank him for his wisdom, guidance, support, and endless hours spent debating with me the finer points of ecology, and placing me back on the right track when I strayed about 2 miles off course. This project was funded by several research grants from the Delta Waterfowl Foundation, and Ducks Unlimited Canada through the Institute for Wetland and Waterfowl Research. I would like to acknowledge the Portage Department of Highways, JonAir, and Resources for Tomorrow for their logistical support. Additionally, numerous travel grants from the Alumni Association, Department of Botany, Faculty of Science, and Graduate Students Association made it possible to present at several student and professional scientific conferences, which I feel are a critical part to the education of a graduate student.

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CHAPTER 1

Introduction and Literature Review: Prairie Marsh Ecosystems, and the Processes Within

1.1 An Introduction To The Prairie Marsh

1.1.1. Wetland or Marsh?

If one encounters a shallow pond vegetated by aquatic plants, and bordered by meadows or agricultural farmland, is it a wetland or a marsh? Essentially, it is both. In general it is a wetland, but more specifically it would be a prairie marsh. Warner and Rubec (1997) define a wetland as land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation and various kinds of biological activity which are adapted to a wet environment. A marsh is defined as a specific type of wetland that has shallow water, with water levels typically fluctuating daily, seasonally or annually due to flooding, seepage loss, evapotranspiration, groundwater recharge or tides (Warner and Rubec 1997). The dominant vegetation community of a prairie marsh consists of graminoids, forbs, shrubs and emergent plants, along with submersed aquatics occupying the shallow water areas. Prairie marshes range in size from small shallow prairie potholes to larger, heavily vegetated lacustrine complexes, and are among some of the world's most productive ecosystems (Murkin 1989). Prairie wetlands are a prominent feature throughout the prairie region covering 40 to 60% of the entire land area. They stretch across an estimated 750,000 km² (Kantrud et al. 1989a) of the Canadian prairie provinces (Alberta, Saskatchewan, Manitoba) and in prairie regions of the upper United States (Montana, North Dakota, South Dakota, Minnesota, Iowa) (**Figure 1.1**).

Prairie wetland systems are considered some of the most dynamic wetland types in North America. This is attributable to the extremely variable climatic conditions associated with the prairie environment (Kantrud et al. 1989a). Alternating periods of flooding and droughts (high and low water years) are characteristic of this region, and whether daily, seasonally or annually these fluctuating water levels cause prairie marshes to undergo drastic vegetation changes (Kantrud et al. 1989a). In understanding the dynamic nature of these wetlands, one must be familiar with not only the complex processes which occur within them, but be aware that the prairie environment itself is responsible for the existence of these wetland systems. This chapter introduces the prairie marsh setting, and its historical significance and

environmental characteristics. The present day classification of marsh systems are also discussed, as well as marsh ecosystem dynamics and theories of competition and coexistence in prairie marshes.

1.1.2. The Prairie region

The prairie region is classified as the Aspen Parkland and Grassland ecoclimatic regions of Canada (Ecoregions Working Group 1989), and Great Plains, Central Lowlands regions of the United States (Kantrud et al. 1989b). The prairie landscape consists of a predominance of grasses and forbs, with a forest-grassland transition area (Aspen Parkland). This transition zone consists of large islands of aspen woodlands towards the north, while clumps and groves of aspen are interspersed with prairie grasses towards the south (Adams 1988). Intermixed among this region is a mosaic of treed river valleys. The prairie region can also be divided into elevation levels: Alberta High Plain (elev. 610 - 1,060 metres above sea level), Parkland and Great Plains region (elev. 320 - 610 m asl) and Lowlands of Manitoba and the Dakotas (elev. 220-335 m asl).

Settlement of the west and beyond

Settlement of the prairie region began during the mid 1800's, and was accelerated by the Homestead Act of 1862, extensions of railroads and stage lines, and road building (Leitch 1989). Prior to European settlement, the entire grassland region covered approximately 370 million ha of North America (Sims 1988). With settlement of the land came clearing and ploughing of the prairie landscape, and draining of wetlands for farming and livestock. Throughout the early settlement of these regions wetlands had survived better than the prairie landscape, being at one time too difficult to drain. Nevertheless, with improved agricultural techniques and machinery following the 1940's, prairie marshes were increasingly drained for agricultural purposes (Leitch 1989). Land practices across the prairies continue to be primarily agriculture, including livestock, and as a result most of the prairie habitat and their associated wetlands have been drained and ploughed under. Drainage in the Canadian prairies occurs primarily by overland trenching or creation of drainage ditches. In the United States methods change from subsurface tiles to surface drains moving northwestward across this region (Leitch 1989). Consequently, remaining prairie marshes are typically surrounded by agricultural land with narrow buffer strips of upland vegetation. As a result of this close proximity, these wetlands receive high inputs of agricultural chemicals, sediments and nutrients (Phillips 1996). It was not until the 1970's that people began to realize the benefits

of wetlands, that they are not just a nuisance, obstacle for farming, waste dump or mosquito breeding ground, and that wetlands should be protected or restored.

1.1.3. Classification of Prairie Wetlands

A wetland is defined as land with pooled surface water or groundwater at, near or above the surface remaining for a significant period of time throughout the growing season. This enables wetland or aquatic processes to occur and growth of wetland vegetation (Kantrud et al. 1989b, Glooschenko et al 1993). Various systems have been adapted for classifying wetland ecosystems in North America, with the more commonly used systems developed by Cowardin et al. (1979) for use in the United States, and the revised Canadian Wetland Classification System developed by the National Wetlands Working Group (Warner and Rubec 1997). Additionally, Stewart and Kantrud (1971) developed a classification specifically for natural ponds and lakes of the prairie region, which is the most commonly used system for detailed classification of prairie marshes. According to Cowardin et al. (1979), prairie marshes can be classified into three groups or systems: palustrine, lacustrine and riverine. These are further subdivided into subsystems, classes and subclasses. Conversely, the Canadian Wetland Classification System, recognizes 8 marsh forms: basin, estuarine, hummock, lacustrine, riparian, slope, spring and tidal, with various subforms to further define each form (Warner and Rubec 1997). For the purposes of this report, the Canadian Wetland Classification System will be used (Warner and Rubec 1997). Although 8 marsh forms are recognized, only basin, lacustrine, and riverine are common within the prairie region.

Basin Marsh

The most familiar prairie marshes found throughout the agricultural prairie region are prairie potholes or sloughs, classified as a type of shallow basin marsh (Warner and Rubec 1997) or palustrine wetland (Cowardin et al. 1979). These unconnected shallow saucerlike depressions dot the prairie landscape, and initially formed during the last glacial advance. Such marshes are situated in well-defined basins or depressions that are far enough away to be influenced by larger water bodies. They receive water from groundwater discharge, rain, snowmelt, surface runoff and inflow from river or streams. The amount of water that they contain fluctuates annually, seasonally and even daily, depending on the amount of snowmelt, spring runoff, precipitation and evapotranspiration they receive (Kantrud et al. 1989a, 1989b; Weller 1994). Consequently, these marshes can be freshwater, brackish or saline. Basin

marshes are the classic prairie pothole marshes found throughout the agricultural prairie region.

Lacustrine Marsh

Throughout the prairie region we also find a variety of wetlands occurring along the shores of inland brackish and freshwater open water bodies or lakes, subjected to periodic flooding and increases in water levels from wave action or wind tides. These are classified as lacustrine marshes (Warner and Rubec 1997) or lacustrine wetlands (Cowardin et al. 1979). These marshes receive their water and nutrient input primarily from adjacent lakes, rivers or streams flowing into the lake as well as rain, snowmelt, surface runoff and groundwater discharge (Warner and Rubec 1997). They typically develop by sediment accumulation, either deposited along the shore from inflowing rivers, ice movement, wave action or from periodic flooding. These sediment accumulations may create sheltered areas or lagoons by trapping water behind barrier beaches or ridges, allowing wetland vegetation to grow. Delta Marsh, Manitoba, Canada (further discussed in Chapter 2) is an example of a lacustrine bay marsh, formed by sediment accumulation and wave drift following the last glacial period. Lacustrine or lake associated marshes are affected by environmental factors in much the same way as smaller prairie marshes are, and are consequently subjected to periodic high and low water periods.

Riparian Marsh

Riparian marshes occupy the riparian areas surrounding rivers and streams. These marshes develop in old glacial deltas where rivers or streams still run over them, on alluvial plains and terraces bordering streams, in abandoned river channels, and on river embankments, channels islands or streambeds (Warner and Rubec 1997). These wetlands receive water from rain, snowmelt, groundwater discharge and surface runoff, but are most closely associated with adjacent streams and rivers. Riverine wetlands are less common throughout the prairie region (Kantrud et al. 1989a, 1989b).

1.1.4. The Midcontinental Prairie Environment

The midcontinental prairies are a semiarid region featuring cold winters and warm summers, with longer winters and shorter summers towards the northern periphery of this region. This region experiences extremely variable conditions of both temperature and

precipitation, which can vary from one year to the next. Annual precipitation ranges from 30 to 100 cm, typically with a descending precipitation gradient from east to west. Annual temperatures range from -40 °C to +40 °C, with less extremes towards the periphery of the region (i.e. Alberta and South Dakota)(Anon. 1982a, 1982b, Kantrud et al. 1989b). Mean January temperatures range from -15 °C to -5 °C, and mean July temperatures from 20 °C to 30 °C, generally following a north-south gradient

1.2. Marsh Ecosystem Dynamics

1.2.1. Hydrology

Prairie marshes are formed where surface or groundwater ponds and remains for a significant period of time throughout the growing season, allowing wetland processes to occur (Kantrud et al. 1989b, Warner and Rubec 1997). Water budgets for these marshes varies according to how they receive and lose water to inflow and outflow respectively. Most marshes receive water from rain, snowmelt, surface runoff, and some sort of groundwater discharge. Basin marshes, or prairie potholes, as well as Riparian marshes also receive water from inflow from rivers or streams. Lacustrine marshes receive their water primarily from their neighbouring water body or lake, as well as some combination of the above sources (Warner and Rubec 1997). Prairie marshes in general lose water primarily by evapotranspiration into the atmosphere, but may also lose water by groundwater recharge (subsurface drainage into the groundwater) or overflowing their depression during high water years (Meyboom 1966, Kadlec 1987, Hubbard 1988, Winter 1989). In each case, the amount of water a prairie marsh contains fluctuates annually, seasonally or even daily, and is dependent on the amount of inflow and outflow it receives (Kantrud et al. 1989b).

Most prairie marshes act as either groundwater recharge sites (supplying water to the water table), groundwater discharge sites (removing water from the water table) or groundwater flowthrough sites (providing both groundwater discharge and recharge) and often change from one to the other depending on the surrounding water table (Meyboom 1966, Hubbard 1988, Winter 1989, Rosenberry and Winter 1997). Climate in the prairie region consists of extremes in both temperature and precipitation. As a result, there is less annual precipitation than annual evapotranspiration, giving prairie marshes a negative water balance (Winter 1989). Since many prairie marshes are nonintegrated basins (not associated with channelized surface water flow), this negative water balance results in extreme changes in mean water depth, which contributes to the dramatic vegetation changes characteristic of prairie marshes

(further discussed in Section 1.3). Surface runoff, subsurface drainage and groundwater discharge in wetlands are highly dependent on the surrounding topography, underlying geology, soil characteristics, surface and groundwater interactions, and atmospheric water exchange (Winter 1989, Kantrud et al. 1989b, Rosenberry and Winter 1997). Ground-water fluxes to and from prairie pothole wetlands are highly variable temporally and spatially and the direction of flux changes frequently (Winter and Rosenberry 1995). Fluctuations in water-table configurations can cause reversals in the water-table gradient, changing directions of groundwater flow and seepage seasonally (Rosenberry and Winter 1997). Since the seasonal water-table configurations of wetlands are quite complex, an accurate knowledge of water budgets is essential for understanding many aspects of wetland ecology (Kadlec 1987).

1.2.2. Wetland Soils

The majority of soils found in wetlands throughout the prairie region can be broadly classified as gleysolic and regosolic soils (Scott 1993). Such soils are characteristic of poorly drained areas with prolonged periods of water saturation. These soils are typically dense and as a result, prairie basins tend to have a high degree of water retention allowing wetland vegetation to grow. Soils found in flooded and waterlogged areas along lakeshores (i.e. lacustrine marshes) tend to have higher contents of silt and sand overlaid by layers of poorly drained organic muck and peat, ranging in texture from sandy loam to silty clay (Shay et al. 1999). Thick organic layers develop through incomplete decomposition of organic material deposited from the marsh, with soil layer thickness varying between and within vegetation zones and communities. Wilson and Keddy (1985) and Dale (1965) indicate that soil and organic matter content contribute to the distribution of some wetland plants. In any case soil properties such as salinity do affect vegetation patterns, which is further discussed in the following section.

1.2.3. Salinity

Salinity is known to significantly affect plant growth, in both aquatic and upland systems (Kenkel et al. 1991). Patterns of plant zonation have been observed along salinity gradients for both inland systems (Badger and Unger 1990, Kenkel et al. 1991) and salt marshes (Barbour 1978, Snow and Vince 1984, Vince and Snow 1984), and it has been suggested that salinity also influences plant growth and long-term distribution within prairie marshes (Stewart and Kantrud 1971, 1972, Leiffers and Shay 1982, Neill 1993). Higher soil salinity often occurs where the water table is at or near the soil surface. Salts are brought to the

surface by capillarity (i.e., upward moving water) and concentrated through surface evaporation (Brady 1990). During a natural state of fluctuating water levels, periodic flooding in prairie marshes effectively reduces soil salinity by flushing away dissolved salts, while dry periods buildup salinity levels as surface waters evaporate (Neill 1993). Conversely, under a stable water level regime salts accumulate and in the absence of flushing water, persist.

Salinity in prairie wetlands, of both soil and water, is a function of the amount of water gain and loss, and the availability of salts. Consequently, water conditions in many prairie marshes tend to be slightly to moderately saline, as a consequence of evapotranspiration rates in these wetlands being higher than their input of freshwater (Winter 1989). Freshwater lake marshes will have greater water gain, and therefore lower salinity levels, whereas isolated prairie marshes will be more saline due to less water gain and more loss due to evapotranspiration. In any case, salinity (both soil and water) has a profound effect on seed germination, plant growth, and vegetation composition and distribution in prairie marshes. Salinity is considered a significant factor affecting a wetland's initial plant composition and zonation patterns (Dale 1964, Stewart and Kantrud 1972, Kantrud et al. 1989a).

1.2.4. Nutrient Cycling

Water transport in a prairie marsh is essential to the input and output of nutrients such as N, P, K, CO₂ and O₂, linking hydrology closely to nutrient dynamics within a prairie marsh. Since these wetlands often occur in basins or low-lying areas with long-term sediment and organic matter accumulation, an effective water budget is essential for suitable nutrient balances (Kadlec 1987). Marshes bordering large lakes, for example, tend to have large surface and ground water inflows and outflows. This can often result in high concentrations of dissolved and suspended particles in the water, which can lead to an extremely productive ecosystem (Kadlec 1987).

Nutrient cycling in a marsh system occurs by many processes within and among the water, organic sediments and inorganic basin. Nutrients can be transferred into and out of the marsh system by atmospheric exchange, incorporated into the biomass and transferred between living plants and litter, and taken in or released by macrophyte plants, epiphytes, algae, small animals and microorganisms (Kadlec 1987). Organic sediments are considered the major source of nutrients for emergent plants such as cattail (*Typha* spp.) and bulrush (*Scirpus*

spp.), whereas submersed plants such as pondweed (*Potamogeton* spp.) or various forms of algae receive nutrients primarily from the water column (Kadlec 1987).

Today, many prairie marshes are surrounded by agricultural fields, and consequently often receive high amounts of nutrients and sediments from agricultural runoff (Phillips 1996). Emergent and submersed plants as well as algae all effectively remove nutrients from water passing through the system. Marshes, therefore, act as successful nutrient sinks helping to preserve local water quality (Neely and Baker 1989). With a healthy diverse plant community, wetlands are effective nutrient sinks removing contaminants from the water column. This enhances filtration of the surrounding runoff thereby improving the overall quality of water (Neely and Baker 1989, Cooper 1993, Phillips 1996). Nonetheless, recent evidence suggests dramatically increased inputs of nutrients affects the overall vegetation community of these marsh systems. For example, heavy runoff from agricultural fields is believed to be responsible for the replacement of dominant emergents by cattail in the Florida Everglades (Davis 1994, Urban et al. 1993). Woo and Zedler (2000) support this, by finding cattail to rapidly replace graminoids within a wet meadow habitat by increasing nutrient input alone. Ultimately, a healthy diverse riparian buffer (vegetated areas) surrounding a prairie wetland is essential in preserving not only the wetland community but the surrounding water quality.

1.3. Vegetation Dynamics

1.3.1. Seed Banks and the Rhizome Reserve

A seed bank is described as the amount and kinds of viable seeds present within the soil, including small vegetative propagules, as well as spores of mosses, liverworts and ferns (van der Valk and Davis 1976a, Murkin et al. 2000). Larger vegetative propagules (bulbs, tubers, rhizomes) are usually not considered part of the seed bank (Murkin et al. 2000), but do play a major part in revegetation of a marsh basin, and so can be considered as the rhizome reserve. Collectively, these viable seed and rhizome stores contain numerous species capable of survival during various types of environmental conditions, ensuring the continuous presence and recolonization of vegetation in a prairie marsh. Accordingly, van der Valk (1981) suggests that a clear understanding of the marsh seed bank and its species characteristics are essential to understanding or predicting vegetation change and plant succession in prairie marsh ecosystems. Seeds within the seed banks of smaller marshes, for example, are usually quite evenly dispersed along the elevation gradient (van der Valk and Davis 1976a). In larger

lake marshes, however, emergent plant seeds are typically distributed within the elevation range where adult plants are found (van der Valk and Welling 1988). As well, seeds in these larger wetlands also become windrowed along the shoreline by water currents resulting in the largest seed densities at the water level elevation (van der Valk and Welling 1988).

Studies indicate that seed banks play a primary role in the initial formation of marsh plant zonation patterns (van der Valk and Davis 1978, Pederson 1981, Pederson and Smith 1988, van der Valk and Welling 1988, Welling et al. 1988a, 1988b, Wilson et al. 1993). The plant community present within a wetland at any given period, however, is not necessarily an indication of the composition of the seed bank, for in this reserve are deposited the seeds of many vegetation communities from the past (Wilson et al. 1993). Ultimately the vegetation present within a marsh at any one time is primarily a function of environmental variables such as water depth, while plant composition is initially a function of the seed bank and rhizome reserve (van der Valk and Davis 1976a).

1.3.2. Zonation

Patterns of plant zonation along environmental gradients are evident in natural ecosystems (Stewart and Kantrud 1971, Sharitz and McCormick 1973, Vince and Snow 1984, Day et al. 1988, Reader and Best 1989). In prairie marshes plants are distributed along a water depth gradient, creating zones that represent the changing dominant plant species along this gradient (Stewart and Kantrud 1971; Adams 1988). As discussed in the previous section, seed banks typically contain higher percentages of seeds where adult plants normally dominate, which contribute to these zonation patterns. The MERP study demonstrated that the genesis of such zonation patterns is not from any single source, but rather from a combination of factors (van der Valk 2000). These patterns occur from the collective result of seed distribution, seedling recruitment, and seedling and adult mortality, further followed by ecological tolerances of species and competition. Accordingly, since more tolerant and competitive individuals predominate, emergent plants found within these zones are usually considered indicators of the marshes hydrologic regime, or elevation and associated water-depth gradient (Kantrud et al. 1989a, 1989b). Nevertheless, these vegetation zones are not assemblages of associated plant species at a given elevation, but rather a collection of independently distributed subdominant and dominant species (van der Valk and Davis 1976b).

The terms used to describe wetland vegetation zones or patches are varied, but generally these zones are summarized as: upland, low prairie, wet meadow, shallow marsh, deep marsh and open water (**Figure 1.2a**), distinguished by water depth (surface water or depth to water-table) and plant community composition (Stewart and Kantrud 1971, Adams 1988, Grosshans in press). **Table 1.1** identifies some of the more common vegetation types inhabiting these zones, representing changes in the dominant plants along an elevation gradient (**Figure 1.2b**). Grosshans (in press) further separates these vegetation zones of a large lacustrine marsh system into vegetation classes, represented by one or more dominant species or composed of one or more distinct species associations.

1.3.3. Vegetation Succession in a Prairie Marsh

Prairie marshes are described as one of the most dynamic wetland types in North America. This is attributable to the extremely variable climatic conditions of the prairie environment (Kantrud et al. 1989b). Annual variations in spring runoff, precipitation during the summer months, and evapotranspiration cause these wetlands to experience natural fluctuations in water levels, resulting in high and low water periods and contributing to the cyclical succession of prairie marshes (Weller and Spatcher 1965, Walker 1965, van der Valk and Davis 1978). Accordingly, seed banks play a critical role in the initial formation of zonation patterns of prairie marsh plant communities (van der Valk and Davis 1978; Pederson 1981; Pederson and Smith 1988; van der Valk and Welling 1988; Welling et al. 1988a, 1988b), while water depth is considered the primary determinant of plant species distribution, growth and survival within these wetlands (McDonald 1955, Harris and Marshall 1963, Walker 1959, 1965, Kadlec 1962, Meeks 1969, van der Valk and Davis 1978, Spence 1982, Galinato and van der Valk 1986, Kantrud et al. 1989a).

Prairie marsh systems undergo a natural cycle of vegetation change as a result of water-level fluctuations first described in prairie potholes by Weller and Spatcher (1965). Walker (1959, 1965) further demonstrated that these vegetation changes are not restricted to small marsh systems, but occur in large lacustrine marsh complexes as well (i.e. Delta Marsh). van der Valk and Davis (1978) described four distinct stages in this succession, which they referred to as a wet-dry cycle, often considered to be the model to describe prairie wetland ecosystem dynamics (Murkin et al. 2000). These stages are the dry, regenerating, degenerating, and lake marsh phases (**Figure 1.3**). In actuality this cycle is much more complex with respect to the composition and distribution of plants within a marsh system, and not every marsh system undergoes this complete cycle. Nevertheless, it does represent

the general vegetation changes a prairie marsh experiences subject to periodic high and low water-level fluctuations. This cycle is, however, typically restricted to deeper and not shallower marshes, or areas of a marsh, where water-levels fluctuate dramatically throughout the growing season (Kantrud et al. 1989a).

The plant or the seed, where does succession begin ...?

Regeneration of a prairie marsh begins as water levels fall during years of drought, exposing mudflat areas when parts of the marsh go dry. Since seeds of most emergents only germinate when there is little or no standing water, many plant species rapidly recolonize when water levels recede reestablishing themselves by recruitment from the seed bank and rhizome reserve (McDonald 1955, Walker 1965, Harris and Marshall 1963, Meeks 1969, van der Valk and Davis 1978, Galinato and van der Valk 1986). The resulting community is a mix of pioneering mudflat annuals and perennials such as goosefoot (*Chenopodium rubrum*), asters (*Aster* spp.) sow thistle (*Sonchus arvensis*), Canada thistle (*Cirsium arvense*), marsh ragwort (*Senecio congestus*), and smartweed (*Polygonum* spp.), as well as seedlings of emergents like cattail (*Typha* spp.), bulrush (*Scirpus* spp.) giant reed (*Phragmites australis*) and whitetop (*Scholocloa festuacea*). The presence of a viable seed bank with species capable of surviving in a wetland during various types of climatic conditions is essential to ensure the presence of vegetation throughout the wet-dry cycle (van der Valk 1981). Annuals and perennials will dominate the marsh system as long as the basin remains dry, with large quantities of annual and perennial plant seeds deposited to the seedbank.

As water levels rise the marsh basin is reflooded beginning the regenerating stage of the marsh (**Figure 1.3**). Flooding eliminates mudflat annuals and perennials while halting further germination of most seeds (van der Valk and Davis 1978). Emergent seedlings thrive spreading by vegetative clonal growth quickly reclaiming the marsh. Bulrush, cattail, sedge (*Carex* spp.), whitetop, and giant reed grass dominate across the underlying water-depth gradient. Standing water promotes germination of submersed and free-floating seeds reestablishing these species among the emergents. Biomass and primary production of the marsh increase dramatically as emergents grow to their full size, with an enormous amount of emergent plant seeds deposited to the seed bank (van der Valk and Davis 1978). A variety of waterfowl, muskrats, blackbirds, rails, wrens, deer and other wildlife increase in abundance during the regenerating stage as the marsh reaches maximum productivity.

As flood conditions persist, dense, closed stands of vegetation develop accumulating copious amounts of standing deadfall marking the beginning of the degeneration stage in the cycle. Plant diversity decreases and many animal species leave the marsh system as valuable wildlife habitat is eliminated. With a persistence of high water emergent vegetation begins to rapidly die off as a result of intolerance of species to prolonged flooding (McDonald 1955, Harris and Marshall 1963, Walker 1965, Millar 1973). Emergent plants do not have enough above water leaf area to take in oxygen causing an inadequate supply to roots and rhizomes, leading to eventual death of the plant (van der Valk 1994). Muskrat damage also contributes, primarily from eating and lodge building, often helping to eliminate emergent vegetation from deeper sections of the marsh. A substantial decrease in overall biomass and productivity occurs throughout this degenerating stage (van der Valk and Davis 1978), as submersed aquatics such as *Potamogeton* spp. and free-floating species like *Lemma minor* eventually dominate.

Eventually, when most emergent vegetation is eliminated the wetland enters the lake-marsh stage. During this time the marsh resembles a small lake or pond with only a band of emergents remaining along the shores. Since emergent plant seeds are unable to germinate underwater these species cannot reestablish while high water levels persist (Harris and Marshall 1963, van der Valk and Davis 1978). With reduced standing emergent cover, submersed aquatics and free-floating vegetation abundance often decline due to increased turbidity as a result of wave action. Algae dominate these lake marshes with blue-green filamentous algal blooms a common occurrence in marshes during this stage (van der Valk 1985). The marsh will remain in this lake-like state until water levels fall during the next drought period, continuing the vegetation cycle (**Figure 1.3**).

These cyclical changes in wetland vegetation have been observed during both naturally occurring and experimental fluctuations of water levels. Walker (1959, 1965) observed changes during high and low water levels in the Delta Marsh, where high water effectively killed off thousands of hectares of emergents, approximately 25% of the marsh vegetation. As water levels receded bare mudflat areas were exposed and recolonized by several pioneer plant species. Eventually water levels increased, emergent vegetation redominated, and the marsh developed into new patterns of zonation similar to those found prior to flooding. Decreases in density of marsh emergents has also been observed as water levels increased in shallow marshes of Saskatchewan (Millar 1973) and along the shores of Lake Erie (McDonald 1955), where emergents were almost completely eliminated if flooding persisted for two or more years. Similar vegetation cycles have also been observed from experimental

manipulations of water levels (Kadlec 1962, Harris and Marshall 1963, Meeks 1969), most recently by the Marsh Ecology Research Program (MERP) (van der Valk 2000). This long-term study is discussed in greater detail in Chapter 2, with the present follow-up studies described in Chapters 3 and 4.

1.3.4. Cyclical Succession in Prairie Marshes

Cyclical changes in wetland vegetation due to fluctuations in water levels, as described in the previous section, represent the fundamental ecological process of plant succession in a natural marsh system. Wetland plant succession has long been observed in prairie marshes and described in the Gleasonian approach (Gleason 1927) of understanding the life-history characteristics of the individual plant species making up the vegetation habitat. Gleason (1927) defines succession as all inclusive, with any change (qualitative or quantitative) in the vegetation cover of an area being succession. Van der Valk (1981, 1982) narrows this definition of succession as occurring whenever a new plant species becomes established and/or an existing plant species is eliminated, leaving quantitative vegetation changes in an area to be considered only fluctuations. In essence, not all marsh systems undergo true cycles of succession since only deeper marshes (or portions of a marsh) undergo succession following a type of cycle as described above, whereas shallower marshes (or shallower areas of a marsh) only undergo fluctuations throughout the growing season. In reality there is no true fixed direction of succession in a marsh system, but rather regular changing vegetation conditions as a consequence of present water levels (van der Valk 1985, Murkin et al. 2000).

1.3.5. Natural Disturbance and Human-Induced Stabilization?

Disturbance in the Prairie Marsh Ecosystem

One of the characteristic features of a prairie marsh is that the vegetation community is critically linked to the hydrology and environmental conditions of the area in which it exists. As a direct result of the highly variable prairie environment, these marshes experience alternating periods of flooding during wet or high water years, and droughts during dry or low water periods, which van der Valk and Davis (1978) refer to as a wet-dry cycle. These fluctuating water levels lead to profound changes in plant composition, where marsh and wet meadow vegetation undergo natural cycles of succession (Weller and Spatcher 1965, Walker 1959, 1965, Miller 1973, van der Valk and Davis 1978). In general, high water levels kill off marsh emergents due to intolerance to prolonged flooding, causing extensive vegetation

diebacks, whereas low water periods expose mudflats allowing plants to recolonize areas from the seed bank. It is clearly recognized that these periodic disturbance events through prolonged flooding and drought events are essential to maintaining habitat diversity and productivity within prairie marshes (Harris and Marshall 1963, Walker 1965, Weller and Spatcher 1965, van der Valk and Davis 1978, van der Valk 1981, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996, van der Valk 2000). Consequently, these marsh systems can be described as resilient, disturbance-driven ecosystems (Kenkel 1997). They can also be considered fairly robust systems, being able to survive in an environment as dynamic as the prairie environment. This need for seasonal instability, though, should not be interpreted as a need for erratic water-level changes at any time of the year. Periodic drying and reflooding is generally beneficial, but fluctuations that are too rapid or frequent may cause mortality to wildlife (i.e., muskrats and waterfowl).

Stability in the Prairie Marsh Ecosystem

One of the most serious impacts we can have on a wetland system is to interfere with the frequency and amplitude of water level fluctuations (Keddy 1989). Artificial stabilization of water levels eliminates the natural wet-dry cycle, which affects the critical link between environmental variation and vegetation composition, consequently preventing the elimination and regeneration of marsh vegetation. With prolonged water permanency, emergent plants are no longer held 'in check' by flood-drought events, and as a result these plant zones become dense, plant monocultures with little open water, and laden with deadfall. Prolonged periods of water level stabilization (i.e., reduction in the magnitude of water level fluctuations) results in reduced habitat complexity, biodiversity, and productivity (Kantrud et al. 1989a), as subordinate understory species, typically beneficial as diverse wildlife habitat, are eliminated. Over time, these dense monodominant zones increase providing little or no open cover, significantly reducing suitable waterfowl and marsh bird habitat (Kantrud et al. 1989a). With no disturbance to rejuvenate the marsh, plant communities enter a state of degeneration or stagnation.

1.4. Function And Value Of Prairie Wetlands

In general, there is still considerable information regarding the function and value of prairie marsh ecosystems that is relatively unfamiliar to the public, including political decision-makers. With little or no understanding of prairie marsh systems they are often considered nothing more than stagnant pools of water where ducks live and mosquitoes breed, a nuisance

for farm machinery, and a waste of good agricultural land better off drained or filled-in. Increasing public awareness is essential for the preservation of prairie marshes, to educate concerning the importance of these wetlands, which extends far beyond their use by waterfowl. Apart from their valuable role as habitat for hundreds of species of wildlife, wetlands also play a significant role in the hydrology of the prairie region. The hydrological function of these wetlands seems to be a much more integral and critical process than previously determined. Ultimately, prairie marshes perform most effectively in all their functions by their abundance and distribution across the prairies by maximizing water retention, groundwater recharge, and waterfowl breeding habitat (LaBaugh 1986).

1.4.1. Hydrological Regime

In general, wetlands play a critical role in the hydrologic regime of the prairie region (Winter 1989, Hubbard 1988) by acting as “sponges”, collecting and storing surface runoff waters and reducing the severity of potential flooding (Phillips 1996). By holding back water, marshes allow it to either evapotranspire into the atmosphere or slowly drain into the groundwater. Artificially draining wetlands increases the flood potential of an area leading to extensive surface erosion of the surrounding watershed, and potential damage to nearby populations and farmland. A further effect of draining wetlands that are closely linked to the groundwater system, is that it may be detrimental to the surrounding soil moisture regime, as well as permanently lowering the underlying water table. Prairie marshes recharge groundwater supplies by collecting surface water and allowing it time to seep down through the ground. Draining these groundwater-linked marshes can also lead to increased soil salinity of the surrounding area (Hubbard 1988), and consequently decreased agricultural yields and vegetation growth. Additionally, with a healthy diverse plant community, a wetland enhances filtration of the surrounding runoff improving the overall quality of water. These wetlands are effective nutrient sinks which help to purify surface water by breaking down, removing, using or trapping contaminants, nutrients, agricultural herbicides and pesticides, and organic wastes from the water column thereby helping preserve local water quality (Neely and Baker 1989, Cooper 1993, Phillips 1996).

1.4.2. Waterfowl and Wildlife Habitat

The prairie region is regarded as one of, if not the most important and productive waterfowl breeding areas in North America (Hawkins et al. 1984, Canadian Wildlife Service 1986, Batt et al. 1989). Between 1955 and 1985 it had been estimated that an average of 21.6 million

ducks used the prairie region as their breeding grounds, representing 51.1% of the total estimated surveyed population in North America (Batt et al. 1989). Nevertheless, these marsh systems not only support waterfowl, but a whole diversity of fauna ranging from large mammals such as deer and moose, to marsh birds and furbearers (i.e., muskrats, raccoons, beavers, etc.), to a variety of fish, amphibians, and small vertebrates and invertebrates (Hubbard 1988, Swanson and Duebbert 1989). Ultimately, conservation of this wildlife is closely linked to the condition and fate of marsh habitats and the availability of suitable plant cover (Kadlec and Smith 1992). A rich diversity of aquatic marsh plants provides a much greater availability of wildlife habitat, maintained only by occasional periods of flooding and drought. During periods of relative wetland stabilization, dense zonation of monodominant plants becomes quite conspicuous, providing little or no open cover and reducing the species richness and diversity of an area (Kantrud et al. 1989). As a result, a significant decline in habitat quality and a loss of suitable wildlife habitat occurs. From a wildlife perspective, the most productive marsh is one with a nearly balanced availability (50:50) of patches of open water and vegetation cover, often referred to as a hemi-marsh (Weller and Spatcher (1965). This optimal balance between open water and vegetation cover is where wildlife diversity, density and production are at their highest. However, like all stages in the wet-dry cycle it is only one phase, and maintaining the entire cycle provides the greatest overall diversity and productivity of species (Murkin et al. 2000).

Further results of prolonged water levels are the impacts of wave action and prevailing winds. Consequently, persistent wave action results in heavily eroded shorelines where sharp drop-offs replace the gently sloping shorelines typical of a prairie marsh, now replaced with ledges dominated by emergent such as *Phragmites* and cattail. These eroded shorelines and loss of vegetation cover not only affect wildlife habitat but fish habitat as well. Fish communities of wetlands also benefit from a diverse marsh with an active hydrology, resulting in less erosion of gently sloping shorelines, and consequently less turbid water. In the absence of fluctuating water-levels, human influence also typically encroaches on these marsh systems in many ways, such as valuable marsh habitat being cleared for haylands and agricultural fields within close proximity of the marsh edge.

1.5. Competition In A Prairie Marsh: Can't We All Just, Get Along...

1.5.1. Competition in General

Introducing Competition

It is generally agreed that competition is an important and common interaction within animal and plant communities (Begon et al. 1990). Numerous definitions and conflicting views regarding competition have been presented in the literature (Keddy 1989). Newman (1992) defines competition as an interaction where: 1) the competitors in question share resources, 2) the supply of at least one resource is reduced by one competitor for the other and, 3) the decreased resource affects the growth, survival and/or reproduction of the affected individual. Alternatively, Keddy (1989) simply describes competition as the negative effects one organism has upon another by consuming, or controlling access to, a resource that is limited in availability. Newman (1992) further comments that competition may not necessarily be reciprocal; one species may affect the other but not necessarily the reverse. With regards to plants, the definition and true influence of competition within these communities has been thoroughly debated (Tilman 1987, Thompson and Grime 1988), often to an extent far exceeding the purpose of using these definitions as a reference for studying natural systems. Competition in plants could simply be described as interactions between two species, which can potentially occupy the same habitat space.

Modes of competition

Two mechanisms of competition have been described in the literature, exploitation competition and interference competition (Keddy 1989). Exploitation competition occurs when the niches of two species overlap, and the presence of one competitor depletes the nutrients in the overlapping area, which affects the growth of the other competitor. Exploitation effects are an indirect passive form of competition, and occur solely through reduction of the available pool of resources in the shared area. An example of exploitation competition in a marsh system would be one emergent plant depleting the soil nutrients within the surrounding area, robbing its neighbouring plants of the availability of these nutrients. Another common form of exploitation is a larger more robust plant shading or crowding its shorter neighbouring plants, decreasing their access to sunlight. The other form of competition is interference competition, this occurs when one individual directly or actively affects another's ability to obtain resources, which affects the growth, reproduction

or survival of the affected individual (Keddy 1989). This interference could be an outright physical attack or a much subtler form such as shows of aggression. An example in plant communities would be allelopathy; the secretion of a toxin that negatively affects a neighbouring species. For the majority of plant competition cases the more passive exploitation competition occurs, rather than the more aggressive interference competition.

Competitive Interactions

Generally, competitive interactions are described as either interspecific or intraspecific competition (Begon et al. 1990). Intraspecific competition is simply the competitive interactions that exist between two individuals of the same species, whether it is for space or resources. Interspecific competition on the other hand, is competitive interactions between individuals of different species. Not surprisingly, competition within a species (intraspecific) is often more intense than between species (interspecific) since individuals of the same species have identical resource requirements (Begon et al. 1990). Nevertheless, one must remember that competitive interactions involve not only pairwise interactions between individuals, but also involves the combined effects of all individuals within a community of neighbouring species. Keddy (1990) refers to multispecies interactions as competition intensity, which is the combined negative effects of all neighbouring populations on the growth and survival of a given population. These types of interactions between plants are often measured by removal experiments, where the area around a given population is cleared of all its neighbours, and the resulting advances of the remaining species is compared to control areas where plants are not removed (Keddy 1989). Keddy (1989) further describes variations in this competition intensity. Diffuse competition is where cumulative effects of neighbours on a target species is relatively equal, whereas if the effects of one neighbour population has the greatest influence on a given species and the combined effects of all others is negligible, this can be termed predominant competition.

1.5.2. Dominance and Competitive Exclusion

It is understood that the effects of competitive interactions among species may not be equal, and that competitive dominance is an outcome of interactions where one species suppresses another through exploitation and/or interference competition. In fact, inter- and intraspecific competition are more often asymmetric than not (Keddy and Shipley 1989, Shipley et al. 1991, Connolly and Wayne 1996). Competitive displacement, or exclusion, from an area can result from the negative effects a dominant plant species has upon another by consuming (or

controlling access to) a limited resource (Grubb 1985, Keddy 1989). As abundance of the dominant species increases and the subordinate decreases within the disputed area, competitive influence from the dominant species is enhanced through a positive feedback loop (Keddy and Shipley 1989). The dominant species decreases the availability of resources for the subordinate while simultaneously increasing its own acquisition of resources by taking control of newly acquired space. This further lowers the resource availability for the subordinate. These increased competitive interactions can result in the elimination of the competitively subdominant species, while consolidating the abundance of dominants. If the effects and difference between the competitive ability of the 2 species to obtain the limited resource is great enough, the subordinate species may be completely eliminated from the area, provided there is an absence of factors such as disturbance.

Obviously, for competition to take place in the first place, lack of some shared resource, or space to obtain resources, must limit plant growth. Since plants are in most cases sessile organisms, the potential for sharing limited resources is great. Within plant communities, the most important shared resources are water, light, nutrients, carbon dioxide and in some cases pollinators (Newman 1992). Essentially, for a plant to be subordinate, its ability to procure a particular resource must be less than its competitive dominant, and the lack of this resource must ultimately affect its growth or survival. Newman (1992) states, that the plant with the greatest and most efficient means of sequestering resources, either through above or below ground methods, should ultimately be the better competitor.

Competitive dominance or simple tolerance?

Although dominance is achieved by competition as described above, it is important to distinguish between competitive dominance and simple dominance due to differences in niche requirements. In other words, abundance need not be a result of competition, a species may achieve dominance in an area because of inherently better abilities to withstand environmental effects, such as fire, flooding, grazing or salinity (Keddy 1989). Zonation patterns in saltmarshes, for example could indeed be a result of competitive interactions along the salinity gradient, but at the same time, those species excluded from highly saline areas simply may not be tolerant of these conditions (Goldsmith 1973). Kenkel et al. (1991), however, determined both tolerance and competitive ability are equally as important. They found that salt tolerant species are outcompeted from areas at the lower end of the salinity gradient, and consequently inhabit highly saline areas because competitive dominants cannot. Ultimately, in an environment with frequent disturbances (i.e. periodic flooding and droughts

in a prairie marsh) dominance is attained more through the ability to survive the environmental conditions. Conversely, when we have a stable regime, abundance is often achieved through traits that aid in exploitation or interference competition for resources, which in turn leads to competitive dominance (Keddy 1989, Kenkel et al. 1991).

1.6. Modelling Competition And Community Coexistence

1.6.1. Resource Partitioning

Fundamental physiological response curves (niches) are described as resource-use patterns that occur in the absence of interspecific competition, indicating the range within a resource gradient a species tolerates (Keddy 1989). Conversely, realized response curves (niches) are patterns that occur in the presence of competition, and consequently are narrower than fundamental responses. In essence, the realized response can be described as a function of the physiological tolerances of a species (i.e., fundamental responses), combined with competitive interactions with neighbouring species (Austin 1990). In any case, it is generally assumed that most species prefer the benign end of the resource gradient, in other words the end where resources are more abundant, and are only restricted to the stressful end of the gradient as a result of competitive interactions (Keddy 1990, Kenkel et al. 1991, Grace and Wetzel 1981, Snow and Vince 1984). As a result of competitive hierarchies species are expected to sort themselves out along resource/habitat gradients, with more competitive species at the benign end and stress tolerants limited to the periphery (Levine et al. 1998). These resource partitioning patterns occur as a result of physiological trade-offs between a plant's ability to compete at the benign end of the gradient, where resource availability will be high but competition from dominants greater, and its ability to tolerate stresses imposed on it at the other end of the gradient where availability is less. This resource partitioning is typically used to explain stable coexistence within plant communities, but is less important in communities that are exposed to recurrent periods of disturbance.

1.6.2. Competing Mechanisms for Competition and Coexistence

Resource partitioning produces obvious patterns in the landscape, which are evident in natural ecosystems. Interspecific competition has often been used to explain zonation patterns in wetland plant communities, arranging species along natural environmental gradients such as water depth (Grace and Wetzel 1981, Shipley et al. 1991), salinity (Snow and Vince 1984), exposure (Keddy 1983), Shipley et al. 1991) and disturbance (Wilson ad

Keddy 1986b). How these patterns of coexistence develop as a consequence of competitive interactions, however, is often debated. Resource partitioning is generally assumed to be a result of fundamental niches or environmental preferences among species, such as flood or salt tolerance, which are narrowed as a result of competitive interactions with neighbouring populations to create differing realized niches (Kenkel et al. 1991). These same resource patterns could also be a result of different fundamental niches between species, in other words species having different tolerances or preferences along the gradient, which would avoid competitive interactions. Two competing models have been presented which account for resource partitioning in natural systems (**Figure 1.4**). Both mechanisms result in identical observed patterns, but they can only be distinguished by further knowledge of the system or experimental trials (Keddy 1989).

The Ghost of Competition Past

One such model to explain coexistence in natural systems is referred to as the ghost of competition past (Connell 1980). This model assumes that competition is relatively unimportant in present communities, only causing minor differences between the realized and fundamental niches. This model assumes that resource partitioning is caused by differences between the true fundamental niches, which differentiated as a result of past competition, which lead to this specialization (**Figure 1.4**). The species within the community adapted to a specialized range along the resource gradient some time in the past, developed to minimize interspecific competitive interactions (Keddy 1989).

The Competitive Hierarchy Model

An alternative model to describe resource partitioning and coexistence of species along natural gradients, is the competitive hierarchy model (**Figure 1.4**). This model (or some form of it) has been used in various studies to describe coexistence of vegetation in natural systems (Sharitz and McCormick 1973, Grace and Wetzel 1981, Wilson and Keddy 1986a, Levine et al. 1998, Snow and Vince 1984, Kenkel et al. 1991). This model first assumes that the species all have inclusive niches; in other words, their tolerance levels along the resource gradient overlap with most species preferring the same end of the resource gradient where resources are more abundant (**Figure 1.4**). Secondly, these species vary in their competitive ability or their ability to acquire resources, which is an inherent characteristic of these species. Lastly it is assumed that there is a trade-off between competitive ability and

physiological tolerances, resulting in a negative correlation between competitive ability and fundamental niche width (Kenkel et al. 1991, Wisheu and Keddy 1992).

Centrifugal organization of communities

Rosenzweig and Abramsky (1986) describe a further variant of the competitive hierarchy model to describe habitat use, and community coexistence and structure, termed centrifugal organization. In such communities, a group of species has shared preference for a central habitat type, as well as each having another peripheral habitat in which it is a highly competitive dominant. This expands on the typical inclusive niche structure model (competitive hierarchy model) where species have overlapping fundamental niches along only a single axis (Keddy 1990). Keddy (1989), and Wisheu and Keddy (1992) further expand this centrifugal model to complex communities, proposing that not just single habitat types, but entire environmental gradients radiate from the central habitat. Towards the central habitat, species may have inclusive fundamental niches, but radiating out towards the peripheries, there will only be a few neighbouring species. Keddy (1989) gives evidence that wetland plant communities follow this organization. The central habitat would have low disturbance and high fertility, and radiating outwards would be different disturbance or stress gradients along which species and vegetation types are arranged. Competitive hierarchies along these biomass gradients produce this centrifugal organization of wetland plant communities (Keddy 1989)

1.6.3. Disturbance, Competition and Marsh Diversity

According to both Grime (1973) and Tilman (1982), within a plant community experiencing no disturbance regime, species with high competitive ability can grow and exclude competitive subordinates, reducing habitat diversity. How this competitive superiority arises, and to what degree competition is actually occurring, however, is often debated. Grime (1973) suggests these species accomplish competitive superiority by rapid resource uptake and high growth rates, whereas Tilman and Wedin (1991) suggest that the species' low resource tolerance limit is the trait most important for determining this superiority. In any event, the result is the same; one species dominates over another, which is less competitive.

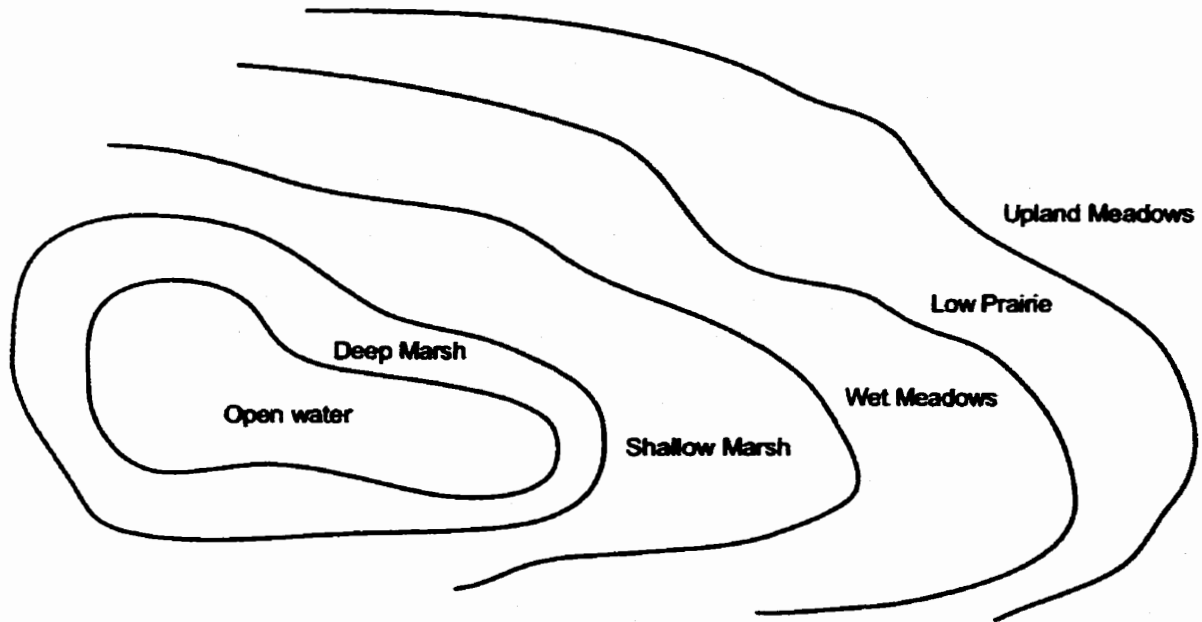
Putting all competition theories and debates aside, it is generally agreed that within a natural disturbance regime (i.e., a prairie marsh) interspecific competition will remain low

(Keddy 1989), resulting in high species diversity and low levels of monodominance (van der Valk and Davis 1980). Conversely, without periodic disturbance events, zonation patterns within these plant communities become very distinct as highly competitive dominants expand unimpeded, eliminating poorer competitors and reducing species diversity (Grace and Wetzel 1981, Czaran 1992). Ultimately, periodic and intermediate levels of disturbance, in combination with competitive interactions, is generally believed to be critical in maintaining high wetland habitat diversity (Harris and Marshall 1963, Weller and Spatcher 1965, Grime 1973, van der Valk and Davis 1976b, van der Valk 1981, Tilman 1982, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996, van der Valk 2000). Nevertheless, although it is generally agreed that competitive interactions do occur within most vegetation communities, the degree to which they determine the actual community composition remains highly debated.



Figure 1.1. Prairie wetland region of North America. Prairie marshes are a prominent feature throughout this region covering 40 to 60% of the entire land area. These wetlands stretch across an estimated 750,000 km of the Canadian prairie provinces (Alberta, Saskatchewan, Manitoba) and prairie regions of the upper United States (Montana, North Dakota, South Dakota, Minnesota, Iowa).

a. Typical patterns of vegetation zonation in a prairie marsh.



b. Characteristic dominant marsh vegetation along a water depth gradient.

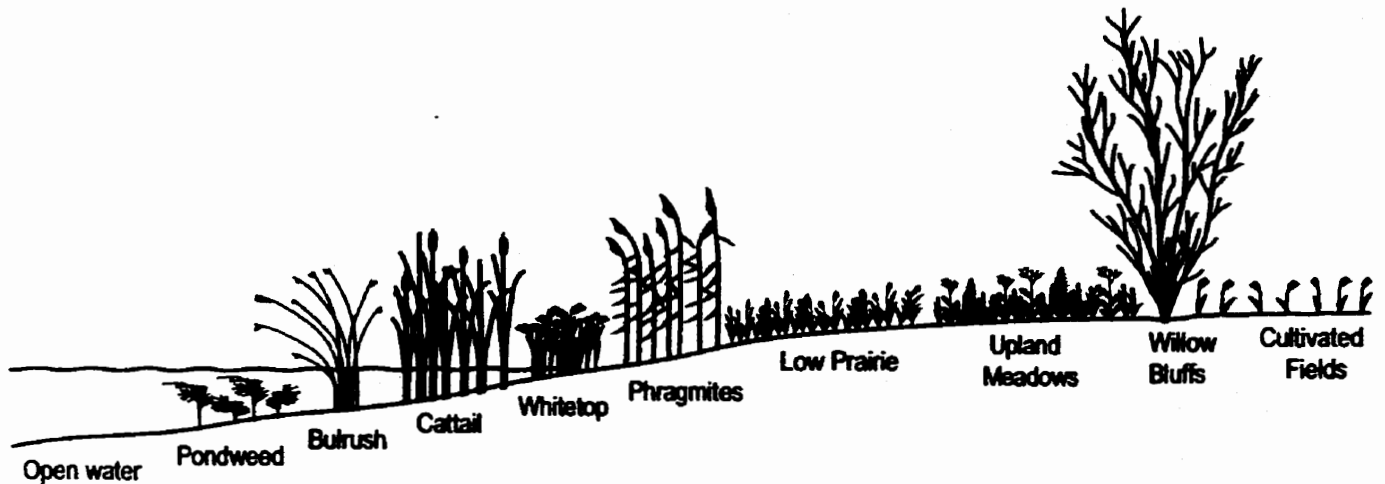


Figure 1.2. a. Typical zonation patterns of prairie marsh and surrounding vegetation, distinguished by water depth (surface water or depth to water-table) and plant community composition. b. Characteristic dominant plant communities are illustrated, arranged along a water-depth gradient.

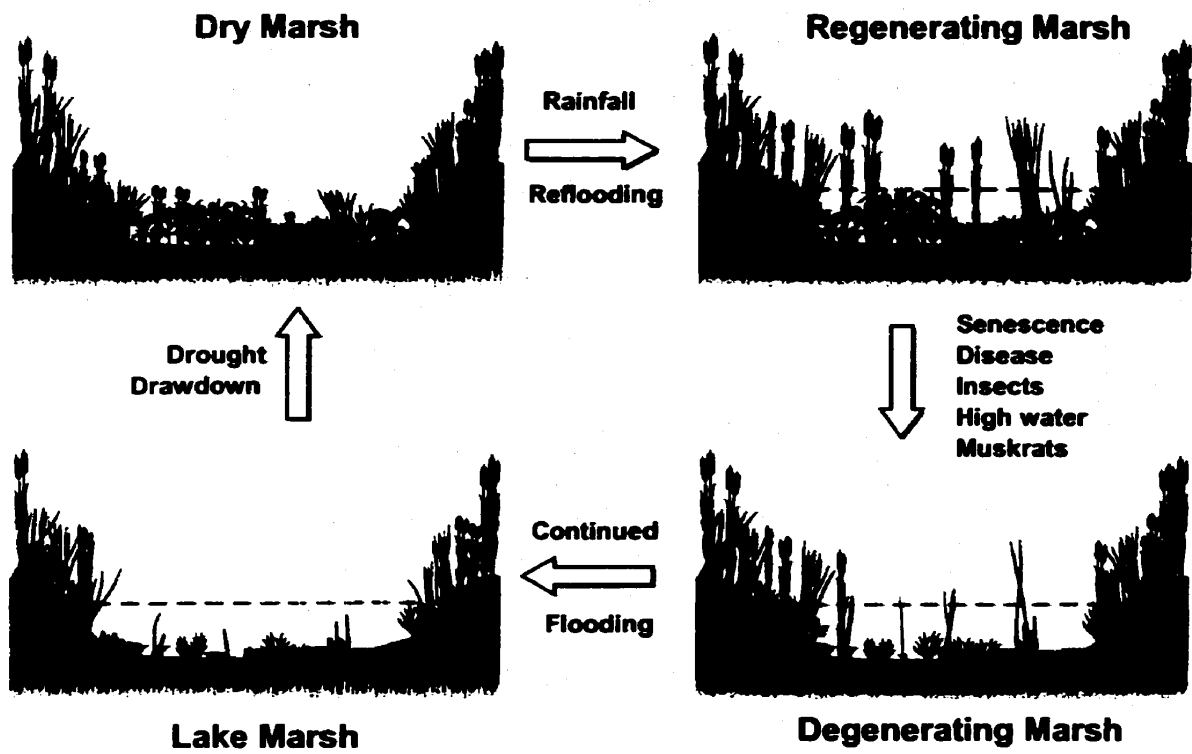


Figure 1.3. The wet-dry cycle experienced by prairie marshes as a result of the dynamic prairie environment. From Murkin et al. (2000), as adapted from van der Valk and Davis (1978).

Partitioning Mechanisms (Process)

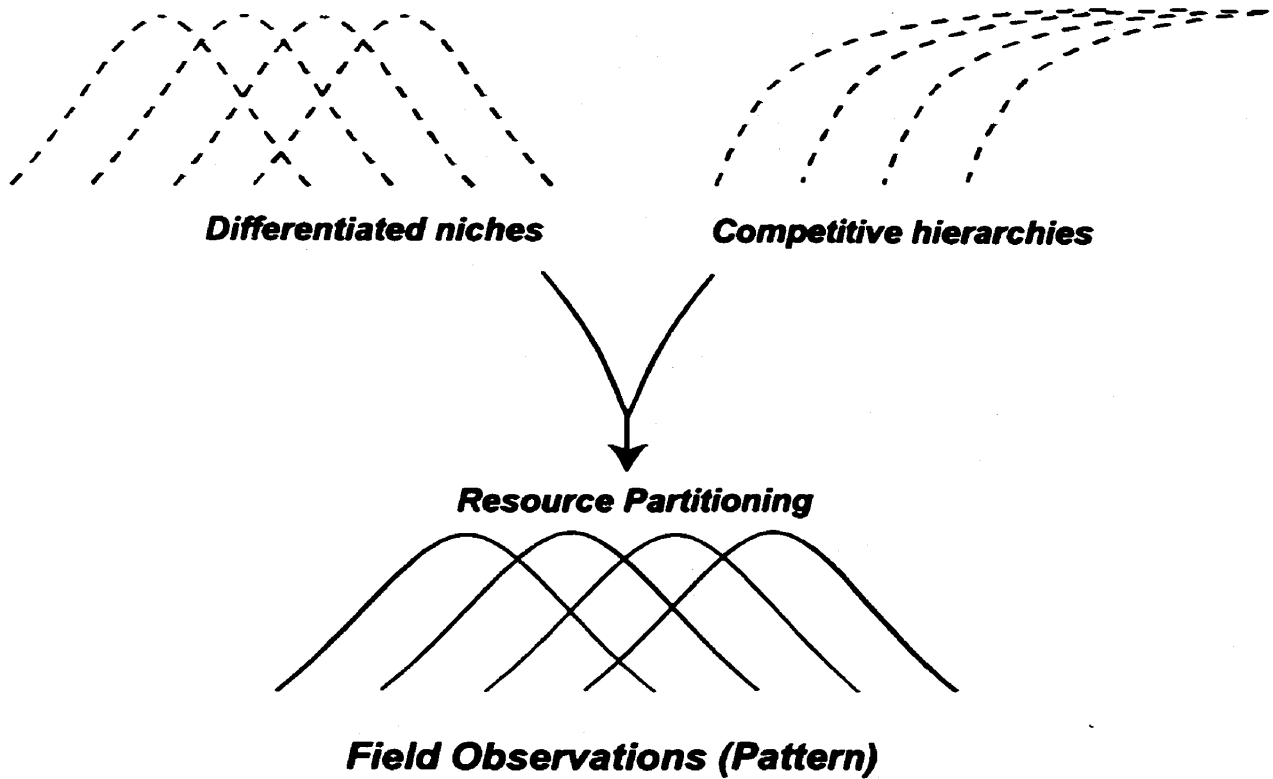


Figure 1.4. Two models are presented to account for resource partitioning and species coexistence. These two models can only be differentiated by experimental trials. The first (left) describes differentiated fundamental niches which avoid competitive interactions, while the second (right) describes competitive hierarchies within inclusive fundamental niches of species. Both mechanisms result in observed resource partitioning, in other words the species realized responses along a natural environmental gradient. (Adapted from Keddy 1989).

Table 1.1. Typical vegetation zones and associated dominant plant species of a prairie marsh. Dominant plant forms, characteristic species and normal inundation period are given for these wetland systems. Zonation classification follows Stewart and Kantrud (1971) and Grosshans (in press). Species names follow Kartesz (1994).

Vegetation Zone	Dominant Plant Form	Representative Plant Species	Typical Inundation Period
Open water	Submersed or free-floating aquatics	<i>Potamogeton</i> spp. <i>Utricularia macrorhiza</i> <i>Ceratophyllum demersum</i> <i>Myriophyllum sibiricum</i> <i>Lemna minor</i> <i>Lemna trisulca</i>	Permanent year-round except for low water years and periods of drought.
Deep marsh	Tall, robust, coarse herbaceous emergents	<i>Typha</i> spp. <i>Scirpus</i> spp. <i>Phragmites australis</i> <i>Utricularia macrorhiza</i> <i>Potamogeton</i> spp. <i>Carex atherodes</i> <i>Lemna minor</i> <i>Lemna trisulca</i>	Generally year round, except during low water years and periods of drought.
Shallow marsh	Medium height coarse herbaceous emergents i.e. grasses, coarse sedges	<i>Carex</i> spp. <i>Scirpus maritimus</i> <i>Eleocharis</i> spp. <i>Juncus balticus</i> <i>Scolochloa festucacea</i> <i>Polygonum amphibium</i> <i>Alisma triviale</i> <i>Glyceria grandis</i> <i>Sparganium eurycarpum</i>	Typically throughout the growing season; from spring to mid-summer, often through fall.
Wet meadow	Low herbaceous sedges, rushes, fine grasses and forbs	<i>Scolochloa festucacea</i> <i>Carex</i> spp. <i>Calamagrostis canadensis</i> <i>Spartina pectinata</i> <i>Chenopodium rubrum</i> <i>Hordeum jubatum</i> <i>Polygonum</i> spp. <i>Cicuta maculata</i> <i>Sonchus arvensis</i> <i>Juncus balticus</i> <i>Mentha canadensis</i> <i>Cirsium arvense</i> <i>Atriplex patula</i>	Temporary flooding for few weeks in spring, or into early summer.
Low prairie	Low herbaceous, fine grasses and forbs (<50% forb cover)	<i>Poa</i> spp. <i>Bromus inermis</i> <i>Cirsium arvense</i> <i>Sonchus arvensis</i> <i>Lactuca tatarica</i> <i>Aster</i> spp. <i>Elytrigia repens</i> <i>Hordeum jubatum</i> <i>Agrostis stolonifera</i> <i>Carex</i> spp. <i>Mentha canadensis</i> <i>Solidago</i> spp. <i>Calamagrostis</i> spp. <i>Lycopus asper</i> <i>Spartina pectinata</i> <i>Eleocharis</i> spp. <i>Melilotus</i> spp.	Temporary flooding to saturated soil in early spring.
Upland	Low herbaceous, coarse and fine, grasses and forbs (>50% forb cover)	<i>Bromus inermis</i> <i>Poa</i> spp. <i>Cirsium arvense</i> <i>Sonchus arvensis</i> <i>Aster</i> spp. <i>Melilotus</i> spp. <i>Lactuca tatarica</i> <i>Solidago</i> spp. <i>Andropogon gerardii</i> <i>Grindelia squarrosa</i> <i>Helianthus</i> spp. <i>Symphoricarpos occidentalis</i> <i>Rosa acicularis</i> <i>Medicago sativa</i> <i>Elytrigia repens</i> <i>Elymus canadensis</i> <i>Hordeum jubatum</i> <i>Agrostis stolonifera</i>	Brief flooding to saturated soil in early spring.

CHAPTER 2

Delta Marsh And The Marsh Ecology Research Program Experimental Marshes (MERP)

2.1. Delta Marsh, And The Influence Of Lake Manitoba Management

2.1.1. Introduction

Location

Delta Marsh is one of the largest and most significant freshwater wetlands in North America (Shay 1999), with past estimates of size at anywhere from 15,000 to 25,000 ha depending on which areas have been included (Bossenmaier et al. 1968, Shay 1999, Batt 2000). The current estimate of its size is now believed to be at 18,500 ha (Grosshans in press). It is situated at the southern end of Lake Manitoba, Canada (50° 11'N, 98° 19'W; **Figure 2.1**), separated from the lake by a natural sand ridge and connected by a series of open channels. Consequently, Warner and Rubec (1997) classify it as a freshwater lacustrine bay marsh. Delta Marsh is a wetland of international importance, being designated a Ramsar wetland in 1982 (Gillespie and Boyd, 1991), and a Manitoba Heritage Marsh in 1988 (Manitoba NAWMP Technical Committee 1988). For further descriptions of the marsh see Bossenmaier et al. (1968), Wrubleski (1998), Shay (1999), Batt (2000) and Grosshans (in press).

2.1.2. Origin and post-glacial history

In the beginning...

Delta marsh finds its origin following the end of the last glacial period, which began almost 12,000 years ago (Teller and Last 1981). As the great ice sheets retreated northward the natural flow of water was blocked, impounding water to the south in front of the glacier. As melt waters collected, a large glacial lake was created in the lower basins, today generally referred to as glacial Lake Agassiz. As ice gradually retreated, this lake extended northward covering much of Manitoba, and some parts of Saskatchewan, Minnesota, North Dakota and Ontario. Around 11,000 yr BP the ice retreated enough to open outlets to the east draining Lake Agassiz into Lake Superior, including the entirety of the Lake Manitoba basin (Teller

and Last 1981). Over the next few thousand years water levels in Lake Manitoba fluctuated in response to varying climatic conditions, readvancing of ice sheets and isostatic rebound (Teller and Last 1981). This resulted in varying periods of deep to shallow waters, as well as dry lakebeds. As a result, high salinity occurred in Lake Manitoba as salts accumulated during the dry and shallow water periods. Without an outflow for the lake, water evaporated leaving behind accumulations of dissolved salts, concentrating in the soil during each subsequent drying period.

This last era of change came to a dramatic end with the diversion of at least part of the Assiniboine River into Lake Manitoba (**Figure 2.2**), bringing about a new hydrological period for the lake. According to Teller and Last (1981), this happened around 4500 years ago although Rannie et al. (1989) believe it to be almost 7000 years ago. In any event, this condition persisted until sometime around 3500 years BP, when Lake Manitoba stabilized at its present level (Teller and Last 1981). Freshwater conditions returned to the marsh with input from the Assiniboine River, as well as flushing of resuspended salts north through the newly reestablished Fairford river outlet. The deviation of the Assiniboine also marked the single most important event in the formation of Delta Marsh. During its flow, the river carried vast amounts of sand with it, which were deposited into the lake. With prevailing northwest winds this sediment and debris flowed eastward to form the beach ridge separating Lake Manitoba from Delta Marsh (**Figure 2.2**), believed to have been completely formed almost 2500 years ago (Sproule 1972). Between 2500 and 2000 yr BP, the Assiniboine river channel flowing into Lake Manitoba was completely abandoned due to sedimentation and a changing hydrological gradient (possibly due to isostatic rebound), diverting the river east again to the Red River. Blind channel still exists today, once the main Assiniboine distributary into Lake Manitoba, now only a remnant of a once much larger channel system. Wave action has since eroded most of the delta that flowed out into Lake Manitoba, with most of it deposited east onto the barrier beach ridge, although an outline of the delta can still be seen as a relict sand area on the lake floor (**Figure 2.2**).

With the formation of the ridge and resultant absence of lake effects, marsh vegetation quickly established itself within this new sheltered region to form the marsh, which still remains today (Löve and Löve 1954). Grasses, trees and shrub species quickly invaded this new barren habitat, slowly building up organic debris and sediment and anchoring the sandy beach ridge with an eventual root system. With alternating wet and dry periods, and in the absence of violent inundations of water from wave action, a gradually sloping marsh shoreline slowly developed with the build up of debris and sediment. Wet meadow species

invaded south of the enclosed basin within these shallow water areas, as larger emergents spread out into the deeper bays and channels. With continued alternating wet and dry periods in the marsh, a rich diverse mosaic of vegetation and open water patches developed forming Delta Marsh.

2.1.3. Ecological Dynamics – Mother Nature vs. Human Influence

Climate

McGinn (1992) summarized the climatological data for the Delta Marsh area for the period 1967-1991 from two weather sites, located at the Delta Marsh Field Station (U of M) (50°11'N, 98°23'W), and the Delta Waterfowl and Wetlands Research Station (50°11'N, 98°18'W). Mean temperatures range from $-19.8 \pm 2.9^{\circ}\text{C}$ in January to $19.1 \pm 1.2^{\circ}\text{C}$ in July, with mean annual temperatures at $1.5 \pm 0.9^{\circ}\text{C}$. The frost-free season of the area averages 128 days, with annual precipitation over this period averaging 498.6 ± 95.2 mm with 374.7 mm/year falling as rain between April and October and 135.0 mm of water equivalent snow falling between October and May (Batt 2000). Evaporation loss from the marsh exceeds precipitation by 54.4 mm annually (McGinn 1992).

As a result of its proximity, Lake Manitoba has a definite effect on the local climate of the Delta Marsh region, especially since the prevailing winds of the area are from the northwest across the length of the lake. When the lake is still frozen in the spring, cooling winds off the lake delay warm temperatures, with daily temperatures on average 2.1-2.4°C cooler than other southern Manitoba areas (McGinn 1992). The lake effect also prolongs warm temperatures in the fall, increasing the growing season by 3, 4 and 6 days longer than the Portage la Prairie (which receives a modified lake effect), Winnipeg and Brandon areas respectively, as well as the number of frost-free days by 6, 10 and almost 30 days respectively.

The size of Lake Manitoba not only has a climatological affect but a seiche tide effect as well. During strong prevailing winds from the north and northwest, surface water can pile up at the southern shores causing what is called wind fetch, or wind tide, up to 0.6 m above normal (McGinn 1992). Similarly, as north winds die down or as strong south winds develop, wind tide can cause levels below normal as waters are pushed north into the lake.

Natural Disturbance and Human-Induced Stabilization

One of the characteristic features of a lacustrine bay marsh is that its water levels are susceptible to dramatic changes due to its close association with the lake (Warner and Rubec 1997). As in most prairie marshes, alternating high and low water periods, attributable to the extremely variable climatic conditions associated with the prairie environment, cause changes in plant composition, where marsh and wet meadow vegetation undergo natural cycles of succession (Weller and Spatcher 1965, van der Valk and Davis 1978). High water levels kill off marsh emergents due to intolerance to prolonged flooding, causing extensive vegetation diebacks. Conversely, low water periods expose mudflats allowing plants to recolonize areas from the rhizome/seed bank. It is clearly recognized that these periodic disturbance events are essential to maintaining habitat diversity and productivity within prairie marshes (Harris and Marshall 1963, Walker 1965, Weller and Spatcher 1965, van der Valk and Davis 1978, van der Valk 1981, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996, van der Valk 2000).

One of the most serious impacts humans can have on a wetland system is to interfere with the frequency and amplitude of water level fluctuations (Keddy 1989). Artificial stabilization of water levels eliminates the natural wet-dry cycle, which consequently prevents the elimination and regeneration of marsh vegetation. Emergent plants are no longer held 'in check' by flood-drought events, resulting in the formation of extensive monocultures of emergent macrophytes. Prolonged periods of water level stabilization (i.e., reduction in the magnitude of water level fluctuations) results in reduced habitat complexity, biodiversity, and productivity (Kantrud et al. 1989a). With no disturbance to rejuvenate the marsh, plant communities enter a state of degeneration or stagnation. These patterns which develop in a marsh ecosystem and the underlying processes involved are discussed in detail in Chapters 3 and 4.

Stabilized Water Level Regime of Delta Marsh.

Delta Marsh, in its natural state, was once a very dynamic ecosystem. Water levels in Lake Manitoba and consequently the adjacent Delta Marsh historically fluctuated within a range of 1.7 metres (5.6 feet). Alternating high and low water periods (**Figure 2.3**) caused vegetation to undergo cyclical succession, maintaining vegetation and habitat diversity within the marsh, and preventing vegetation from filling in open-water areas. With the 1961 completion of Fairford dam at Lake Manitoba's outlet (Anon 1974), lake levels have been

maintained at a mean level of 247.6 metres (812 feet) asl, dampening water level fluctuations to less than 0.6 metres (2 feet). Disruption of the natural flood-drought cycle has prevented the removal and regeneration of marsh vegetation, resulting in dramatic changes in emergent macrophytes. Consequently, this vegetation has rapidly filled in many areas of open water (Shay et al. 1999, Goldsborough 1987). In the absence of disturbances since completion of Fairford dam, plant communities have entered a state of degeneration or stagnation resulting in greatly reduced habitat diversity and productivity. The marsh has rapidly reached a successional stage of monodominant plant zones with low species and habitat diversity (Shay 1999, Grosshans in press).

Wildlife and Stabilization Effects.

Wildlife productivity is closely related to the condition of prairie marshes, i.e. the availability of suitable habitat and plant cover. Most marsh wildlife prefer diverse open habitat with a mixed diversity of vegetation patches and open water (Weller and Spatcher 1965). Prior to the mid 1950's, habitats in Delta Marsh were mixed and diverse, creating not only an important breeding and staging ground for waterfowl (Ducks Unlimited Canada 1981), but also an important breeding area for furbearers such as muskrats (Bossenmaier et al. 1968). Since stabilization, however, both muskrat and waterfowl numbers have decreased dramatically within the marsh during both the spring breeding season and fall migration (Olsen 1959, Jones 1978, Ould 1980). This is widely believed to be a result of the marsh's low habitat diversity and unattractiveness to both waterfowl and furbearers.

2.1.4. Investigating Delta Marsh.

Vegetation prior to stabilization

The first vegetation descriptions of Delta Marsh were sporadic and often qualitative in their abundance measurements, but nevertheless represent the past vegetation communities of the marsh. Hinks (1936) observed giant reed grass and softstem bulrush to be the main dominant emergents, with cattail found patchily distributed. Hinks (1936) also noted thick beds of submersed plants throughout Delta Marsh, predominantly sago pondweed, water milfoil, redhead grass and coontail, as did Soper (1941) within Lake Francis. McLeod et al. (1948) noted the die-off of large areas of emergents due to high water levels, and describe some of the first plant succession trends for Delta Marsh (McLeod et al. 1948). The most extensive description of Delta Marsh flora was by Löve and Löve (1954), who described a

diverse plant community dominated by giant reed grass (*Phragmites australis*) interspersed with patches of whitetop (*Scolochloa festucacea*). Open water was fringed with bulrush (*Scirpus* spp.) and broad-leafed cattail (*Typha latifolia*). As a consequence of high water levels in the 1950's, Olsen (1959) suggested softstem bulrush was replaced with the more flood tolerant hardstem bulrush, while Bossenmaier et al. (1968) noted a 21% reduction in *Phragmites* cover during this time. Walker (1959, 1965) noted that *Phragmites* dominated revegetated mudflats following the flood of the 1950's, and continued to dominate the marsh well into the 1970's. Miller and Moore (1967) indicated that *Phragmites* still occupied the greatest area in 1965, approx. 75% of the marsh, followed by submersed aquatics then bulrush.

Vegetation following stabilization

Following stabilization of the marsh in 1961, the marsh began a new era in its vegetation composition. It was during this time that cattail abundance throughout the marsh increased, while *Phragmites* and bulrush abundance decreased dramatically, resulting in a shift in the dominant vegetation community. By early 1980 there was a definite shift from a *Phragmites* and bulrush marsh to a cattail dominated system (Shay 1986, Shay et al. 1999). Shay (1986) and Waters and Shay (1990) attributed this shift to the increasing dominance of a robust hybrid cattail species, *Typha x glauca* (between *T. latifolia* and *T. angustifolia*) which first appeared in the marsh following the high water years of the 1950's (Walker 1965). Today, cattail, *Phragmites* and whitetop are the three dominant emergent species within Delta Marsh, while bulrush is represented by only a few remaining sparse beds. The dominant vegetation creates large continuous zones following the water depth gradient, rather than intermixed vegetation patches typical of prairie marshes (Grosshans in press). These zones are often dense monodominant stands with thick accumulations of fallen and standing deadfall. In the absence of water level fluctuations cattail (believed to be composed largely of the hybrid *T. glauca*) has increased dramatically over the past 40 years to become the predominant taxon throughout Delta Marsh. *T. x glauca*'s success and rapid expansion is due in part to its dynamic growth patterns and tolerance to a wide range of water levels (Weller 1975, Bedish 1967, Waters and Shay 1990, Squires and van der Valk 1992). Additionally, recent evidence from the Florida Everglades (Davis 1994, Urban et al. 1993) and wet meadows in Wisconsin (Woo and Zedler 2000) suggests that increased inputs of nutrients from agricultural runoff through the Portage Diversion could very well be aiding the expansion of cattail in Delta Marsh.

Present Communities of Delta Marsh

As is typical with prairie marsh habitats, the dominant vegetation zones of Delta Marsh follow an elevation-moisture gradient (Kantrud et. al. 1989b) (Figure 1.2b). This progression begins with permanent open water too deep for emergents, often populated by submersed aquatics such as pondweed (*Potamogeton pectinatus*). The emergent species cattail (*Typha* spp.) and bulrush (*Scirpus* spp.) typically occupy permanently flooded shorelines, followed by giant reed grass (*Phragmites australis*) which generally borders open water along dykes and heavily eroded shorelines. Although *Phragmites* can be found in water depths up to 0.6 metres within Delta Marsh, it is typically found further up the moisture gradient than cattail or bulrush as well as many wet meadows, growing in waterlogged organic soils above the water table. Wet meadows dominated primarily by whitetop grass (*Scolochloa festucacea*), sedges (*Carex* spp.) and rushes (*Juncus* spp.) fringe the emergent zones at seasonally flooded elevations, where soils remain waterlogged throughout the growing season. Low prairie grasses composed of mixed communities of low herbaceous grasses and forbs continue the transition from wet meadows to uplands, with increasing proportions of forbs as moisture levels decrease. This transition ends in prairies, pastures (prairie grasses and small shrubs) and woodlands at the furthest edges of the marsh before reaching cultivated fields. These vegetation communities have been classified and described by Grosshans (in press) accompanied by a 1997 vegetation composition map for the marsh (Grosshans 2000).

Soils in Delta Marsh are poorly developed, broadly classified as gleysols and regosols (Walker 1965). Flooded and waterlogged areas of the marsh result have resulted in poorly drained organic muck and peat overlying a high content of silt and sand, ranging in texture from sandy loam to silty clay (Shay et al. 1999). These thick organic layers develop through incomplete decomposition of organic material deposited from the marsh, with soil layer thickness varying between and within vegetation zones and communities.

Other than emergent vegetation?

Additional vegetation surveys of Delta Marsh have described not only the emergent community, but also seed bank characteristics (Pederson 1981, 1983), distribution of submersed plants (Anderson and Jones 1976, Anderson 1978, Wrubleski and Anderson in press), the forested beach ridge (MacKenzie 1982, Kenkel 1986), and the riverbottom forest Oxbow Woods (Barker and Kenkel 1994). Vegetation cover maps of Delta Marsh have been

produced several times in the past. Partial maps have been produced by Dillon (1953) for a portion of east Delta Marsh and Smith (1976) of the Centre Marsh Unit. The entirety of the marsh has been mapped by Miller and Moore (1967), Evans (1972), Ducks Unlimited (1979) and Grosshans (2000).

2.1.5. The future of Delta Marsh

Although a large marsh system like Delta Marsh is considered today to be a staging ground for migrating waterfowl, it was once a very productive spring breeding ground, as well as a refuge for flightless ducks in the summer molting period, during its natural disturbance regime (fluctuating water levels) (Hochbaum 1940, 1944, Bell and Ward 1984). In any event, Delta Marsh remains an integral part of the Mississippi flyway, one of the major waterfowl migratory routes across North America (Hawkins et al. 1984).

Concerns over the health of the marsh have been raised repeatedly in the past, accompanied by possible management recommendations (Bossenmaier et al. 1968, Jones 1978, Ould 1980, Ducks Unlimited Canada 1981, Bond 1996). Additionally, in an effort to document habitat conditions, de Geus (1987), Goldsborough (1983, 1987) and Shay et al. (1999) examined vegetation changes and ingrowth within the marsh, describing possible future conditions of Delta Marsh. Nonetheless, little to-date has been done towards management of this marsh system. Currently, Ducks Unlimited has undertaken a study in an effort to further the understanding of vegetation communities and changes within this stabilized regime (Grosshans in press). A new digital vegetation map (1997) along with digital versions of historical vegetation maps (1965, 1979) have been created, to be used for future management studies within Delta Marsh.

2.2. The Marsh Ecology Research Program (MERP)

2.2.1. Introduction to the MERP Experimental Marshes

History, purpose, present

Ducks Unlimited Canada and the Delta Waterfowl Foundation, in response to a need for a further understanding of prairie wetland ecology developed the Marsh Ecology Research Program in 1979 (Murkin et al. 1985, Murkin et al. 2000). The overall objective was to examine changes that occur within prairie wetlands exposed to water-level fluctuations.

Areas of interest concerning the structure and function of prairie marshes included: algae, plant, vertebrate and invertebrate ecology; wetland management; nutrient dynamics; hydrology and water chemistry. The MERP experimental marshes were constructed in 1979 to carry out this long-term manipulation study to examine the effects of a simulated wet-dry cycle on prairie marsh habitats (van der Valk and Davis 1978). The MERP program ran for ten years, from 1979 - 1989, with vast amounts of information collected in many areas of wetland ecology.

The MERP experimental marshes comprise a large research complex located in Delta Marsh. They are a series of 10 continuous sand-diked marshes, or cells, each 5-7 hectares in size, constructed so water levels in each could be independently manipulated. Each cell was built with a stop-log water control structure, with an automatically controlled electric pump to maintain and adjust water levels (Murkin et al. 2000). These marshes were constructed with the natural beach ridge (which separates Lake Manitoba from Delta Marsh) as their northern boundary, with constructed sand dikes forming the remaining boundaries (**Figure 2.1**). Besides the experimental marshes two undiked areas of similar size within the main marsh (marshes 11 & 12) were monitored as controls, or representative areas, for the surrounding Delta Marsh. The long-term biological information available from the MERP study makes these experimental marshes ideal for studying long-term vegetation dynamics of a prairie marsh following long-term water level stabilization. For a more detailed description of the MERP project refer to Murkin et al. (1985), van der Valk (1986, 1994), van der Valk et al. (1994) and Murkin et al. (2000).

Vegetation of the MERP marshes

When first constructed in 1979, the experimental marshes were similar to those areas within the surrounding marsh, containing all vegetation zones (many monodominant) and the elevation gradient (approx. 1.5m) present within the adjacent Delta Marsh (van der Valk 1994). The dominant vegetation zones in Delta Marsh consist of: wet-meadow vegetation at higher elevations (i.e. grasses, forbs and shrubs); giant reed grass (*Phragmites australis*), sedge (*Carex* spp.) and whitetop (*Scolochloa festucacea*) at seasonally flooded elevations; cattail (*Typha* spp.) and bulrush (*Scirpus* spp.) at lower permanently flooded elevations; and submersed plants (e.g., pondweed, *Potamogeton pectinatus*) in water too deep for emergents. A more detailed description of Delta Marsh vegetation is given in section 2.1.4.

2.2.2. Water Level Manipulations and Vegetation Change: The experimental design

The primary objective of the MERP project was to examine changes that occur within a prairie marsh system subjected to a wet-dry cycle (Murkin et al. 2000), accomplished by a series of water level manipulations on these cells (Table 2.1). The initial years before and after construction of the complex (1979 and 1980) were used as baseline years before any manipulations had occurred, for comparison of conditions between the experimental and surrounding marsh. The next two stages were deep flooding and drawdown of the cells to simulate the wet-dry cycle (Table 2.1), and essentially begin all the marshes at the same stage. Following this were five years where the marshes were divided into 3 groups and each group subjected to a different treatment water-level, in order to examine marsh dynamics subjected to different flooding regimes.

Flooding

The experimental marshes were subjected to deep flooding for 2 years as outlined in Table 2.1. This prolonged flooding period was intended to kill off most emergent vegetation in an attempt to reduce variability between the experimental marshes (Murkin et al. 2000). This high water almost completely eliminated 3 of the 5 dominant emergent species from all marshes (whitetop, bulrush and sedge) with the two more flood tolerant surviving species (*Phragmites* and cattail), reduced by 75% and 60% respectively (van der Valk 1994). In order to prevent any influences from the dikes and ditches surrounding the cells, vegetation within a 10 m area of the ditch or dike was excluded from any analysis (van der Valk 1994).

Decomposition of plant litter for four of the dominant emergents (whitetop, bulrush, cattail and *Phragmites*) was compared between the normal water level regime during 1980, and during the flooded regime of 1981 (van der Valk et al. 1991). Mean decomposition rates were higher during the flooded period for all emergents. Whitetop, cattail and bulrush all had a much higher rate of decomposition than *Phragmites* debris (Murkin et al. 1989). Changes in N and P concentrations were also examined and varied with emergent species, age of litter and the water level (van der Valk et al. 1991). Ultimately, the flooding period was effective in eliminating dense monodominant vegetation patches.

Drawdown

Following 2 years of flooding, 8 of the marshes were drawn down for two years while the remaining 2 only for one, in an effort to compare different drawdown durations (Murkin et al. 2000). During this dry period vegetation was reestablished on open mudflats by recruitment from the rhizome and seed banks. Mudflat annuals rapidly recolonized during both years of the drawdown, while most seedlings of emergent species appeared only during the earlier part of the first drawdown (Welling et al. 1988a, 1988b). Additionally, seedlings of 4 of the 5 emergent species were distributed along the elevation gradient at the same heights where adult plants were found prior to flooding. *Phragmites* did not conform, however, due primarily to the presence of dense stands of this species found at higher elevations not eliminated by deep flooding (Welling et al. 1988a, 1988b, van der Valk and Welling 1988). Higher percentages of seeds were also found in the seed bank along the elevation where adult plants dominated prior to flooding. These differences in distributions along the elevation gradient suggest that survival of seedlings during the drawdown stage and subsequent reflooding events, contributed significantly to the eventual development of zonation patterns found within these marshes (Welling et al. 1988a).

Treatment Period

In 1985 all 10 marshes were reflooded to 3 different randomly assigned treatment water levels (normal, medium, and high) (Table 2.1), which were maintained and monitored for 5 years (1985-1989) (Murkin et al. 2000). These levels were established to compare differing rates of change in productivity for prairie marshes, believed to be determined largely by water depth (van der Valk and Davis 1978). Results from the treatment period show that persistent high water levels affect the distribution and abundance of plant species within a marsh. Consequently, reduced abundance of emergent vegetation occurred accompanied by increased open water, usually after a lag time of 2 to 3 years when plants exceeded their flooding tolerances (van der Valk and Squires 1992). Prolonged flooding also resulted in an increase in submersed and free-floating species, large accumulations of plant litter, as well as a decrease in plant diversity and heterogeneous vegetation zones in all 3 treatment levels (van der Valk et al. 1994). These results are consistent with previous studies of increased water levels in marsh systems (Harris and Marshall 1963, Weller and Spatcher 1965, Walker 1965, Millar 1973, Weller and Frederickson 1974, van der Valk and Squires 1992).

The new vegetation communities established after reflooding were similar to those found prior to initial flooding in 1981, with emergent zones dominated by cattail, *Phragmites*, whitetop and bulrush at comparable elevations where previously found. These new communities, however, differed substantially from initial ones because they were no longer dense monodominant stands. The location of species along the elevation gradient after reflooding appeared to be determined from a combination of plant life history characteristics, i.e. initial seed dispersal, germination, seedling survival, and adult mortality (van der Valk and Welling 1988).

2.2.3. Years following the MERP study.

Since completion of the Marsh Ecology study in 1989, water levels in the experimental marshes have been relatively stable. No further water level manipulations were performed on the majority of these marshes. Unfortunately, in the earlier part of the 1990's three of these marshes (2, 4 and 5) were indiscriminately manipulated for waterfowl management purposes (P. Ward pers. Comm.). Nevertheless, the remaining seven have been left to equilibrate with the adjacent Delta Marsh, having limited water level fluctuations since 1961 (i.e., no flood-drought cycle). Consequently, since soil found in this region of the marsh has a high content of silt and sand, the sand dikes surrounding these marshes are relatively "leaky", and will equilibrate fairly rapidly with the surrounding marsh (H. Murkin pers. Comm.). In any event, all marshes have been in a stable state anywhere from 5-12 years, which represents a range of stable water level regimes and elevation ranges (**Table 2.2**). Those marshes flooded above normal experienced a lowering of water levels following 1989, whereas those maintained at normal levels essentially experienced no significant change in water level (**Figure 2.4**). As a result of the stabilized regime, the vegetation composition of the MERP marshes has rapidly reached a stage of dense monodominant vegetation patches. These communities are not unlike those of the surrounding Delta Marsh, as well as the initial vegetation communities present in these marshes prior to deep flooding (pre-1980). Observation of the three recently managed marshes (2,4 and 5), indicates they contain much more open water and open vegetation patches, providing habitat that is much more attractive to waterfowl and other marsh wildlife. As a result, these recently manipulated marshes house a much larger number of waterfowl than those untouched since 1989 (Murkin et al. 1982, 1989).

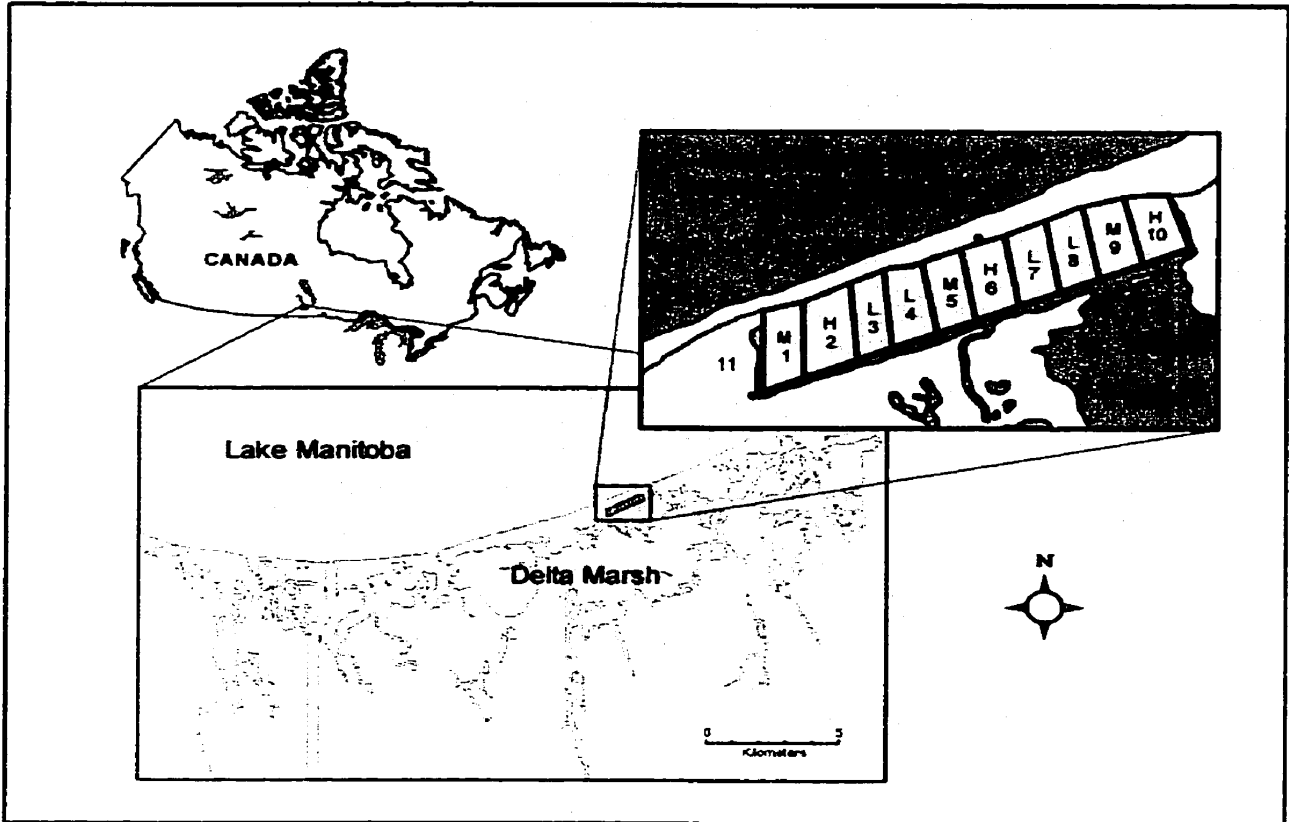


Figure 2.1. Delta Marsh, Manitoba, Canada and the Marsh Ecology Research Program (MERP) experimental marshes. Delta Marsh is an 18500 ha freshwater wetland situated at the southern end of Lake Manitoba, Canada (50° 11'N, 98° 19'W).

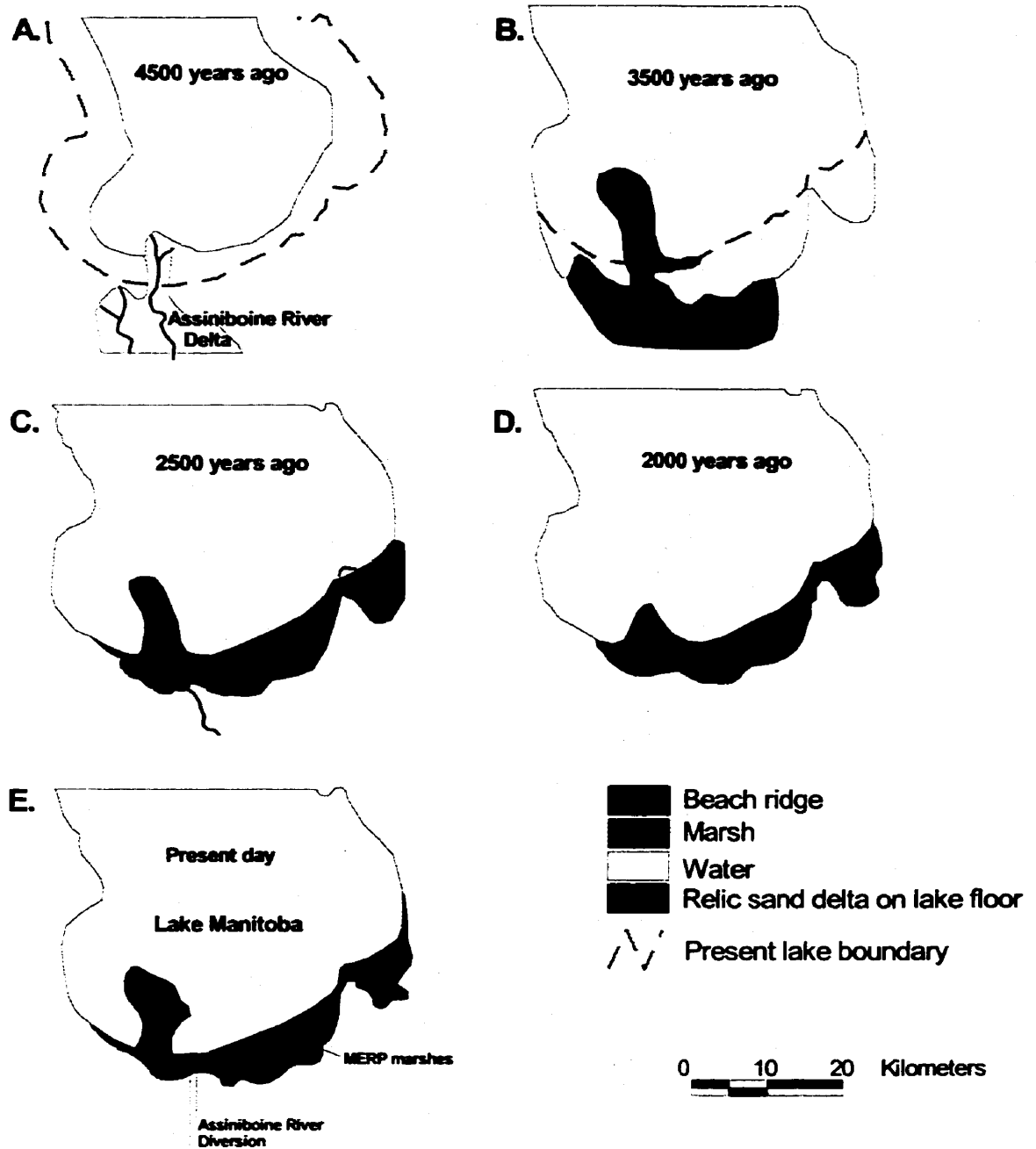


Figure 2.2. Origin and post-glacial history of glacial Lake Agassiz and the formation of Delta Marsh on the southern shore of Lake Manitoba. A. Assiniboine River begins to flow into Lake Manitoba. B. Massive amounts of sediment are deposited from the river into the lake. C. Debris flowed eastward to form the beach ridge separating Lake Manitoba from Delta Marsh. D. Approximately 2000 years ago the marsh and lake were formed. E. Delta Marsh as it exists today. From Teller and Last (1981).

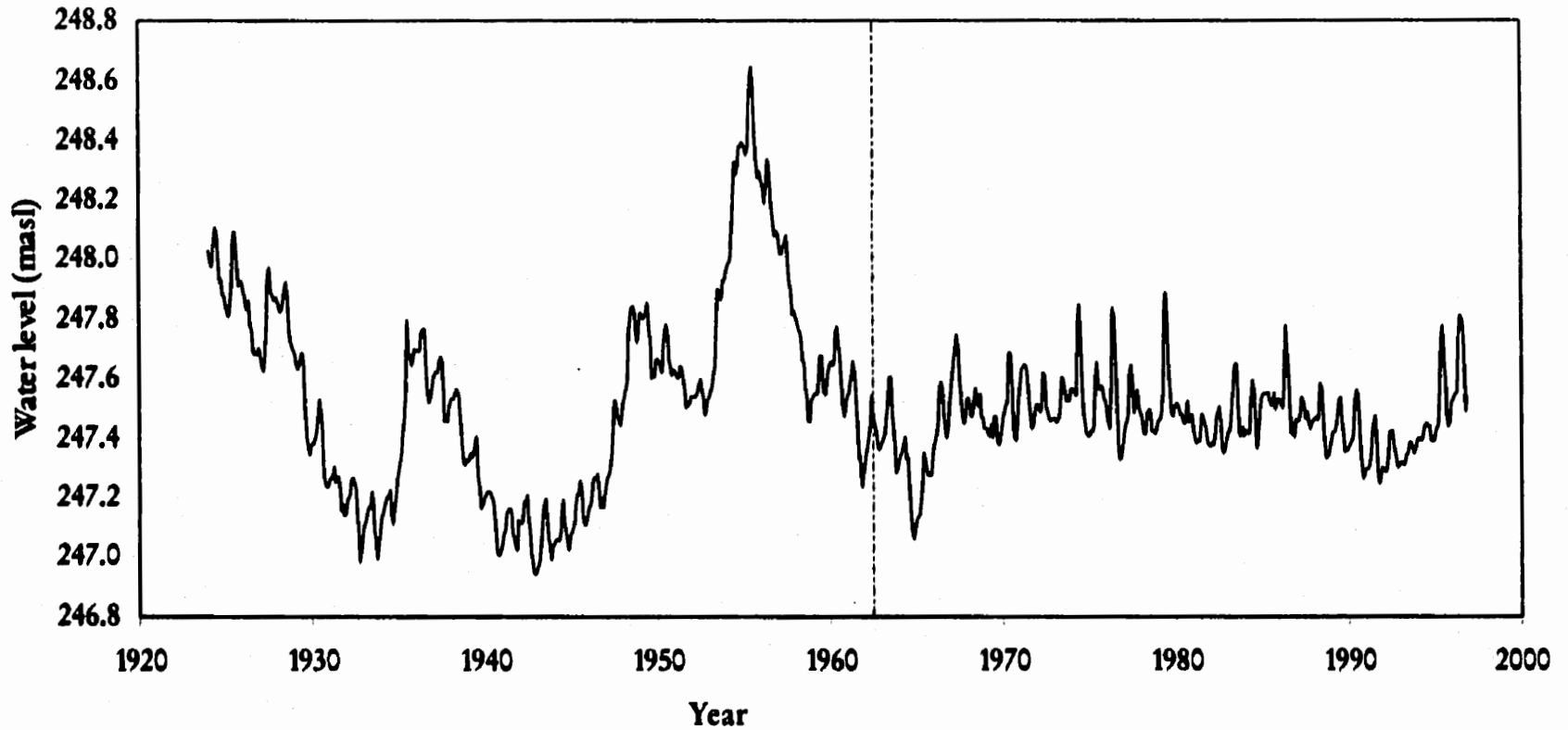
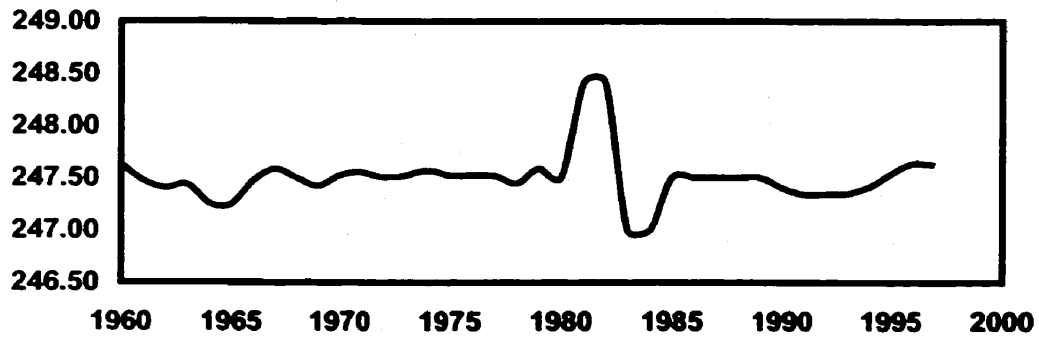
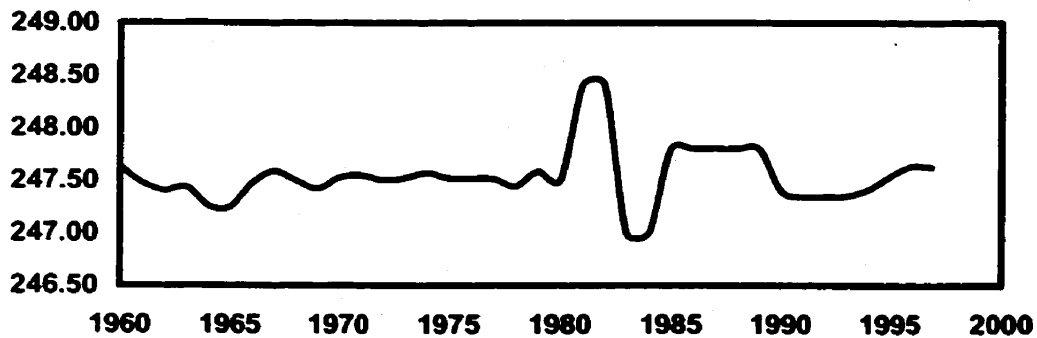


Figure 2.3. Lake Manitoba water level history (Steeprock Station) 1914-1997, indicating the completion of the Fairford dam and resulting 36-year stable water-level period (1961-1997). Presently, Delta Marsh is connected to the lake by four main openings, although this number has been greater in the past. These channels allow exchange of water between the marsh and lake, and as a result Delta Marsh follows the water-level regime of the lake.

a. Normal treatment group (marshes 3,7, and 8).



b. Medium treatment group (marshes 1 and 9), flooded 30 cm above normal.



c. High treatment group (marshes 6 and 10), flooded 60 cm above normal.

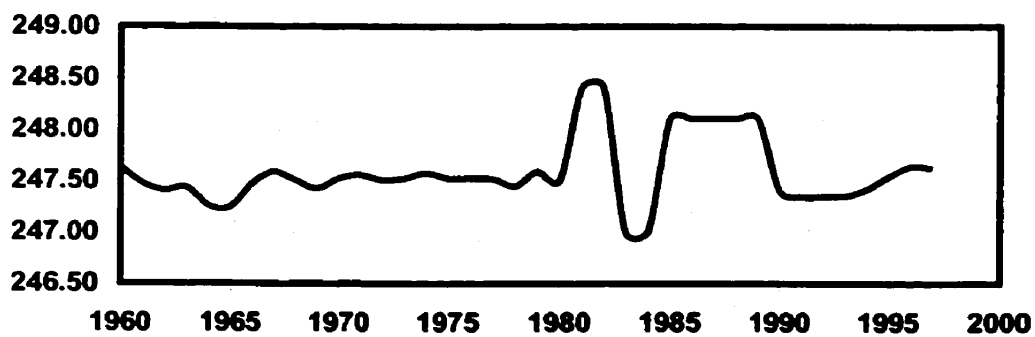


Figure 2.4. Water-level history of the MERP experimental marsh area: following lake stabilization in 1961, prior to MERP construction, during the MERP study period (1980-1989), and following 1989 when water levels returned to the stabilized regime of the surrounding marsh.

Table 2.1. History of water level manipulations during the Marsh Ecology Research Program (MERP) (Murkin et al. 2000).

YEAR	WATER LEVELS
1980	All 10 marshes at normal levels of Delta Marsh (247.5 masl) (baseline monitoring of all marshes)
1981	8 marshes flooded to 1 m above normal (248.4 masl) 2 marshes (3 and 7) at normal levels of Delta Marsh (247.5 masl)
1982	All 10 marshes flooded to 1 m above normal (248.4 masl)
1983	8 marshes drawdown (247.0 masl) 2 marshes (3 and 7) remain flooded 1m above normal (248.4 masl)
1984	All 10 marshes drawdown (247.0 masl)
1985 - 1989	4 marshes (3,4,7, and 8) flooded to normal level (247.5 masl) 3 marshes (1,5, and 9) flooded to medium level (247.80 masl) 3 marshes (2,6, and 10) flooded to high level (248.10 masl)

Table 2.2. Periods of water level stabilization of the MERP experimental and control marshes, located within Delta Marsh, Manitoba, Canada. Given are the marsh numbers, treatment they were subject to during the Marsh Ecology study (Treatment group), period of stabilization, years of stabilization, and associated mean water levels (masl).

Marshes	Treatment			
	Treatment group (1985 - 1989)	Water level (masl) (1985 - 1989)	Stabilization period (Time Period)	Stabilization years (Years)
2	High	248.1	1992 - 1997	5
4	Normal	247.5	1992 - 1997	5
5	Medium	247.8	1992 - 1997	5
6	High	248.1	1989 - 1997	8
10	High	248.1	1989 - 1997	8
3	Normal	247.5	1985 - 1997	12
7	Normal	247.5	1985 - 1997	12
8	Normal	247.5	1985 - 1997	12
1	Medium	247.8	1985 - 1997	8
9	Medium	247.8	1985 - 1997	8
11	n/a	247.55	1961 - 1997	36

CHAPTER 3

Long-Term Vegetation Changes Following Water Level Stabilization in a Prairie Marsh: Markovian succession of a freshwater wetland.

3.1. Introduction

3.1.1. Natural disturbance and human-induced stabilization.

In their natural state, prairie wetlands experience fluctuations in water levels caused by the highly variable climatic conditions of the continental prairie environment. Annual variations in spring runoff, precipitation, and evapotranspiration result in prairie wetlands experiencing high and low water years. These alternating periods of flooding and drought cause changes in plant community structure and composition, as marsh and wet meadow vegetation undergo natural cycles of succession (Weller and Spatcher 1965, van der Valk and Davis 1978). As a result of their intolerance to prolonged flooding, marsh emergents are killed off during flood conditions causing vegetation diebacks, or degeneration of the plant community. Conversely, low water periods begin a period of regeneration by exposing mudflats, allowing plants to regenerate from the rhizome/seed bank. It is recognized that these periodic disturbance events are essential to maintaining habitat diversity and productivity within prairie marshes (Harris and Marshall 1963, Walker 1965, Weller and Spatcher 1965, van der Valk and Davis 1978, van der Valk 1981, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996, van der Valk 2000). Consequently, prairie wetlands can be described as resilient, disturbance-driven ecosystems (Kenkel 1997). Accordingly, the water regime is considered to be one of the primary determinants of plant composition and zonation patterns within these marshes (Harris and Marshall 1963, Spence 1982, Kantrud et al. 1989a), with recruitment dependent upon the rhizome/seed bank (van der Valk and Davis 1978, Walker 1959, 1965, Pederson and van der Valk 1984, Welling et al. 1988). Distribution of dominant macrophytes proceeds along a water depth gradient reflecting differential tolerances to flooding (Stewart and Kantrud 1971),

It is believed one of the most serious impacts on a wetland system is to interfere with the frequency and amplitude of water level fluctuations (Keddy 1989). Without the wet and dry periods, elimination and regeneration of marsh vegetation is prevented, while simultaneously increasing the intensity of interspecific competition (further discussed in Chapter 4). With stabilization emergent vegetation is no longer held 'in check' by flood-drought events,

allowing it to spread uninhibited. Prolonged periods of stability (i.e., reduction in the magnitude of water level fluctuations) produce distinct zonation patterns, as extensive monodominant vegetation zones develop reducing habitat diversity and productivity (Weller and Fredrickson 1974, Kantrud et al. 1989a). With no disturbance to rejuvenate the system, the marsh community enters a state of degeneration or stagnation. The long-term effects of water level stabilization on these prairie marsh systems and the ecological processes driving vegetation changes are incompletely understood. To ensure the long-term survival of these ecosystems, a more complete knowledge of their successional dynamics and driving mechanisms is required.

3.1.2. Remote sensing and GIS for vegetation mapping.

Detailed wetland analyses can be accomplished through the use of geospatial and conventional data, such as georeferenced aerial photographs and the delineation of these photos, utilized within a geographic information system (GIS) such as ArcView (Welch et al. 1992, Remillard and Welch 1992, 1993, Welch et al. 1995, Williams and Lyon 1997, Kowalski and Wilcox 1999). Kowalski and Wilcox (1999) used aerial photographs in conjunction with historical and geospatial data to examine long-term changes of a degraded coastal wetland in western Lake Erie, in order to guide its restoration. Similarly, the Marsh Ecology Research Program (MERP) heavily utilized infrared aerial photography and ArcView GIS within an experimental context (van der Valk 2000). van der Valk (1994), and van der Valk and Squires (1992) describe the use of time-series photographs to monitor detailed plant community changes within the MERP marshes subject to a series of experimental water level manipulations. Here, in a follow-up examination of the MERP vegetation community, we also present historical and geospatial data to examine long-term changes within this prairie marsh system now subject to prolonged water level stabilization. Long-term spatial data was used to examine the effects of stabilization on plant succession, and the formation of patterns of plant zonation under the stabilized regime. Additionally, a Markov transition matrix model (Horn 1975) was utilized to predict future marsh plant communities.

3.1.3. Markovian properties of wetland succession.

When a prairie marsh undergoes a disturbance newly exposed areas are quickly recolonized by various pioneering species. Over time, a wetland will continue to undergo succession towards a final marsh community, often resembling the original community prior to

disturbance. Horn (1975) stated that the most striking property of succession is that the same final community composition can be repeatedly reached from many different starting points. This can be described using a Markov chain, defined as a transition of various states whereby the probabilities of these transitions depends only on the immediately preceding state and not dependent on any other previous state (Jeffers 1988). Although ecological communities such as prairie marshes show great variability, the preceding marsh community fundamentally influences the probability of a given future state (Jeffers 1988).

Markov models have been used in various forms to describe vegetation dynamics (Lippe et al. 1985, Usher 1981). The model presented here is a regular Markov chain based on Horn's (1975) model primarily intended for examining forest succession dynamics. There has been some criticism, however, of how the model determines the necessary starting and final transition states (Facelli and Pickett 1990). In forest succession studies these are determined by examining a present forest community and its understory plants, and by assuming the understory community to be the future final state. The understory community, however, is not an accurate representation of the future forest, and the time span needed to confirm such transitions would be decades. Despite this criticism the model can be used successfully to determine transition patterns in wetland communities. Prairie marsh systems have a very rapid rate of succession providing many transition generations, which allows future transition states to be examined in the field. Long-term vegetation transitions determined in this study were based on actual marsh vegetation changes, and not inferred changes as in forest studies. These transition patterns were used to examine long-term changes within a prairie marsh system subject to prolonged periods of water level stabilization, and the overall robustness of a prairie marsh plant community.

3.2. Objectives

The principle objective of this study is to examine the effects of long-term water-level stabilization (i.e., absence of disturbance from water level fluctuations) on prairie marsh vegetation. Emphasis of this chapter is on the long-term changes in plant distribution and patterns of zonation following this stabilization. It is hypothesized that disruption of the natural disturbance regime (i.e., flood-drought cycle), and resulting persistent stable water levels is expected to lead to increasingly distinct monodominant plant zones over time. Chapter 4 further examines these landscape patterns, specifically the processes involved in causing such changes during the stabilized regime.

3.3. Study Area

This study was conducted in the Marsh Ecology Research Program (MERP) experimental marshes, located in Delta Marsh, both introduced in Chapter 2. Delta Marsh is an 18 500 ha freshwater wetland situated at the southern end of Lake Manitoba, Canada (50° 11'N, 98° 19'W; **Figure 2.1**), separated from the lake by a natural sand ridge and connected by a series of open channels. In its natural state, Delta Marsh experienced dramatic changes in water levels caused by its association with the lake (Warner and Rubec 1997). Water levels in Lake Manitoba and consequently the adjoining marsh historically fluctuated within a range of 1.7m (**Figure 2.3**). These recurrent periods of flooding and drought caused vegetation to undergo cyclical succession, maintaining plant and habitat diversity within the marsh (Walker 1965, van der Valk and Squires 1992). Since 1961, lake levels have been artificially stabilized at a mean level of 247.6 m asl, dampening lake fluctuations to less than ca. 60 cm. Disruption of the natural wet-dry cycle has prevented marsh regeneration, resulting in dense monodominant plant zones of low species and habitat diversity.

The MERP experimental marshes (constructed to examine water level fluctuation affects on prairie marsh habitats, Murkin et al. 1985) are a series of 10 continuous sand-diked marshes (approx. 5-7 ha. each) constructed so water levels in each could be independently manipulated. The northern boundary lies along the natural beach ridge separating Delta marsh from the lake, with constructed sand dikes forming the remaining boundaries (**Figure 2.1**). Additionally, an undiked area of similar size within the surrounding Delta Marsh was monitored as a control (marsh 11). A more detailed description of the MERP project is in Murkin et al. (1985), van der Valk (1986, 1994), van der Valk et al. (1994) and Murkin et al. (2000).

When first constructed in 1979, the 10 experimental marshes contained all vegetation zones (many monodominant) and the elevation gradient (approx. 1.5m) consistent within the adjacent Delta Marsh (van der Valk 1994). From 1985-1989, these marshes were subjected to one of 3 different water level treatment groups: normal=247.5 masl, medium=30cm above normal (247.8 masl), high=60 cm above normal (248.10 masl) (**Table 2.1**). Following 1989, water levels in these marshes were left to equilibrate with the surrounding Delta Marsh, which has limited water level fluctuations (i.e., no flood-drought cycle) due to its association with the lake. Consequently, since soil found in this region of the marsh has a high content of silt and sand, sand dikes surrounding these marshes are relatively "leaky", and will equilibrate with the surrounding marsh quite rapidly (H. Murkin pers. comm.). Although 3

of the marshes were manipulated in the early 1990's, all marshes have been in a stable state for anywhere from 5-12 years, representing a range of stable water level states and elevation ranges (Table 2.2).

3.4. Methods

3.4.1. Field methods

Aerial and Ground Photography

The MERP marshes (10 experimental and 1 control) were photographed in August 1997 when plant development and biomass were at maximum. Colour infrared aerial photographs were taken by Northwest Geomatics Ltd., Edmonton, Alberta, Canada, produced at a scale of 1:4,000. 1997 photography was done with a Wild 15/4 UA6-S large format camera, at a setting of 1/200 at f5.6. Film used was Kodak Aerochrome Infrared film type 2443. Similar photos are also available from the MERP study, for 1980-1989 inclusive, all taken in early August. Additionally, true colour aerial photographs were taken of the marshes in 1998 during early spring (May), early summer (June) and mid-summer (August), as well as monthly photographs taken across each marsh at ground level. This series of infrared and true colour photos was used to create vegetation maps to examine changes in plant composition from 1989 to 1997 as well as 1980, the year prior to initial manipulations of the MERP study.

GPS sampling and GIS Integration

Aerial photographs from 1997, 1989 as well as 1980 were scanned using a flatbed scanner and imported into the mapping software MapInfo. A Trimble Geoexplorer mapping grade GPS unit was used to collect UTM coordinates (Universal Transverse Mercator – zone 14, NAD 83) of all dyke intersections and visible landmarks on the aerial photographs to aid in georeferencing scanned images. Collected UTM data was differentially corrected using data obtained from base stations operated by RFT (Resources For Tomorrow) and the Province of Manitoba, utilizing the Trimble Pathfinder software. This spatial data was imported into MapInfo, and used to georeference the scanned colour infrared images from 1997, 1989 and 1980. 1989 and 1997 images were then utilized to create the overlying vegetation composition maps, used to examine plant zonation patterns and long-term vegetation trends occurring within the MERP marshes.

3.4.2. Vegetation Mapping and Classification

Vegetation cover-mapping was undertaken in 1997 with a follow-up in 1998 to determine the dominant vegetation types. Plant communities of the MERP marshes were categorized into five groups distinguished by water depth (surface water or depth to water-table) and plant community composition. Three of these groups were further separated into vegetation zones represented by one or more dominant species, or composed of one or more distinct species associations. Generally, vegetation zones or patches are dominated by one species, although usually composed of several species (van der Valk 1992, Shay et al. 1999). Vegetation classification descriptions are given in **Appendix I**, based on Grosshans (in press).

1. Non-vegetated (no emergent macrophytes)
 - 1A. Open water (no emergents, little submergents)
 - 1B. Submergents and free floating
2. Emergent Vegetation (permanently-seasonally flooded)
 - 2A. Bulrush (*Scirpus*)
 - 2B. Cattail (*Typha*)
 - 2C. Giant reed grass (*Phragmites australis*)
 - 2D. Dead emergents
3. Wet meadow (seasonally-temporarily flooded)
 - 3A. Sedges and rushes (*Carex*, *Eleocharis*, *Juncus*)
 - 3B. Whitetop (*Scolochloa festucacea*)
 - 3C. Foxtail/salt flat species (*Hordeum*, *Puccinellia*, *Suaeda*)
4. Grasses and forbs (i.e. low-prairie, temporary-no flooding)
5. Trees (i.e. tree and shrub cover, little to no flooding)

1997 map creation

Plant communities of 1997 were identified on the aerial photographs by ground verification, with vegetation boundaries ultimately determined by viewing stereopairs of aerial photos with a Dietzgen mirror stereoscope. These patches were determined by colour, tone, texture, shape and height (Shay et al. 1999), with an interpretation key developed for vegetation identification (**Table 3.1**). Vegetation zones were painstakingly differentiated and traced on clear plastic sheets with a micro thin permanent marker. These clear vegetation boundary overlays were scanned into a computer using a flat bed scanner. The resulting

images were edited in Adobe Photoshop to create line diagrams of the vegetation boundaries with transparent backgrounds. These vegetation boundary maps were imported into MapInfo and overlain onto the georeferenced scanned aerial photos in MapInfo. Initial vegetation maps were created and analyzed with MapInfo. With the availability of ArcView in following years, however, these vegetation boundary maps were georeferenced with on-screen digitizing in MapInfo and exported to ArcView for final creation of the digital vegetation maps. In ArcView these maps were converted to a polygon theme and colour coded with a unique value approach based on the vegetation classification. Final vegetation maps were subsequently verified in the field using ground surveys.

1989 map creation

Vegetation composition maps for 1989 were based on existing 1989 maps created during the Marsh Ecology Research Program (MERP) study (van der Valk unpubl.). Essentially, for long-term plant zone comparisons the present study required much more detailed vegetation zone delineation than that required by the MERP study. For this reason alone, vegetation zone boundaries were redrawn in greater detail to aid in calculating long-term changes and resulting transitional trends. Additionally, to minimize subjectivity and to maintain consistency in mapping techniques, the 1989 vegetation boundary maps were recreated following the same techniques used to create the 1997 boundary maps. Stereo pairs of 1989 colour infrared photos were used to create the modified vegetation maps based on the 3D characteristics of colour, texture and height (Table 3.1). Final vegetation map creation followed the above 1997 methods, with final 1989 composition maps verified with the original 1989 MERP vegetation maps (van der Valk unpubl.).

3.4.3. Vegetation changes

Analysis of the total area of vegetation for 1989 and 1997 was performed using ArcView 3.2. Extent of vegetation zone overlapping and vegetation changes from 1989 to 1997 were calculated using the geoprocessing wizard extension in ArcView. Individual vegetation themes from 1989 and 1997 were overlaid, and using the geoprocessing wizard, vegetation zones of 1989 were clipped based on the overlap of vegetation zones in 1997. These “cookie cutouts” were used to calculate how much of the original area from a given vegetation zone from 1989 remained as it was still dominated by itself in 1997, and how much was other vegetation in 1997. These total area changes were converted to proportional area changes, to create a transition probabilities matrix of vegetation change from 1989 to 1997 (Table 3.2).

Emphasis was placed on the six main dominant vegetation zones: open water, cattail (*Typha* spp.), whitetop (*Scolochloa festucacea*), giant reed grass (*Phragmites australis*), bulrush (*Scirpus* spp.) and low prairie dominated by grasses and forbs. The remaining vegetation zones were omitted from most analysis because their abundance within the MERP complex is very low and considered negligible.

3.4.4. Use of a Markov model for wetland succession.

The model presented here is a regular Markov chain model, which determines future projected proportions of the dominant plants based on a matrix of dominance transition probabilities (Jeffers 1988) (**Table 3.2**). 1989 and 1997 dominant plant communities determined the actual starting and final transition states respectively, used for creation of the transition probabilities matrix. Here, we have two fixed time periods with known vegetation patterns spanning an 8-year "generation" period from 1989-1997. By creating a matrix of species dominance transition probabilities from 1989 to 1997, future communities can be determined by using this matrix with the transition model created as a Microsoft Excel macro (**Appendix II**). Using ArcView GIS, the initial transition probabilities were determined by calculating the proportion of overlap of dominant vegetation zones between 1989 and 1997. Essentially, how much of the original vegetation in 1989 remained as it was dominated by a given species, and what proportion was invaded, and so converted to other vegetation in 1997. For example, by calculating the total area dominated by species A in 1989, of that area how much remained dominated by species A, how much changed from species A to be dominated by species B, or species C and so on. These areas were converted to proportions, creating a transition matrix of succession probabilities representing proportional changes in the dominant species (**Table 3.2**). Beginning with any initial generation of species proportions (i.e. 1989 proportions of dominant species), the model calculates future transition states based on the table of vegetation changes (i.e. transition matrix). Using the Transition Matrix macro, future dominant plant communities of the MERP marshes subjected to a stabilized water level regime can be determined (**Appendix II**). Additionally, since succession in a wetland environment takes place very rapidly, future projected transition states can be easily examined in the field.

3.5. RESULTS

3.5.1. Plant composition.

Vegetation patterns within the MERP experimental marshes are typical of those found throughout Delta Marsh. Plant zonation progresses from open water with submersed aquatics (e.g., pondweed, *Potamogeton* spp.) bordered by the emergent macrophytes cattail (*Typha* spp.) and bulrush (*Scirpus* spp.) at lower permanently flooded elevations, through giant reed grass (*Phragmites australis*), whitetop (*Scolochloa festucacea*), sedges and rushes (*Carex* spp., *Juncus* spp and *Eleocharis* spp.) at seasonally flooded elevations to low prairie grasses and forbs finally surrounded by *Phragmites* grass and willows along the dykes (Figure 1.2b). This progression follows a decreasing moisture gradient as we proceed further away from the waters edge. Species found within the following vegetation zones are listed in Table 3.3, with the dominant and characteristic species of each zone given. Additionally, Appendix III contains a complete plant species list for the MERP experimental marshes and immediate surrounding area. Vegetation classification follows Grosshans (in press), with plant scientific names adopted from Shay (1999) and Kartesz (1994).

3.5.2. Vegetation changes from 1989-1997

Vegetation composition maps of the MERP experimental marshes were produced for 1989 and 1997 (Figures 3.1, Appendix IV) from mosaics of colour infrared photos (Figure 3.2). Additionally, vegetation maps are available for every year of the original MERP study, particularly from 1980, prior to any manipulations taking place (Figure 3.3). This time-series of maps illustrates clear changes in area within these marshes dominated by the respective vegetation zones from 1989 to 1997. In 1989, 42% (27.8 ha) of the total 67.0 ha of the MERP marshes consisted of open water (Figure 3.4), with cattail, *Phragmites* and whitetop occupying 15.4 ha (23%), 11.8 ha (18%) and 6.9 ha (10%) respectively (Figure 3.4). In 1997, open water cover decreased from 27.8 to 15.2 ha (Table 3.4) with cattail almost doubling its cover to 26.9 ha, almost 40% of the total MERP area. *Phragmites* cover increased slightly while whitetop cover decreased to only 5.0 ha. From 1989 to 1997, the three dominant emergents expanded from 34.1 to 46.6 ha, increasing from 51 to 69% of the total MERP marshes. In both 1989 and 1997 open water, the three dominant emergents and grass/forb cover accounted for approximately 97% of the cover in the MERP marshes

(Figure 3.4) with small isolated patches of bulrush, sedges, foxtail/salt flat species, trees and dead emergents making up the remaining 3% (Table 3.4).

Long-term vegetation changes were calculated in ArcView by overlaying 1989 and 1997 vegetation maps. From this, the proportional changes in dominant species cover were calculated: how much of the original 1989 vegetation (Figure 3.1) remained as it was dominated by a given species, and what proportion was invaded, and so converted to other vegetation in 1997 (Table 3.5, Figure 3.5). Only 52% of the open water area from 1989 remained in 1997, the remaining was invaded by vegetation. The greatest loss of this open water was to the encroachment of cattail where 36% of the total 1989 open water area was invaded and overgrown with cattail by 1997 (Figure 3.5). Cattail is extremely resilient with 85% of its 1989 area remaining in 1997 (Table 3.5b). Only very small proportions changed to other vegetation, with less than 10% being invaded by *Phragmites*. This large marsh reed is as equally resilient as cattail, with some 78% of its 1989 area remaining in 1997 (Table 3.5b). Some of its area (11%) was lost to cattail with minor changes to whitetop and low prairie as well (Table 3.5b, Figure 3.5). Whitetop patches on the other hand exhibited extensive changes, with only 41% of 1989 whitetop areas remaining in 1997. Cattail, *Phragmites* and grasses/forbs invaded into and dominated 27, 19 and 12% of 1989 whitetop areas respectively (Table 3.5b, Figure 3.5). Grass/forb areas experienced moderate change, with 51% remaining, while 43% was invaded by *Phragmites*, and much smaller proportions taken over by whitetop (3%) and cattail (2%) (Table 3.5b, Figure 3.5). The largest change was experienced by bulrush, where virtually no 1989 bulrush areas remained in 1997. The majority of this area (74%) converted to cattail cover, with 13 and 12% invaded by whitetop and *Phragmites* respectively (Table 3.5b, Figure 3.5). Most bulrush patches present in 1997 (91%) were more recently established from previously open water (Table 3.5c).

The vegetation zone with the largest overall increase in total cover was cattail, almost doubling its area from 1989 to 1997 (Table 3.4). A vast majority of its new area (37% of total 1997 cattail cover) was from invading into regions previously open water in 1989. The remaining was gained from areas previously whitetop, *Phragmites* and bulrush comprising 6.8, 4.9 and 2.2 % of 1997 cattail cover respectively (Figure 3.5, Table 3.5c). Total area of *Phragmites* and whitetop increased and decreased moderately, respectively (Table 3.4). An increase in *Phragmites*-dominated areas was primarily from invading into cattail, whitetop, and grass/forbs at 10.0, 9.2 and 8.3 % of the 1997 *Phragmites* cover respectively (Figure 3.5, Table 3.5c). Loss in whitetop from 1989 to 1997 was primarily to cattail (26.7 %) and *Phragmites* (19.2%) but at the same time new area was obtained from previously open water

as well as *Phragmites* (25.0 and 11.9% of 1997 whitetop area respectively) (**Figure 3.5, Table 3.5c**). Grasses and forbs had little change in overall cover losing almost half their original 1989 area to emergent vegetation, while regaining new area in 1997 from previously whitetop and *Phragmites* occupied areas in 1989 (27.7 and 16.7 % of 1997 grass/forb area respectively) (**Figure 3.5, Table 3.5c**). As mentioned previously, bulrush maintained itself within the MERP marshes only by more recently colonizing areas previously open water.

3.5.3. The prairie marsh Markov transition matrix model

Long-term changes in the dominant plant species were examined in the previous section, with the creation of a transition matrix of vegetation area changes from 1989 to 1997, i.e. a period of NO fluctuations or “steady-state” (**Table 3.5a**). These area exchanges were converted to percentages to create the transition matrix given in **Table 3.5b**. A transition probabilities diagram for a stable water level regime was created (**Figure 3.6**) using these transition probabilities, indicating that when water levels are stabilized many of the strongest transitions lead towards cattail and *Phragmites*. The transition matrix (**Table 3.5b**) was used with the transition matrix macro (**Appendix II**) to calculate transition populations over an indefinite stable water level state (**Figure 3.7**). From any given starting generation the proportions of plant species in the next generation can be calculated, and using those proportions to calculate the next generation following, and so on. In this case, the community generation used in the model covers an 8-year period, since the probabilities were calculated for the period 1989 to 1997. Transitions matrices (**Table 3.6**) were also created for each treatment group (normal, medium or high) (**Table 2.1**) and run through the transition matrix macro.

Figure 3.7 shows the transitions calculated from the matrix model, over a 15-generation period (120 years) for each treatment group (normal, medium and high) as well as the post-1989 manipulated group (marshes 2, 4 and 5) in a marsh system beginning with 100 percent open water. The 2 treatment groups flooded higher than mean normal levels of Delta Marsh [**Figure 3.7 a. medium: 30cm above normal (247.8 masl), Figure 3.7 b. high: 60 cm above normal (248.10 masl)**] show successions leading to *Phragmites* dominated systems. Cattail rapidly dominates these systems eliminating open water within the first 2-3 generations, but then slowly declines as *Phragmites* abundance steadily increases. These predicted trends are contradictory to what is occurring in the surrounding Delta Marsh (Grosshans in press). Conversely, the normal treatment group (**Figure 3.7 c. normal: 247.5 masl**) shows cattail dramatically dominating and continuing to dominate up to 80% of the marsh system.

Marshes 2,4 and 5 (**Figure 3.7 d.** post-1989 manipulated) are similar to the normal group but to a lesser degree of cattail dominance.

In order to suppress prominent localized trends and focus on landscape transitions, the transition data of all marshes was combined. **Figure 3.8** shows the transitions calculated from the model, over a 15-generation period (120 years) for all marshes combined in a marsh system beginning with 100 percent open water. Following current vegetation trends, the model predicts cattail will quickly invade a large proportion of the marsh (60%) within the first 4 generations, a time period of approximately 32 years. *Phragmites* is not far behind, its invasion occurring at a much slower rate, but a gradually increasing rate nonetheless (**Figure 3.8**). **Figure 3.8 inset** shows an expanded version of the lower 10 percent range of percent cover to examine low abundance changes in the remaining vegetation zones, their values suppressed by the larger increases of the two main dominants. Grass/forbs and whitetop-dominated areas appear to be holding their own, gradually increasing their area over time. Whitetop abundance increases more rapidly than low-prairie regions, but slowly drops below low-prairie abundance, as does the proportion of open water (**Figure 3.8**). Bulrush abundance peaks within the first 3 generations, and then slowly decreases in abundance as stable water levels persist (**Figure 3.8**). Regardless of initial starting generation, the model predicts that the overall succession of the marshes is towards a cattail-dominated system secondarily dominated with *Phragmites*. These two dominants, however, do not completely take over upland areas; these areas remain dominated by low prairie and wet meadow vegetation. Bulrush is consistently reduced very early in succession by cattail.

3.5.4. Colour Infrared Photointerpretation

Stereoscopes were very effective in identifying vegetation zones on infrared photos, adding height as an excellent feature for identification. Cattail, *Phragmites* and trees in particular appear quite tall with the use of stereoscopes, whereas whitetop and grasses/forbs appear quite flat making vegetation boundaries easier to distinguish (**Appendix IVd, Figure 3.2**). As well, *Phragmites* patches appear quite grainy, almost spongy, whereas cattail appears spiked with intermixed white spots representing deadfall (**Table 3.1**). Certain features are very characteristic of vegetation zones or plant communities and proved effective for vegetation identification (**Table 3.1**). The Emergent zones are fairly easy to distinguish, while whitetop and grasses/forbs can be more difficult to distinguish and required ground-verification. Cattail is very characteristic with regards to its general appearance, specifically its smooth to grainy dark red colour (**Figure 3.2**). *Phragmites* also has a characteristically

grainy to lumpy light pink appearance (Table 3.1) often clearly shadowed when bordering areas of Wet meadow. Tree and disturbed patches (appearing bright white) are all characteristic and easiest to identify on colour infrared photos (Table 3.1, Figure 3.2).

3.6. DISCUSSION

3.61. Long-term vegetation changes with prolonged periods of stabilized water levels.

Results of this study further demonstrate that fluctuating water levels are essential to species and habitat diversity within prairie marshes (Harris and Marshall 1963, Walker 1965, Weller and Spatcher 1965, van der Valk and Davis 1978, van der Valk 1981, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996), and that the water regime is considered the primary determinant of plant composition and zonation patterns within these wetlands (Harris and Marshall 1963, Spence 1982, Kantrud et al. 1989a, Wilson and Keddy 1985). Within a relatively short period following 1989, water levels stabilized to levels comparable to those within the surrounding Delta Marsh as water leaked through the sand dykes. As the experimental marshes equilibrated with the surrounding stable water level state, four of the marshes remained at their normal levels experienced during the MERP study (247.5 m asl being essentially the same as the mean level of Delta Marsh), while the remaining six experienced a lowering of water from the previously maintained higher levels (Table 2.2).

As water level fluctuations were dampened with stabilization mudflats and shallow waters were revealed, allowing vegetation to encroach into areas previously beyond their water depth tolerances (Squires and van der Valk 1992). Cattail (*Typha* spp.) rapidly recolonized newly exposed areas along its borders, resulting in a dramatic decline in open water. As this aggressive species quickly spread to dominate these regions, its cover doubled within the 8 years to dominate almost half of the total area within the MERP complex by 1997. Most of this increase in cattail-dominated area can be attributed to its invasion into previously open water cover from 1989. Consequently, open water in 1997 decreased to almost half of its 1989 total area, with the largest loss attributable to the invasion of cattail. Stabilization of water levels also allowed *Phragmites* to slowly expand along its borders, invading open water, as well as previously cattail, grasses/forbs and whitetop dominated regions. Without fluctuating water levels, transition areas between species no longer received inundations of water, which allowed cattail and *Phragmites* to invade new habitats. Similarly, Bossenmaier et al. (1968) indicated during the low water periods of the 1960's, recolonization of Delta

Marsh was primarily by mudflat annuals and wet meadow perennials, followed by rapid colonization by cattail, *Phragmites* and whitetop.

Unlike cattail, which predominantly invaded neighbouring plant zones, most species within the MERP marshes lost considerable area to, while at the same time gaining area from, neighbour species. Typically, boundaries or transition zones between vegetation shift due to seasonal variations in water depth and competitive interactions (Stewart and Kantrud 1972, Kantrud et al. 1989b). Whitetop, *Phragmites* and grasses/forbs for example exchanged areas amongst each other as minor fluctuations in environmental conditions occurred. Within a stabilized regime, however, water level fluctuations are not great enough to cause major shifts in plant composition or large transition zones, which allows dominant species to persist. Whitetop grass experienced considerable loss of habitat to *Phragmites* as well as cattail, but nonetheless, maintained itself within its habitat range. Additionally with no fluctuating water levels, low prairie vegetation (dominated by grasses and forbs) encroached into areas that no longer received inundations of water. As these regions remained dry for extended periods, wet meadow (i.e. whitetop) plant abundance slowly declined, tolerating dry conditions only for so long. These wet meadows areas where grass and forb abundance was previously low, slowly converted to low prairies. Other vegetation such as sedges, rushes and foxtail grass for example have much lower abundance, and a few small patches occur within some marshes during both 1989 and 1997.

One of the most striking changes with stabilized water levels in the MERP marshes was the loss of bulrush. Very few bulrush patches from 1989 remained in 1997, most of them being replaced primarily by cattail. Bulrush maintained itself within these marshes only by more recently colonizing areas that were previously open water. Evidence from the three MERP marshes recently manipulated for waterfowl management purposes (marshes 2, 4 and 5, further discussed in section 3.6.4.) indicates bulrush is decreasing not only from the invasion of cattail, but also because it seems to prefer fluctuating water levels. The recent fluctuations in water levels (i.e. disturbances) have resulted in higher bulrush abundance remaining within these marshes.

Overall, 1997 vegetation zones within the experimental marshes have reached a similar successional state to those in control marsh 11 (**Appendix IVd**). Vegetation patches have become dense, homogenous zones laden with deadfall. Dominant emergent plant zones include: cattail, *Phragmites*, whitetop, bulrush, and grasses and forbs, with minor species of much lower percent cover independently distributed within the understories. The degree of

single plant dominance in monoculture zones of the experimental marshes, however, is not yet as high as those in marsh 11. Many mixed transition zones of the dominant emergents are still present within the experimental marshes, whereas monodominance in marsh 11 is extremely high. Additionally, plant zones in marsh 11 are so overloaded with deadfall, that proportionally there is more dead than live growth. Also, previously *Phragmites* patches and whitetop meadows in marsh 11 are slowly progressing into low prairie meadows, while *Phragmites* slowly encroaches on low prairie as well.

Comparison to 1980:

Similar long-term trends seen in marsh 11 are confirmed in the 1980 vegetation maps of the MERP marshes (van der Valk 2000), which represent the vegetation community following almost 20 years of stabilized water levels. Grasses/forb and *Phragmites*-dominated areas, for instance, existed in 1980 where whitetop currently inhabits today. This confirms that with persistence of water levels *Phragmites* and grass/forbs in the future could slowly invade present whitetop-dominated regions. Overall, the 1997 vegetation community appears to be returning to a state similar to that of 1980, before any manipulations had taken place. A dramatic difference, however, was the presence of a substantial amount of bulrush in 1980 inhabiting deeper waters bordering cattail, still present after almost 20 years of stabilization (Figure 3.3.). Many factors can affect the survival of bulrush during reduced water level fluctuations, such as shoreline erosion, muskrat herbivory and cattail invasion (van der Valk and Davis 1978, Coops and van der Velde 1996, Grosshans in press). In 1997 cattail abundance was much greater compared to 1980, which could account for the loss of bulrush because of competitive exclusion. From 1965 to 1979 cattail had begun expanding throughout Delta Marsh almost doubling in its area by 1997, attributed to the appearance of the invasive hybrid cattail, *Typha x glauca* (Shay et al. 1999).

Despite the dramatic schedule of flooding, drawdowns, and reflooding that these marshes were subjected to during the original MERP study, the vegetation community has come full circle with the return of a stable water level regime. This demonstrates that these systems are extremely robust in their overall succession, and when subjected to stabilization of their water levels, the critical link between environmental variability and plant diversity is severed. Stabilization allows formation of distinct vegetation communities, with a dramatic loss in species diversity. Without occasional disturbances from fluctuating water levels, these marsh systems rapidly become overgrown with vegetation, which fundamentally results in a loss of species and habitat diversity.

3.6.2. The Vegetation Invasion

Cattail, *Phragmites* and whitetop remain the three dominant emergent species within the MERP complex, as well as the whole of Delta Marsh (Shay et al. 1999, Grosshans in press). These three species and their associated understory flora form distinct zonation patterns, which follow a water depth gradient. Cattail, in particular, has within a very short time become the most abundant species within these marshes. It continues to dominate flooded areas, while *Phragmites* and whitetop dominate wet meadows to low prairie habitats. All three species have formed extremely distinct, dense monodominant vegetation zones, resulting in habitat with very low diversity. These trends are not surprising. These same trends have been documented within the surrounding Delta Marsh repeatedly over the last 40 years (de Geus 1987, Goldsborough 1983, 1987 and Shay et al. 1999). So what has allowed these species to dominate these marsh systems, and what are the implications for the future of these wetland habitats? Invasive characteristics of these species are discussed below.

i. Aggressive Cattail.

Cattail is by far the predominant macrophyte within the MERP marshes. It is well known across North America as an extremely competitive and invasive species throughout its habitat range, and often dominates wherever shallow water persists (Stewart and Kantrud 1971, Weller 1975, Beule 1979, Toivonen and Back 1989, Ball 1990, Sojda and Solberg 1993, Solberg and Higgins 1993). Fluctuating water levels are considered the most natural and effective means to control cattail spread, eliminating or opening up dense stands (Weller 1975, Beule 1979, Ball 1990, Sojda and Solberg 1993). Without disturbances to restrict it, this invasive species has taken advantage of the stable water level regime of the MERP marshes to rapidly spread into shallow waters. Cattail has quickly dominated areas bordering open water forming dense monodominant patches laden with deadfall. This rapid spread of cattail can be attributed to the increasing dominance of the hybrid *Typha x glauca*, a robust, resilient species first appearing in Delta Marsh during the 1960's (Walker 1965). Shay et al. (1999) and Grosshans (in press) describe its dramatic spread throughout the marsh, having filled many open water areas.

Shay et al (1999) attribute *T. x glauca*'s expansion to its dynamic growth patterns, clearly demonstrated in the present study by its rapid expansion within the MERP marshes. This hybrid's success is due in part to its adaptation in height to a range of water levels (ability to survive in water depths of up to 1 m) (Smith 1987, Waters and Shay 1990, Squires and van

der Valk 1992), as well as rapid vegetative growth (Weller 1975, Waters and Shay 1990, Shay et al. 1999). de Swart et al. (1994), for example, found *T. x glauca* abundance to increase within the MERP marshes as small stands expanded vegetatively while exposed to the three treatment water levels from 1985-1989 (0, 30 and 60 cm above normal). Following 1989, *T. x glauca* increased dramatically throughout the marshes while subject to prolonged stabilization. *T. x glauca*'s ability to germinate in water depths of 2.5-15 cm (Bedish 1967) also contributes to its expansion, as well as its efficiency at creating new habitats and small floating islands by rapid accumulation of organic matter and debris (Shay et al 1999). Recent evidence from the Florida Everglades (Davis 1994, Urban et al. 1993), wet meadows in Wisconsin (Woo and Zedler 2000), a lake in southern Finland (Toivonen and Back 1989), as well as Delta Marsh (Grosshans in press) attribute the rapid spread of *T. x glauca* to not only management, but to increased nutrient inputs from agricultural runoff.

ii. The Not-So-Aggressive Phragmites

Phragmites, or giant reed grass, is the second main dominant species within the MERP complex. Like cattail, it is also described as a very competitive and invasive species, having increased substantially in abundance within wetlands across North America (Cross and Fleming 1989, Rice et al. 2000, Blossey and McCauley 2000, Rooth and Windham 2000). Its abundance within the MERP marshes, however, has not increased as dramatically, which can be attributed to the existence of various genetic clones (Koppitz 1999, Kühl et al. 1999). A much more aggressive *Phragmites* clone for example, plagues coastal wetlands of the southeastern US (Rice et al. 2000), whereas the clonal variety at Delta Marsh has been described as a less aggressive variety as compared to cattail (J. Lissner pers. comm.). Although not as invasive, *Phragmites* has been extremely successful in competitively maintaining areas that it occupies.

Following a disturbance, *Phragmites* is an excellent colonizer and will slowly invade a wide habitat range to form extensive mixed zones with other marsh plants (Haslam 1971a,b, Rice et al. 2000). Under fluctuating water levels *Phragmites* expansion is limited (Cross and Fleming 1989), whereas in their absence it can slowly expand into bordering areas. While seed germination is uncommon and seedling survival quite low (Cross and Fleming 1989), this tall marsh grass spreads by extensive creeping rhizomes and suckers extending up to 20m from the parent plant (Walker 1965, Coops and van der Velde 1996). *Phragmites* can survive under various environmental conditions from its extensive underground reserve, which is provided from the dense network of underground rhizome masses (Haslam 1971b).

Within the experimental marshes, this rhizome layer is often so thick that there is little soil remaining within the root zone. *Phragmites* plants grow up to 2 - 4 m in height and produce copious amounts of standing and fallen deadfall, which does not deteriorate for years (van der Valk and Davis 1978, Wrubleski et al. 1997). These dense impenetrable stands provide little opportunity for recolonizing plants including young *Phragmites* (Haslam 1971a, Cross and Fleming 1989). Rice et al. (2000) indicate that *Phragmites* spreads relatively quickly following a disturbance and once established it is very difficult to eradicate. Without fluctuating water levels to remove plants and accumulated debris (Wrubleski et al. 1997), these stands persist and remain closed.

iii. The comparisons

Shay et al. (1999) suggest that with a stabilized water level regime, dense cattail (*T. glauca*) stands limit the growth of shade-intolerant *Phragmites*, and that cattail could expand up the water depth gradient into areas once occupied by this emergent. Cattail does appear to outcompete *Phragmites* for areas at and below the water table, however, this does not seem to be the case within areas above the water table. From 1989 to 1997, there was very little invasion of cattail into *Phragmites*-dominated regions, with *Phragmites* invading into an equivalent of previously cattail-dominated areas as well. Cattail invaded newly exposed shallow waters following 1989, which proportionally provided much more potential habitat to expand into. Cattail and *Phragmites* may not be equally as invasive, but nonetheless, both are extremely robust in maintaining the areas they previously occupy. Both species produce extensive rhizomes and copious amounts of litter and standing deadfall making them very difficult to eradicate once established.

3.6.3. The Markov Transition Matrix Model: Utilized For A Wetland System?

Treatment group transitions

For all three treatment groups, the transition matrix model indicates that cattail will dominate quite rapidly following stabilization. For both the medium and high treatment groups, however, the model shows cattail abundance decreases as *Phragmites* abundance slowly and steadily increases, giving the impression that *Phragmites* would dominate during a stabilized regime. This does not agree with what is occurring in the surrounding Delta Marsh (Shay et al. 1999, Grosshans in press) or in the MERP marshes, both subject to a common stabilized regime. Cattail is by far the predominant species, and continues to

steadily increase in abundance. Comparing current conditions of Delta Marsh and the MERP marshes to predicted conditions reveals how sensitive the transition matrix model is to prominent data trends.

During the 1985-1989 treatment period, cattail and *Phragmites* were the only dominant emergents to survive in deep flooded areas of the medium and high treatment marshes (van der Valk et al. 1994). As water levels dropped following 1989, shallow and waterlogged areas were revealed allowing whitetop and *Phragmites* to spread into these areas, while cattail abundance declined as a result of drier conditions. At the same time, cattail took advantage of lower water levels and invaded down the elevation gradient into areas previously beyond its water depth range (de Swart et al. 1994). As a result of receding water levels, *Phragmites* moved into areas which were previously occupied by cattail during the flooded regime. The transition matrix extrapolates this trend, which is what could happen if water levels would indeed continue to recede within these systems. *Phragmites* would most likely move into previously cattail dominated areas as cattail abundance within these areas declined. In the present stabilized regime, however, this proposed succession would not occur. Water levels ceased to continue lowering when they reached the stabilized level, and so by 1997 *Phragmites* had moved as far as it could down the elevation gradient before encountering a wall of cattail. Nevertheless, with continued accumulation of deadfall and organic matter, shallow areas could become filled in eliminating deeper standing water and providing optimal *Phragmites* habitat. This event seems unlikely, however, since organic matter accumulation within the MERP marshes is extremely low. Additionally, *Typha x glauca* is extremely resilient, and once established it is not easily eradicated regardless of standing water level (Toivonen and Back 1989, Urban et al. 1993, Davis 1994, Shay et al 1999, Woo and Zedler 2000).

Transition results from the model for the normal treatment group show a very definite cattail dominated system, similar to present conditions of the marsh. These marshes better represent transitions occurring during a stabilized regime, because these water levels did not decrease following 1989, but rather have existed at the same mean level since 1985. Essentially, vegetation patterns in these marshes were farther along than those flooded above normal levels. By 1989, species had already sorted themselves along the elevation gradient, subsequently continuing to form dense homogenous zones up to 1997. Marshes 2, 4, and 5 (marshes manipulated in 1992) show a similar trend to the normal group with cattail rapidly dominating, although to a lesser extent. Each of these 3 marshes are originally from a different treatment group (high, normal, medium respectively), and each experienced

different management during 1992; some combination of flooding, burning, mowing, and drawdown. Yet when pooled together they show a trend similar to existing conditions, of cattail dominating.

Landscape transitions

By pooling the transition data from all MERP marshes we can examine what happens on the landscape level of all the MERP marshes, rather than on an individual marsh level. The transition model appears to be sensitive to localized factors, so by pooling the data we place less emphasis on individual discrepancies, and can identify landscape level trends rather than concentrated ones. Horn (1975) stated that the most striking property of succession is that the same final community composition can be reached from many different starting communities. Here this is clearly the case. Pooling the data identifies a robust trend where cattail continues to dominate waterlogged areas of the marsh with *Phragmites* dominating uplands, regardless of starting proportions.

With 100% open water as the initial community, the model indicates bulrush peaks in abundance fairly rapidly following stabilization, suggesting it expands into these open habitats. In each case bulrush abundance levels off at a low level, and is never completely eliminated from the marsh. This is consistent with vegetation changes within the MERP marshes, where bulrush will colonize areas after disturbances (i.e. starting with 100 percent water), but will lose out fairly rapidly to other dominants, specifically cattail. Consequently, as cattail abundance increases, bulrush decreases dramatically. With stabilization cattail abundance increases rapidly, while *Phragmites* abundance slowly increases to a level lower than that of cattail. This in part is a consequence of the greater proportion of shallow flooded habitat to saturated uplands within the marsh (i.e. optimal cattail and *Phragmites* habitat respectively). The model also indicates that with stabilization whitetop abundance levels off after 3 generations and remains fairly constant between generations, presumably exchanging areas with neighbouring species as minor environmental fluctuations occur. Additionally, abundance of grasses/forbs will increase higher than that of whitetop, consistent with what is observed within control marsh 11 and the surrounding Delta Marsh (Grosshans in press). In the absence of fluctuating water levels certain areas no longer receive inundation of water, remaining dry for extended periods. Wet species such as whitetop only tolerate unsuitable conditions for so long (Smith 1972), and are slowly invaded by grasses and forbs, converting wet meadows to low prairies. Proportionally, cattail and *Phragmites*-dominated areas rapidly comprise 60 and 20 percent of the marsh respectively. In any event, cattail, or *Phragmites*,

never completely dominate, unable to invade low prairie and wet meadow upland areas. These successional trends are surprisingly robust, where eventually after only about 9 generations (72 years) all final community compositions become identical.

3.6.4. Comparisons of Water Level Treatments

Although these marshes were subject to very different experimental water levels from 1985-1989 (van der Valk 2000), the overall long-term vegetation trends were the same once stabilized water levels were initiated. Four of the MERP marshes (marshes 3, 4, 7 and 8) had been stabilized in 1985 to levels comparable to the mean of Delta Marsh (247.55 m asl; **Table 2.1**), and essentially experienced no major change in these levels following 1989. By this time, these marshes showed extensive vegetation cover, more so than most of the other marsh sites (**Figure 3.1**). In essence, by 1997 these marshes had been stabilized at this level for almost 12 years, rather than 8 years. The difference in vegetation cover to the other treatment groups would have been the length of time needed to reach the 1997 state of dense monodominant plant zones, dominated by cattail and *Phragmites*. Changes within these four marshes are farther along in succession than the other marshes. Examples in 1997 are *Phragmites* spreading into previously 1989 whitetop areas of marsh 7, the encroachment of cattail into previously *Phragmites* and bulrush in marsh 3, and invasion of cattail into whitetop areas of marsh 8 (**Appendix IV, Figure 3.1**). With 1989 stabilization, the remaining marshes experienced a lowering of water levels, revealing unoccupied mudflats, and so are merely at a younger stage of succession. Despite extremely varied management histories of the marshes, the pooled transition of the entire MERP area shows the eventual dominance of cattail, clearly evident in 1997.

Additionally, the three marshes (2, 4 and 5), which were manipulated in 1992 for waterfowl management purposes, show the youngest stages of succession for the ten experimental marshes, in essence only stabilized for the last five years. These marshes typically possess more patchy open vegetation cover with intermixed open water patches and submersed aquatics. These conditions provide more suitable waterfowl habitat (Murkin et al. 1982), and consequently house a greater number of waterfowl than those marshes untouched since 1989. Also present in these marshes are areas of bulrush, mixed transition zones, and a rich understory of numerous minor species not normally found within the remaining seven marshes. Following current trends in the MERP marshes and those of Delta Marsh (Grosshans, in press), however, with continued stabilized water levels most of these bulrush beds will most likely disappear.

3.6.5. Long-Term Implications

This long-term study indicates that minor changes or shifts in vegetation boundaries will result from the ingrowth of cattail, *Phragmites* and whitetop as these transition zones constantly shift due to seasonal variations in water depth and competitive interactions between species. Although areas were lost to respective species from 1989 to 1997, these species also gained area back from the same species. Nevertheless, water level fluctuations during the stabilized regime are not drastic enough to cause any major vegetation changes, or to open up dense monodominant stands of vegetation and accumulated deadfall. This study indicates that if stable water levels persist, cattail and *Phragmites* will continue to spread uninhibited, leaving very little open water. This has very serious ramifications for the wildlife habitats within these marshes, which are already seriously degraded. Since waterlogged and flooded areas proportionally make up most of the area of the MERP marshes, this has provided plenty of habitat for cattail and *Phragmites* to dominate. Without disturbances by occasional fluctuating water levels, the experimental marshes will remain overgrown with dense homogenous vegetation stands of low species and habitat diversity; a fate similar to the surrounding Delta Marsh (Grosshans in press).

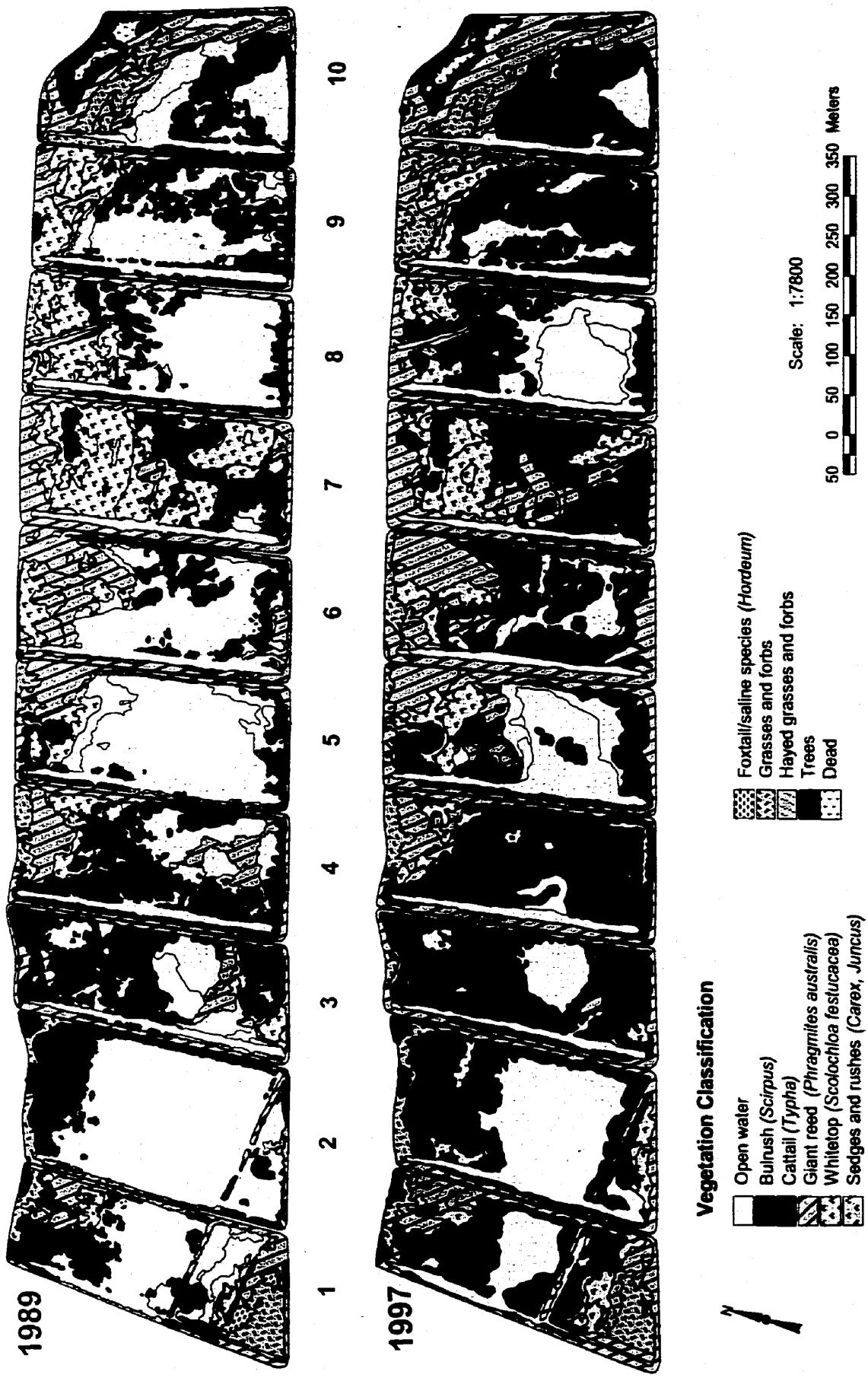


Figure 3.1. Vegetation classification of the Marsh Ecology Research Program (MERP) experimental marshes, Delta Marsh, Manitoba, Canada, 1989 classification is based on IR photos and previous vegetation maps (van der Valk 2000). 1997 classification is based on IR photos and ground verification.

1989



1997

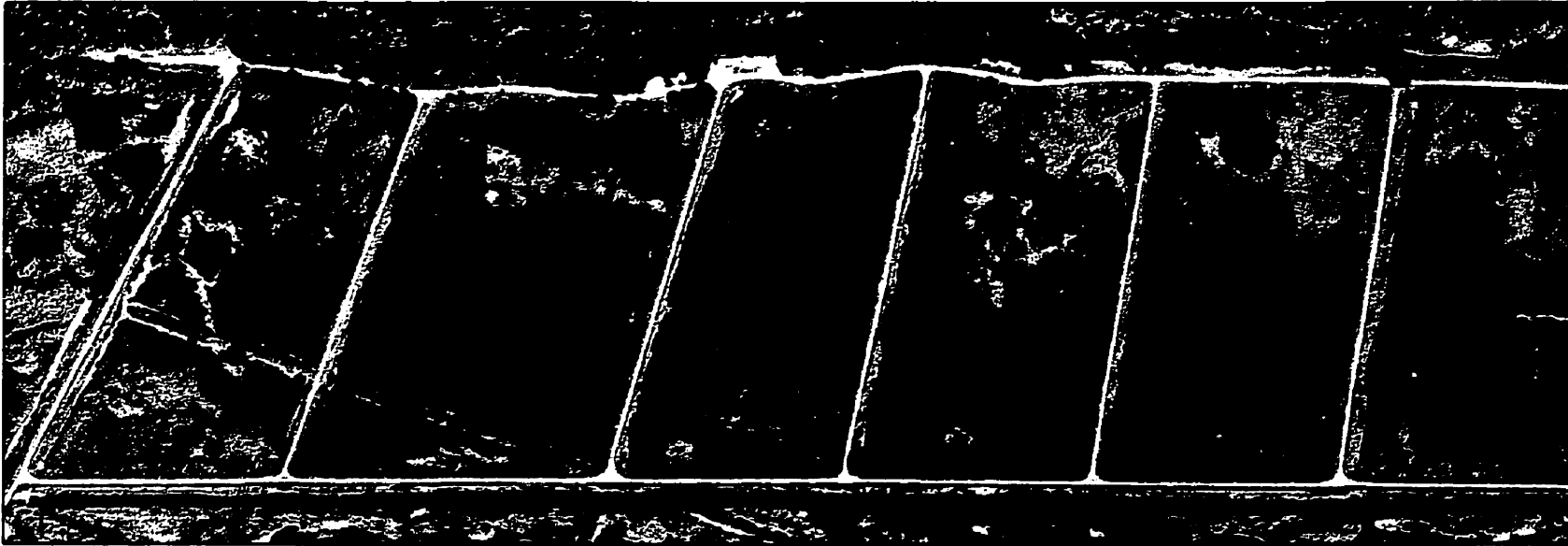
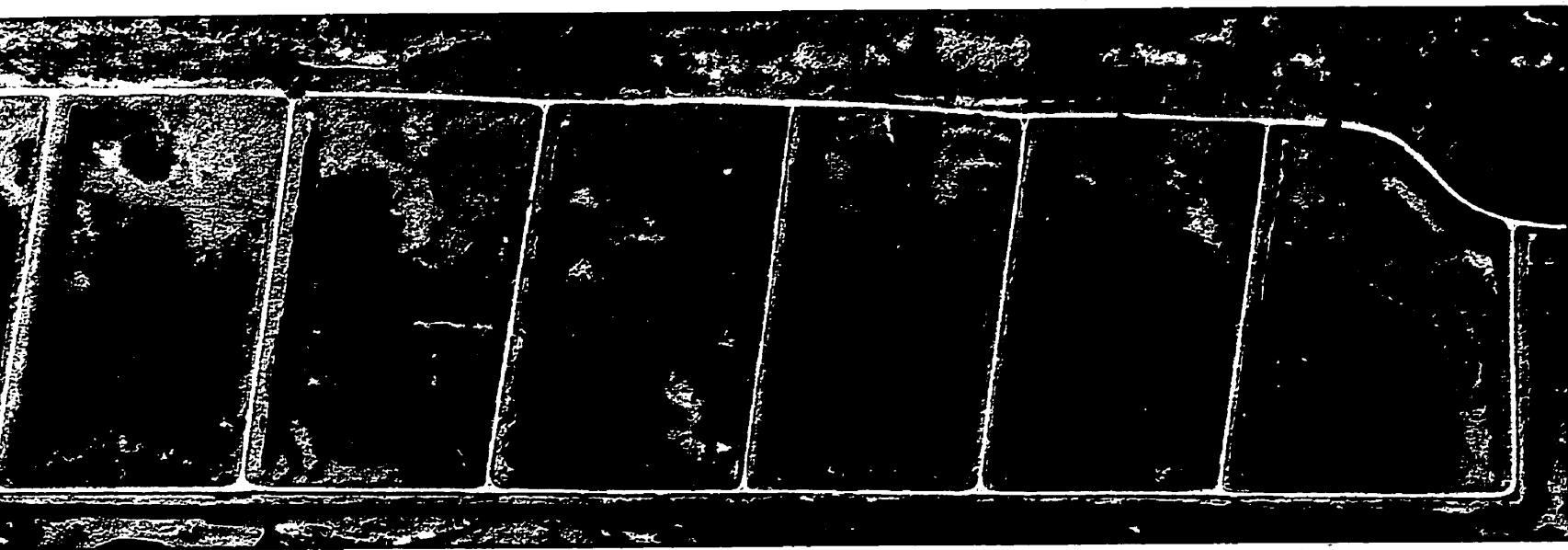
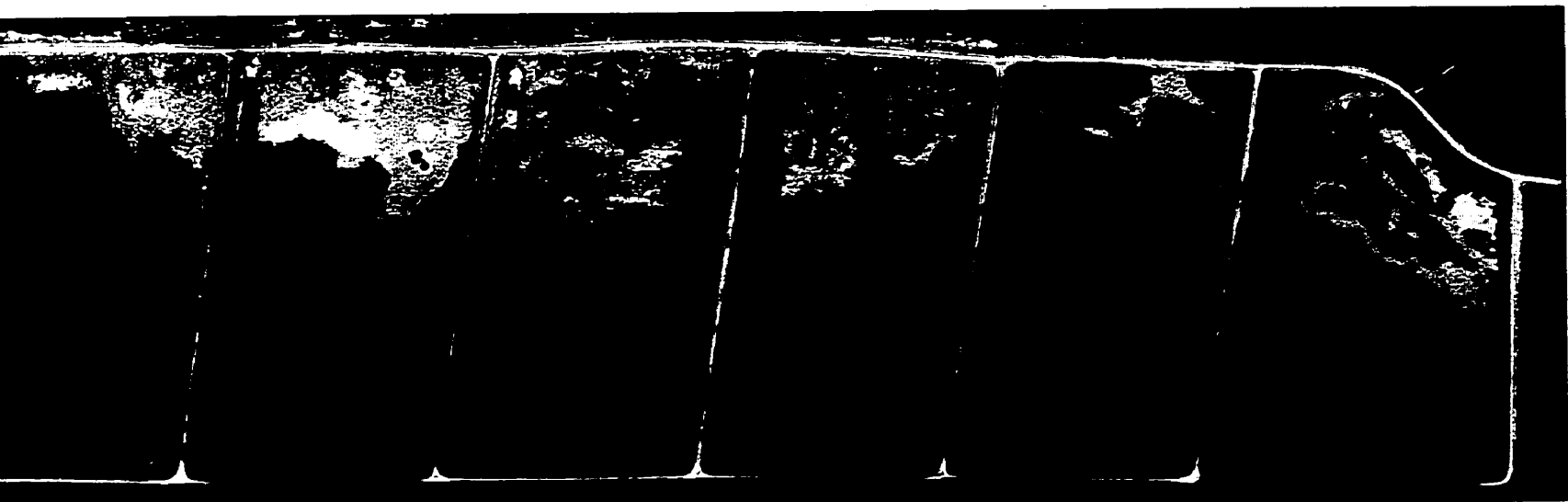


Figure 3.2. Mosaics of colour infrared aerial photographs for 1989 and 1997, flown at a scale of 1:4000. All 1997 photography was done with a infrared film type 2443.





000. All 1997 photography was done with a Wild 15/4 UA6-S large format camera, at a setting of 1/200 at f5.6. Film used was Kodak Aerochrome



1980

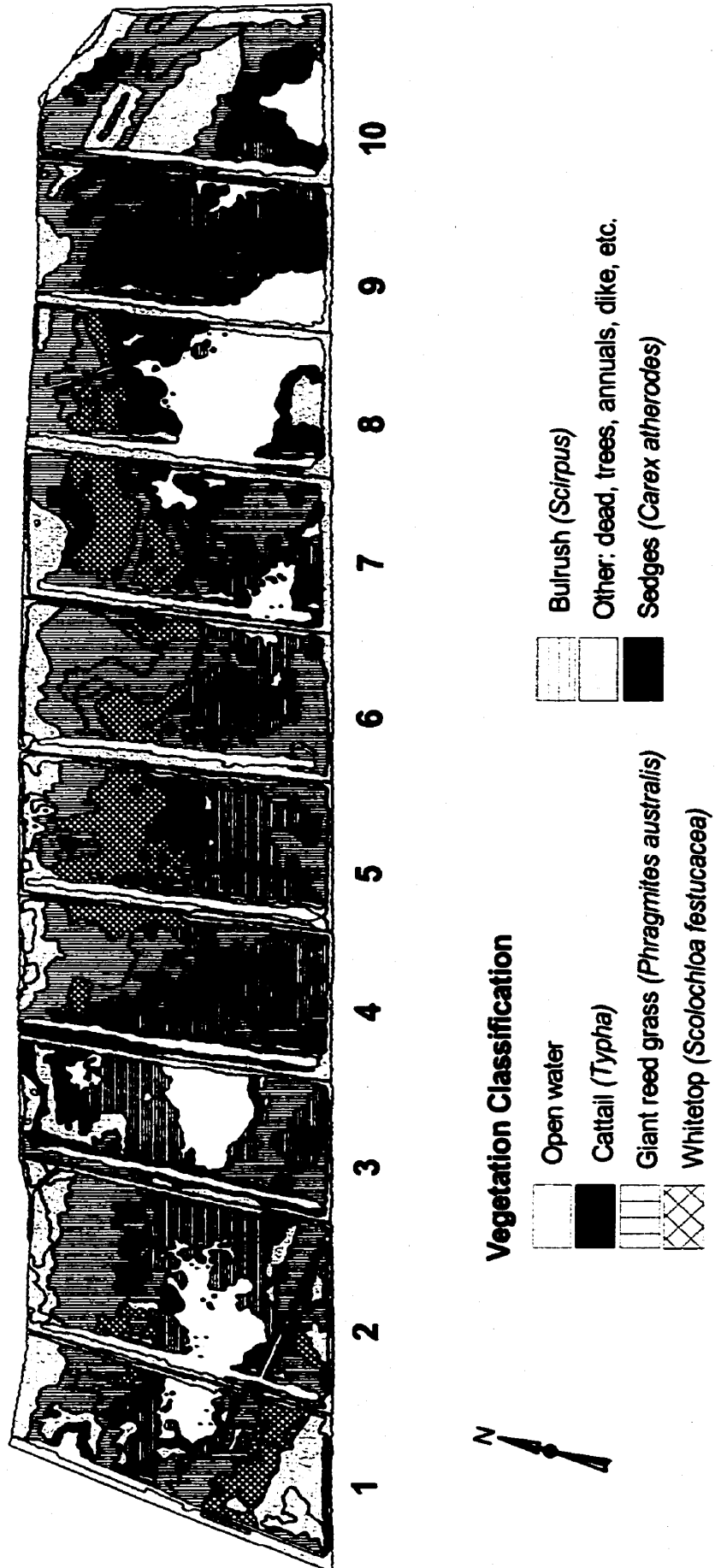
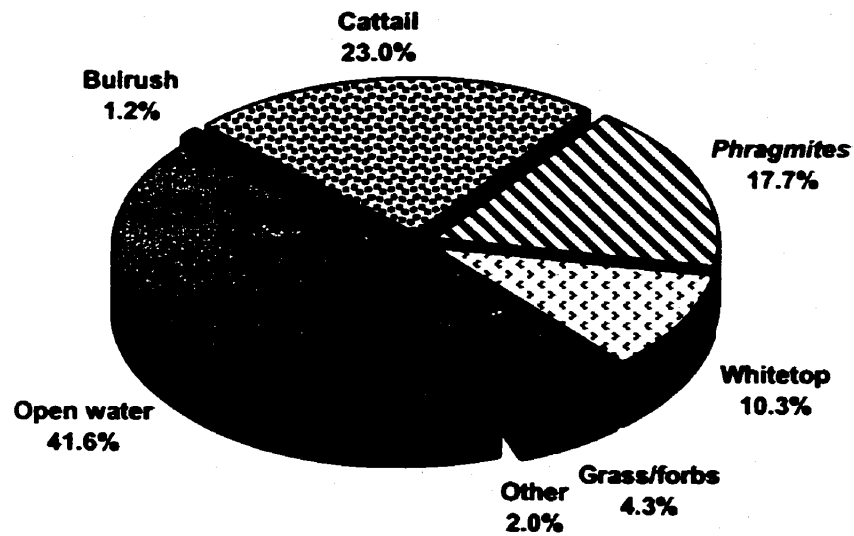


Figure 3.3. 1980 vegetation classification of the Marsh Ecology Research Program (MERP) experimental marshes, prior to any manipulations taking place (from van der Valk 2000). This vegetation community was established after experiencing almost 20 years of stabilized water levels (1961-1980).

a. 1989 vegetation composition of the dominant vegetation zones in the MERP experimental marshes.



b. 1997 vegetation composition of the dominant vegetation zones in the MERP experimental marshes.

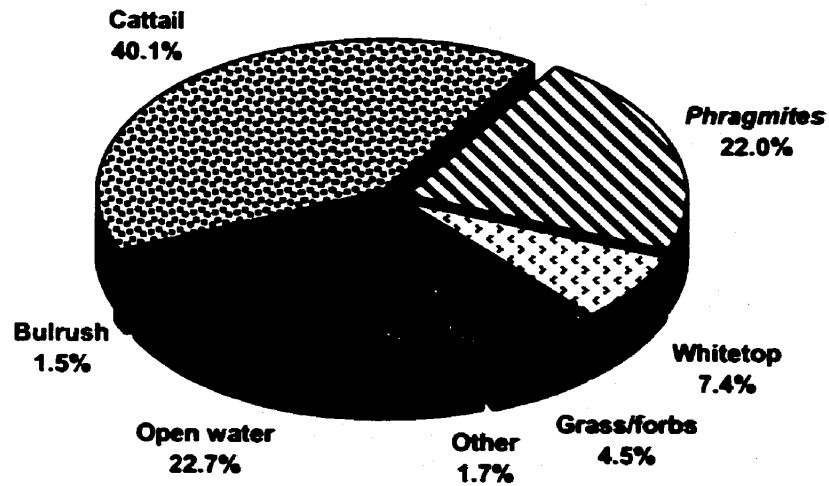


Figure 3.4. Vegetation composition of the dominant vegetation zones in the MERP experimental marshes from 1989 and 1997. Values are expressed as the proportional percentage of the entire MERP complex that the dominant zone occupies

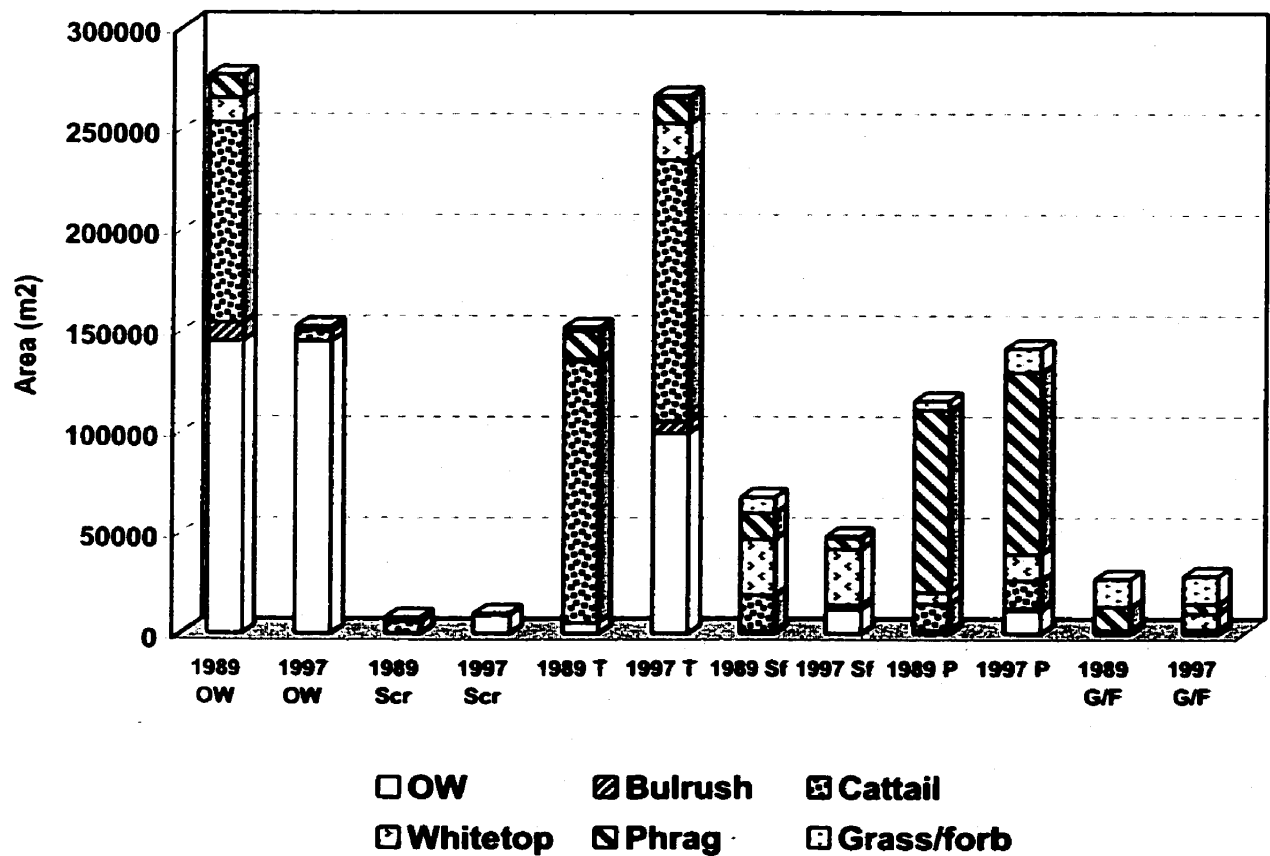


Figure 3.5. Changes in total vegetation areas from 1989 to 1997. 1989 columns give the proportion of the total area of the respective vegetation zone which was lost to invading species in 1997. Essentially, proportions show how much of the original vegetation from 1989 remained as it was still dominated by itself in 1997, and what proportion was invaded, and so converted to other vegetation zones in 1997. Conversely, 1997 columns give the proportion of the total area of the respective zone that is made up areas that remained the same, and what proportion was previously other vegetation in 1989, now newly acquired and dominated by the respective vegetation zone.

Transition matrix of total proportional area changes.

	Veg Zone	1997 OW	1997 Bul	1997 Cattail	1997 Whtop	1997 Phrag	1997 GF	1989 Total
1989	OW	0.524	0.033	0.359	0.044	0.041	0.000	1.000
1989	Bul	0.007	0.002	0.738	0.133	0.119	0.000	1.000
1989	Cattail	0.035	0.001	0.853	0.006	0.093	0.013	1.000
1989	Whtop	0.008	0.006	0.267	0.410	0.192	0.117	1.000
1989	Phrag	0.011	0.003	0.113	0.050	0.782	0.041	1.000
1989	GF	0.004	0.000	0.024	0.028	0.434	0.510	1.000

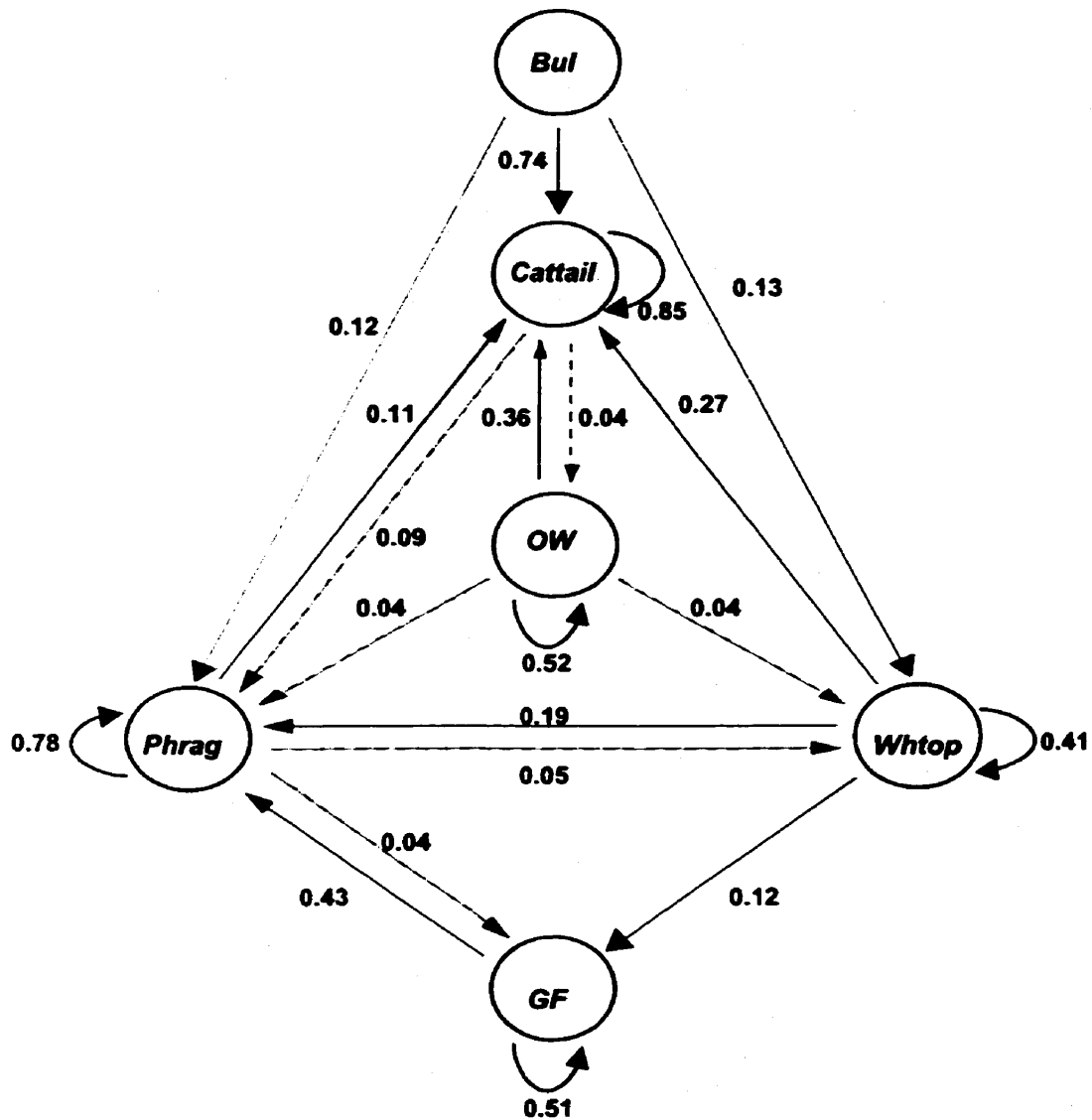
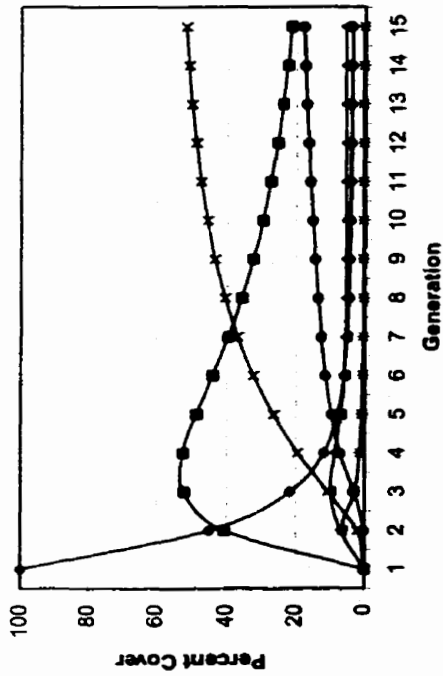
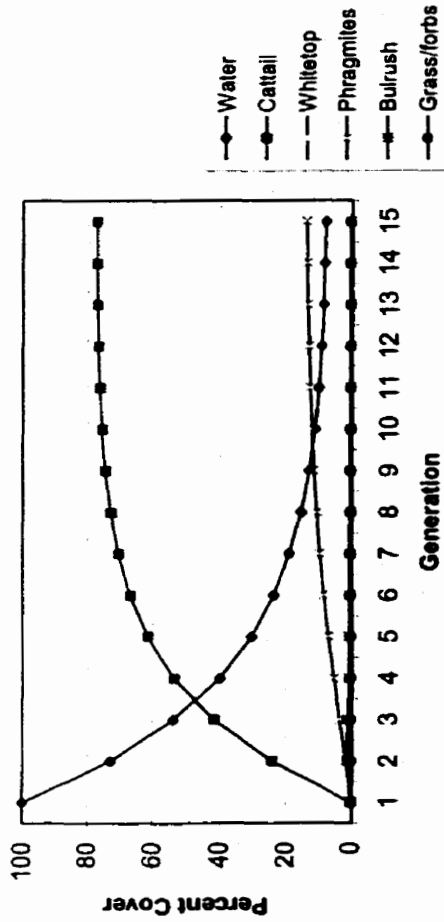


Figure 3.6. A transition matrix of total proportional changes from 1989 to 1997 (above) was used to create the transition probabilities diagram (below) for a prairie marsh subject to a stabilized water level regime. Dominant zones include open water (OW), cattail, bulrush (Bul), whitetop (Whtop), *Phragmites* (Phrag), and grass/forb (GF). Solid arrows indicate dominant trends, while dotted arrows indicate minor trends.

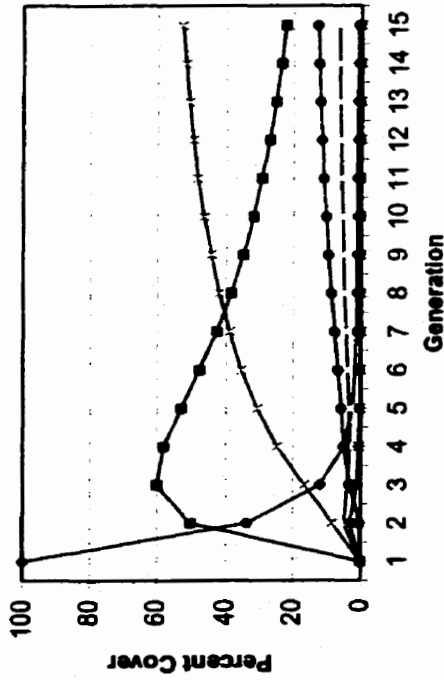
a. Medium treatment group (1 and 9)



c. Normal treatment group (3,7 and 8)



b. High treatment group (6 and 10)



d. Post-1989 manipulated (marshes 2,4 and 5)

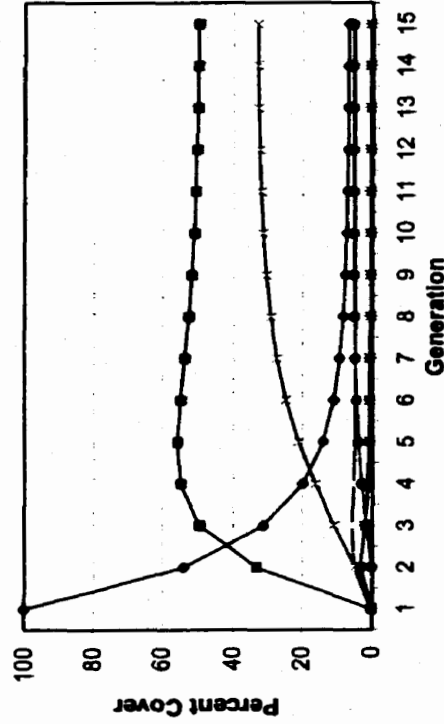


Figure 3.7. Transitions of the dominant marsh vegetation over 15 generations (120 years) within the 3 treatment groups and the post-1989 manipulated group of the MERP experimental marshes. The 2 treatment groups flooded higher than mean normal levels of Delta Marsh [a. medium: 30cm above (247.8 masl), b. high: 60 cm above (248,10 masl) 247.5 masl] show successions leading to *Phragmites* dominated systems, whereas the normal treatment group (c. normal: 247.5 masl) shows cattail dramatically dominating. Marshes 2,4 and 5 (d. post-1989 manipulated) are similar to the normal group but at a much lesser degree of cattail dominance.

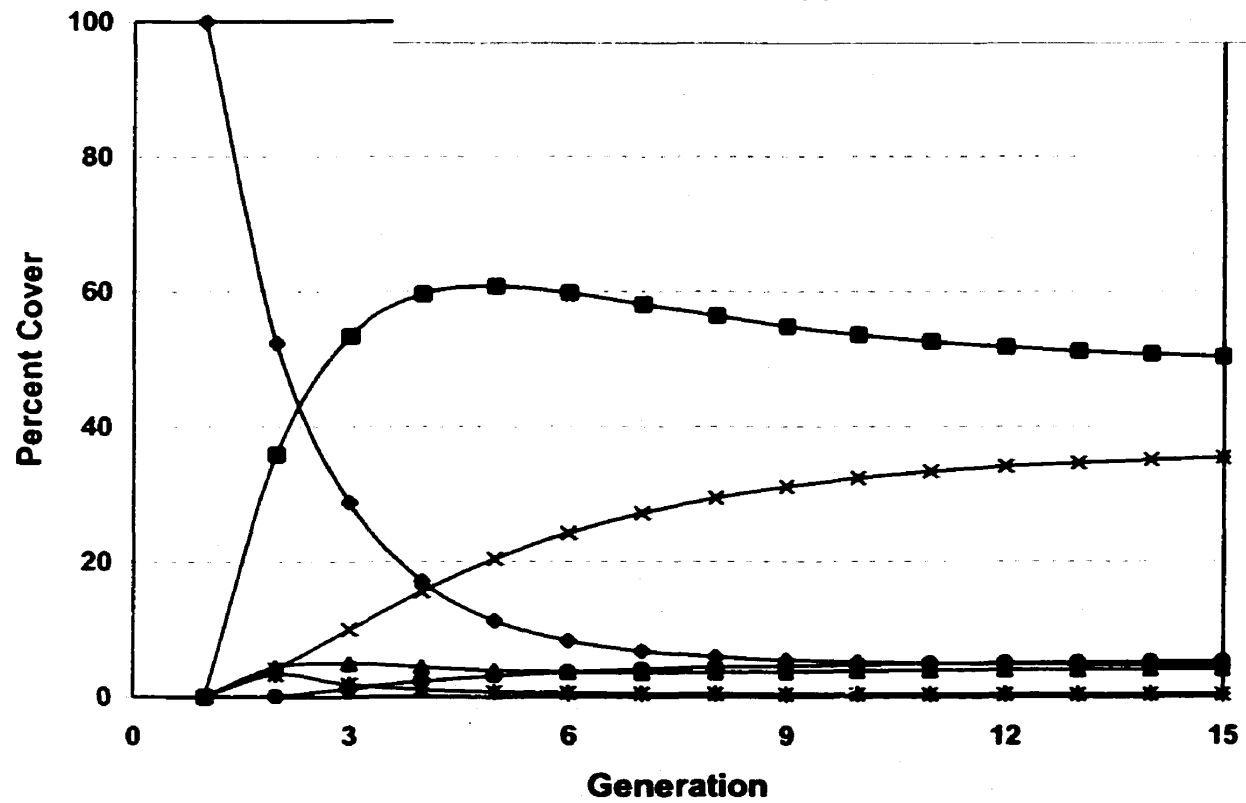
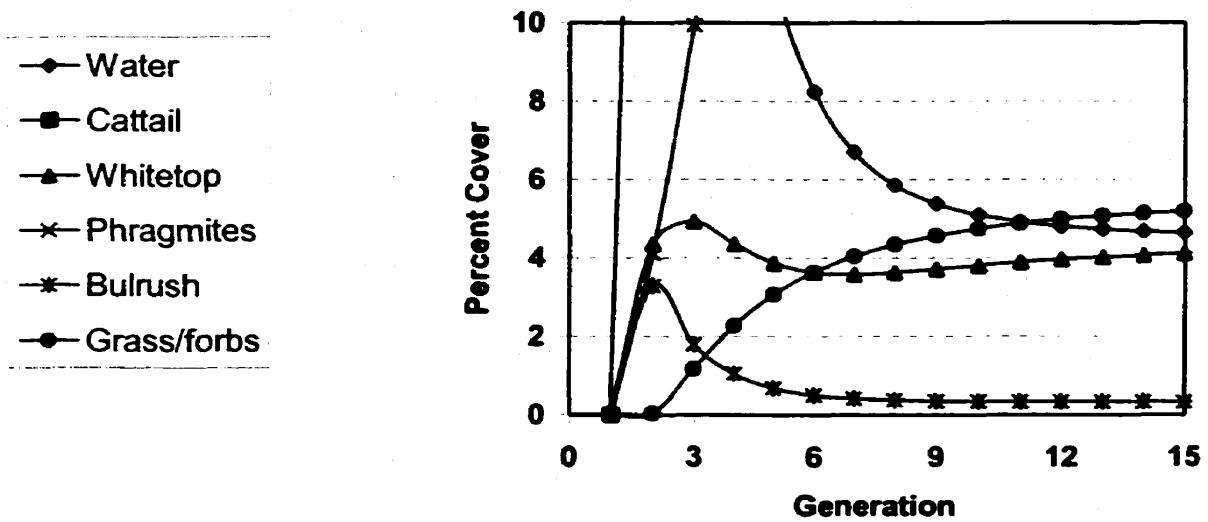


Figure 3.8. Transitions calculated from the transition matrix model of the dominant marsh vegetation for all MERP experimental marshes combined. Predicted compositions cover 15 generations (120 years) in a marsh system beginning with 100 percent open water as a starting generation. Inset shows lower 10 percent range of percent cover expanded to show low abundance trends suppressed by the 2 main dominants cattail and *Phragmites*.

Table 3.1. Interpretation key of vegetation signatures for colour infrared aerial photographs of the MERP experimental marshes. 1997 photos were flown 13 August 1997 at a scale of 1:4,000. Similar scale photos are also available from 1989.

Vegetation Zone	Colour	Texture	Location/Comments
Open water	Blue/black White to green/white	Smooth, rippled in some areas from wave action.	Very dark and distinct. Shallow water or reflections off water will often appear white to green/white.
Mudflat	White to blue/white, to greeny black	Navy/greeny black and white patches.	Found bordering water, disturbed areas.
Bulrush (<i>Scirpus</i>)	Dark deep red, brick red to dark navy, to brownish red	Blurry appearance and patchy. Open water patches due to sparseness.	Found in water, along water's edge, or deeper water areas. Sparse patches appear as shadowed areas on open water.
Cattail (<i>Typha</i>)	Medium to deep red	Smooth to grainy. Peck marked appearance from open water, and intermixed patches of deadfall.	Found mainly bordering open water to low water filled areas. Also borders Whitetop, <i>Phragmites</i> as well as Sedges/rushes.
Giant reed grass (<i>Phragmites australis</i>)	Pink to dark pink	Grainy to lumpy, shadows along edges gives depth to these these patches appearing almost 3D on photos, and much higher than surrounding areas with stereoscopes.	Found bordering water, upland areas, Cattail and Whitetop. Also borders Sedges and rushes, and Grasses and forbs.
Sedges and rushes (<i>Carex, Eleocharis, Juncus</i>)	Dark red to dark pink (not a bright red like cattail)	Appears flatter on photos, does not have 3D appearance as Cattail does. With stereoscopes appears flat.	Usually occurs around/near Whitetop areas, as well as Cattail Also borders Foxtail/saline, and Grasses and forbs. Found in wet waterlogged areas.
Whitetop (<i>Scolochloa festucacea</i>)	White, to pale/light pink to green (shallow water)	Fine mottled appearance. White or green patches from open water areas.	Often found bordering Cattail, wet meadows, and <i>Phragmites</i> . Also borders Sedges/rushes, and Grasses and forbs. Foxtail/ saline species often found bordering or in close proximity.
Sow thistle (<i>Sonchus arvensis</i>)	Light brown, gray to cream. Some light pink.	Flat smooth texture. Patchy and mixed creams, light brown and gray, with mixed light pink.	Occurs near Whitetop, Foxtail/Saline, Sedges/rushes and and Grass/forbs. Difficult to distinguish from other low prairie area.
Foxtail/saline species (<i>Hortemum, Puccinellia</i>)	Cream, brown to brownish red.	Flat smooth texture, low flat appearance with use of stereoscopes.	Occurs all over, but usually associated with mudflats, Whitetop Sedges/rushes and Grass/forb areas as well.
Grasses and forbs	Light pink, light brown, to grey and cream.	Flat smooth texture, often patchy and mixed light pink brown, grey to cream.	Low prairie areas found bordering wet meadows of Whitetop and Sedges/rushes. Presence of forbs cause mixed patches of browns and greys.
Trees and shrubs	Burgundy, maroon to dark red.	Lumpy, patchy, gravelly with shadows. Cauliflower appearance. Tall, 3D appearance with stereo scopes.	High upland areas, borders next to Grass/forbs and <i>Phragmites</i> patches. Willow bluffs appear as smaller, lumpy, dotted areas.
Disturbed	Brownish-grey, grey to white. Light green.	Smooth to grainy appearance. Freshly disturbed bare soils and deadfall appear white to light green.	Disturbed areas very distinct. Usually found in Grass/forb areas.

Table 3.2. Transition matrix of successional changes in dominant species. Essentially, how much of the original vegetation from 1989 remained as it was dominated by a given species, and what proportion was invaded, and so converted to other vegetation classes in 1997. Typical dominant changes are highlighted in each table.

		1997	1997	1997	1997	1989
Species		A	B	C	D	Totals
1989	A	A to A	A to B	A to C	A to D	100
1989	B	B to A	B to B	B to C	B to D	100
1989	C	C to A	C to B	C to C	C to D	100
1989	D	D to A	D to B	D to C	D to D	100

Table 3.3. Vegetation zones and typical dominant plant species of the MERP experimental marshes. Species presence is highly dependent on locational water depth and moisture conditions. Species abundance given as either a dominant, secondary or minor species.

VEGETATION ZONES		CHARACTERISTIC PLANT SPECIES	ABUNDANCE	PLANT LIFEFORM
Non-vegetated	Open water	<i>Potamogeton</i> spp. <i>Ceratophyllum demersum</i>	Dominant Secondary	submergent submergent
	Submergents	<i>Potamogeton</i> spp. <i>Utricularia macrorhiza</i> <i>Ceratophyllum demersum</i> <i>Myriophyllum sibiricum</i> <i>Lemna minor</i> <i>Lemna trisulca</i>	Dominant Dominant Secondary Secondary Secondary Secondary	submergent submergent submergent submergent free floating free floating
Emergent Vegetation (permanently- seasonally flooded)	Bulrush (<i>Scirpus</i>)	<i>Scirpus acutus</i> <i>Scirpus tabernaemontani</i> <i>Scirpus maritimus</i> <i>Utricularia macrorhiza</i> <i>Potamogeton</i> spp. <i>Myriophyllum sibiricum</i> <i>Lemna minor</i> <i>Lemna trisulca</i>	Dominant Dominant Dominant Dominant Secondary Secondary Secondary Secondary	emergent emergent sedge submergent submergent submergent free floating free floating
	Cattail (<i>Typha</i>)	<i>Typha latifolia</i> <i>Typha angustifolia</i> <i>Typha x glauca</i> <i>Scolochloa festucacea</i> <i>Phragmites australis</i> <i>Carex atherodes</i> <i>Ranunculus sceleratus</i> <i>Utricularia macrorhiza</i> <i>Scirpus</i> spp. <i>Lemna minor</i> <i>Lemna trisulca</i>	Dominant Dominant Dominant Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary	emergent emergent emergent emergent emergent sedge forb submergent emergent free-floating free-floating
Wet meadow (seasonally- temporarily flooded)	Giant reed grass (<i>Phragmites australis</i>)	<i>Phragmites australis</i>	Dominant	emergent
		<i>Cirsium arvense</i> <i>Sonchus arvensis</i> <i>Cicuta maculata</i> <i>Urtica dioica</i> <i>Scutellaria galericulata</i> <i>Teucrium canadense</i> <i>Mentha canadensis</i> <i>Lycopus asper</i> <i>Stachys palustris</i> <i>Typha</i> spp. <i>Scolochloa festucacea</i> <i>Carex atherodes</i> <i>Calystegia sepium</i> <i>Echinocystis lobata</i> <i>Polygonum convolvulus</i> <i>Lemna minor</i> <i>Lemna trisulca</i>	Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Minor Minor Minor Minor Minor	forb forb forb forb forb forb forb forb forb emergent emergent sedge forb forb forb forb free-floating free-floating
Wet meadow (seasonally- temporarily flooded)	Sedges and rushes (<i>Carex</i> , <i>Eleocharis</i> , <i>Juncus</i>)	<i>Carex atherodes</i>	Dominant	sedge
		<i>Carex retrorsa</i>	Dominant	sedge
		<i>Scirpus maritimus</i>	Dominant	sedge
		<i>Eleocharis</i> spp.	Dominant	sedge
		<i>Juncus balticus</i>	Dominant	rush
		<i>Scolochloa festucacea</i>	Secondary	emergent

Table 3.3. Vegetation zones and typical dominant plant species cont'd.

MARSH ZONE	VEGETATION CLASS	CHARACTERISTIC PLANT SPECIES	ABUNDANCE	PLANT LIFEFORM
	Whitetop grass (<i>Scolochloa festucacea</i>)	<i>Scolochloa festucacea</i> <i>Carex uterodes</i> <i>Carex retrorsa</i> <i>Teucrium canadense</i> <i>Mentha canadensis</i> <i>Lycopus asper</i> <i>Stachys palustris</i> <i>Sonchus arvensis</i> <i>Cirsium arvense</i> <i>Cicuta maculata</i> <i>Polygonum sp.</i> <i>Hordeum jubatum</i>	Dominant Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary	emergent sedge sedge forb forb forb forb forb forb forb forb grass
	Foxtail/saline species (<i>Hordeum</i> , <i>Puccinellia</i>)	<i>Hordeum jubatum</i> <i>Puccinellia nuttalliana</i> <i>Suaeda calceoliformis</i> <i>Atriplex patula</i> <i>Sonchus arvensis</i> <i>Chenopodium album</i> <i>Elytrigia repens</i> <i>Scirpus maritimus</i> <i>Cirsium arvense</i> <i>Scolochloa festucacea</i> <i>Poa palustris</i>	Dominant Dominant Dominant Dominant Dominant Secondary Secondary Minor Minor Minor Minor	grass grass forb forb forb forb grass sedge forb emergent grass
Grasses and forbs (low prairie, temporary - no flooding)		<i>Poa palustris</i> <i>Poa pratensis</i> <i>Cirsium arvense</i> <i>Sonchus arvensis</i> <i>Solidago canadensis</i> <i>Lactuca tatarica</i> <i>Aster spp.</i> <i>Elytrigia repens</i> <i>Puccinellia nuttalliana</i> <i>Hordeum jubatum</i> <i>Bromus inermis</i> <i>Carex spp.</i> <i>Teucrium canadense</i> <i>Symphoricarpus occidentalis</i> <i>Agrostis stolonifera</i> <i>Elymus canadensis</i> <i>Hordeum jubatum</i>	Dominant Dominant Dominant Dominant Dominant Dominant Dominant Secondary Secondary Secondary Secondary Secondary Secondary Secondary Secondary Minor Minor Minor	grass grass forb forb forb forb forb grass grass grass grass sedge forb herb grass grass grass
Trees (tree,shrub cover)		<i>Salix spp.</i> <i>Prunus virginiana</i> <i>Ulmus americana</i> <i>Cornus sericea</i> <i>Urtica dioica</i> <i>Poa palustris</i> <i>Cirsium arvense</i> <i>Solidago canadensis</i> <i>Bromus inermis</i> <i>Calystegia sepium</i> <i>Echinocystis lobata</i> <i>Polygonum convolvulus</i> <i>Eupatorium maculatum</i>	Dominant Dominant Dominant Dominant Dominant Dominant Dominant Dominant Secondary Minor Minor Minor Minor	tree tree tree shrub forb grass forb forb forb grass forb forb forb forb

Table 3.4. Vegetation composition of the MERP Experimental Marshes in 1989 and 1997. Total area is expressed as m² and hectares.

Vegetation Zone	1989 Total Area (m²)	1989 Total Area (ha)	1997 Total Area (m²)	1997 Total Area (ha)
Open water	278161.76	27.82	152086.97	15.21
Bulrush (<i>Scirpus</i>)	7892.57	0.79	9993.82	1.00
Cattail (<i>Typha</i>)	153585.46	15.36	268899.12	26.89
Giant reed grass (<i>Phragmites australis</i>)	118182.54	11.82	147539.33	14.75
Whitetop (<i>Scolochloa festucacea</i>)	68878.80	6.89	49842.38	4.98
Grass/forbs (<i>Poa, Bromus, Aster</i>)	28451.13	2.85	30175.76	3.02
Other	13165.00	1.32	11373.65	1.14
Submergents (<i>Potamogeton</i>)	956.28	0.10		
Sedges (<i>Carex</i>)	808.53	0.08	1357.05	0.14
Dead emergents	4728.85	0.47	4684.92	0.47
Foxtail/Saline (<i>Hordeum, etc.</i>)	1829.08	0.18	483.11	0.05
Trees	4842.27	0.48	4848.57	0.48
Total	681482.26	68.15	681284.67	68.13

Table 3.5. Total vegetation changes within the MERP experimental marshes from 1989 to 1997. Tables a. and b. show essentially, how much of the original vegetation from 1989 remained as it was dominated by a given species, and what proportion was invaded, and so converted to other vegetation classes in 1997. Dominant changes are highlighted in each table.

a. Total area (m²) changes from 1989-1997.

Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989 Open Water	144847.04	9089.67	99173.48	12043.83	11343.87	95.69	276593.57
1989 Bulrush	56.71	17.02	5823.97	1050.28	938.73	1.73	7888.44
1989 Cattail	5237.44	98.69	129338.52	923.47	14115.67	1913.96	151627.74
1989 Whitetop	548.80	409.06	18041.86	27652.00	12977.22	7890.25	67519.20
1989 Phragmites	1254.56	379.39	13017.71	5724.00	90184.76	4768.32	115328.73
1989 Grass/forbs	100.99	0.00	655.24	763.09	11783.96	13866.11	27169.39
1997 totals	152045.53	9993.83	266050.77	48156.67	141344.20	28536.06	646127.06

b. Transition matrix of total proportional area changes given as percentages.

Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989 Open Water	52.37	3.29	35.86	4.35	4.10	0.03	100
1989 Bulrush	0.72	0.22	73.83	13.31	11.90	0.02	100
1989 Cattail	3.45	0.07	85.30	0.61	9.31	1.26	100
1989 Whitetop	0.81	0.61	26.72	40.95	19.22	11.69	100
1989 Phragmites	1.09	0.33	11.29	4.96	78.20	4.13	100
1989 Grass/forbs	0.37	0.00	2.41	2.81	43.37	51.04	100

c. Percentage of total 1997 area that is made up areas that remained the same, and what proportion was previously other vegetation in 1989, now newly acquired and dominated by the respective vegetation zone

Vegetation Zone	1989 Open Water	1989 Bulrush	1989 Cattail	1989 Whitetop	1989 Phragmites	1989 Grass/forbs	1997 Totals
1997 Open Water	95.27	0.04	3.44	0.36	0.83	0.07	100
1997 Bulrush	90.95	0.17	0.99	4.09	3.80	0.00	100
1997 Cattail	37.28	2.19	48.61	6.78	4.89	0.25	100
1997 Whitetop	25.01	2.18	1.92	57.42	11.89	1.58	100
1997 Phragmites	8.03	0.66	9.99	9.18	63.81	8.34	100
1997 Grass/forbs	0.34	0.01	6.71	27.65	16.71	48.59	100

Table 3.6. Transition matrices of total proportional vegetation changes within the treatment groups [a. medium: 30cm above (247.8 masl), b. high: 60 cm above (248.10 masl) normal (c.) of 247.5 masl] of the MERP experimental marshes from 1989 to 1997. Dominant changes are highlighted.

a. Medium treatment group (1 and 9), transition matrix of total proportional changes (%).

	Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989	Open Water	44.84	6.06	40.63	6.59	1.85	0.03	100
1989	Bulrush	0.00	0.00	0.09	57.67	41.96	0.28	100
1989	Cattail	3.62	0.09	82.65	1.83	11.28	0.52	100
1989	Whitetop	0.24	0.00	2.17	39.28	19.21	39.11	100
1989	Phragmites	2.26	0.00	2.22	4.52	85.66	5.35	100
1989	Grass/forbs	0.00	0.00	0.31	1.28	24.66	73.75	100

b. High treatment group (6 and 10), transition matrix of total proportional changes (%).

	Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989	Open Water	33.56	3.16	50.04	4.90	8.18	0.15	100
1989	Bulrush	0.00	0.00	0.00	0.00	0.00	0.00	100
1989	Cattail	1.28	0.01	85.76	0.07	12.47	0.39	100
1989	Whitetop	0.80	0.00	0.77	29.99	18.25	50.18	100
1989	Phragmites	0.38	0.00	2.95	8.78	82.36	5.53	100
1989	Grass/forbs	0.00	0.00	0.00	0.00	46.54	53.46	100

c. Normal treatment group (3,7, and 8), transition matrix of total proportional changes (%).

	Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989	Open Water	72.88	1.12	24.25	0.32	1.42	0.00	100
1989	Bulrush	0.07	0.29	79.33	11.59	8.21	0.00	100
1989	Cattail	2.14	0.00	93.49	0.14	4.23	0.00	100
1989	Whitetop	1.07	0.92	33.72	41.18	20.25	2.85	100
1989	Phragmites	1.80	0.99	19.83	0.65	74.53	2.19	100
1989	Grass/forbs	0.00	0.00	25.97	5.60	62.77	5.66	100

d. Post-1989 manipulated (2,4, and 5), transition matrix of total proportional changes (%).

	Vegetation Zone	1997 Open Water	1997 Bulrush	1997 Cattail	1997 Whitetop	1997 Phragmites	1997 Grass/forbs	1989 Totals
1989	Open Water	53.89	3.12	33.18	5.09	4.71	0.00	100
1989	Bulrush	3.53	0.00	81.45	1.40	13.59	0.00	100
1989	Cattail	5.89	0.14	76.88	0.57	11.06	3.48	100
1989	Whitetop	0.17	0.00	37.73	46.14	13.59	0.37	100
1989	Phragmites	0.41	0.19	18.22	5.30	72.07	3.80	100
1989	Grass/forbs	0.00	0.00	1.09	5.12	50.06	43.71	100

CHAPTER 4

Long-Term Response Of Marsh Vegetation To Water Level Stabilization: Delayed Influences Of Competition

4.1. Introduction

4.1.1. Prairie wetland dynamics

The prairie marsh is one of the most dynamic wetland types because of the highly variable climatic conditions (i.e. wet and dry years) that characterize the prairie environment. Water levels in these wetlands are highly dependent on marsh basin size, and the amount of snowmelt, spring runoff, and precipitation they receive (Kantrud et al. 1989a,b; Weller 1994). Consequently, these systems experience natural fluctuations in water levels (i.e., alternating periods of flooding and drought) that result in dramatic changes in plant community composition and structure, which contribute to the cyclical succession of prairie marshes (Weller and Spatcher 1965, Walker 1965, van der Valk and Davis 1978). Under a naturally fluctuating regime, vegetation present in a marsh is primarily a function of water depth, while initial overall plant composition is a function of the soil seed bank and rhizome reserve (van der Valk and Davis 1976a).

Patterns of plant zonation along environmental gradients are evident in natural ecosystems (Stewart and Kantrud 1971, Sharitz and McCormick 1973, Vince and Snow 1984, Day et al. 1988, Reader and Best 1989). In prairie marshes plants are distributed along a water depth gradient, reflecting the differential tolerances of dominant macrophytes to flooding (**Figure 1.2b**) (Stewart and Kantrud 1971, 1972; Spence 1982, Adams 1988). Accordingly, seed banks play a critical role in the initial formation and perpetuation of these patterns (van der Valk and Davis 1978; Pederson 1981; Pederson and Smith 1988; van der Valk and Welling 1988; Welling et al. 1988a, 1988b). Nevertheless, water depth is only one part of a complex gradient of elevation, which combines a series of physical factors ultimately affecting plant position in a prairie marsh (Day et al. 1988). The elevation gradient includes such factors as spring flooding, growing season water depth and fluctuations, litter accumulation, and organic matter content. Although the exact mechanisms involved are often unclear (Shipley and Keddy 1987), additional secondary factors such as wave action disturbance (Wilson and Keddy 1985, 1986a, b), litter and standing crop (Day et al. 1988), salinity (Barbour 1978,

Snow and Vince 1984b, Kenkel et al. 1991) as well as competition (Grace and Wetzel 1981) can further affect the exact position of plant species along this gradient.

4.1.2. Cyclical vegetation changes and marsh succession

Van der Valk and Davis (1978) recognize four distinct stages in the vegetation cycle of a prairie marsh subject to natural flood-drought disturbances: dry, regenerating, degenerating, and lake marsh phases, collectively referred to as the wet-dry cycle (further discussed in Chapter 1). Although many factors influence the distribution of marsh plant species throughout this cycle, water depth is considered the primary determinant for plant distribution, growth, and survival (McDonald 1955, Harris and Marshall 1963, Walker 1959, 1965, Kadlec 1962, Meeks 1969, van der Valk and Davis 1978, Spence 1982, Galinato and van der Valk 1986, Kantrud et al. 1989b). Degeneration of the marsh results from persistent water levels and prolonged flooding, which eliminates standing vegetation, whereas regeneration occurs during droughts, which allows species to reestablish by recruitment from underground reserves (i.e. seeds and rhizomes) (**Figure 4.1**). It is recognized that these periodic cycles of disturbances as a result of natural flood-drought cycles, are essential in maintaining species and habitat diversity in prairie marshes (Harris and Marshall 1963, Weller and Spatcher 1965; van der Valk and Davis 1976b, 1978; van der Valk 1981; Pederson and van der Valk 1984; Kenkel 1992; Bornette and Amoros 1996). Consequently, these wetlands can be described as resilient, disturbance-driven ecosystems (Kenkel 1997). Disruption of the natural wet-dry cycle through artificial stabilization, results in a decoupling of the critical link between environmental variation and vegetation composition. As a result, prolonged periods of water level stability (i.e., reduction in the magnitude of water level fluctuations) greatly reduce habitat complexity and biodiversity (Kantrud et al. 1989a). With no disturbance to rejuvenate the marsh system, the community enters a state of degeneration or stagnation. With limited space for colonization one would presume to find increased competitive interactions among plant species.

4.1.3. Salinity

Even though water depth primarily determines wetland plant distribution, many secondary factors, such as salinity (Barbour 1978, Snow and Vince 1984), further affect the position of plant species. Higher soil salinities are often found where the water table is near the soil surface. Salts are brought to the surface by capillarity (i.e., upward moving water) and concentrated through surface evaporation (Brady 1990). During a natural state of fluctuating

water levels, flooding effectively reduces soil salinity by flushing away these dissolved salts (Neill 1993). Since patterns of plant zonation have been observed along salinity gradients for both inland systems (Badger and Unger 1990, Kenkel et al. 1991) and salt marshes (Barbour 1978, Snow and Vince 1984, Vince and Snow 1984), and increased salinity has been found to affect plant growth in prairie marshes (Stewart and Kantrud 1971, 1972, Leiffers and Shay 1982, Neill 1993), salinity may also influence plant distribution over prolonged water level stabilization where salts accumulate and persist.

4.1.4. Plant Competition

For plants, competition can be described as interactions between two species that can potentially occupy the same habitat unit. Since inter- and intraspecific competition are more often asymmetric (Keddy and Shipley 1989, Shipley 1994, Connolly and Wayne 1996), competitive displacement (or exclusion) from this habitat may result from the negative effects one dominant plant species has upon another by consuming (or controlling access to) a limited resource (Grubb 1985, Keddy 1989). Although dominance is achieved by competition, abundance is not necessarily a result of competition. A species rather may achieve dominance in an area because of inherently better abilities to withstand environmental conditions. In an environment with frequent disturbances (i.e. periodic flooding and droughts in a prairie marsh) dominance is attained through the ability to survive environmental conditions. Conversely, abundance within a more stable regime is achieved through traits that aid in competition for resources, leading to competitive dominance.

A fundamental physiological response curve is a resource-use pattern that occurs in the absence of interspecific competition, indicating the range of a resource gradient a species tolerates (Keddy 1989). Generally, most species grow better at the benign end of a gradient where resources are more abundant. (Keddy 1990, Kenkel et al. 1991, Grace and Wetzel 1981, Snow and Vince 1984). Conversely, a realized response curve is a pattern that occurs in the presence of competition, consequently narrower than a fundamental response (Keddy 1989). In essence, a species realized response is a function of its physiological tolerances (i.e. fundamental responses) combined with competitive interactions with neighbours (Austin 1990). Due to competitive hierarchies, species are expected to sort themselves along resource or habitat gradients, with more competitive species at the benign end and more stress tolerant at the peripheral ends (Levine et al. 1998). This idea of resource partitioning is used to explain stable coexistence within plant communities, but is less important in communities exposed to recurrent periods of disturbance. Generally, competition for space

will remain low in a system experiencing fluctuating environmental conditions, whereas in the absence of these disturbances competitive interactions will increase (Keddy 1989). Ultimately, periodic and intermediate levels of disturbance in combination with competitive interactions are critical for maintaining high habitat diversity (Harris and Marshall 1963, Weller and Spatcher 1965, Grime 1973, van der Valk and Davis 1976b, van der Valk 1981, Pederson and van der Valk 1984, Kenkel 1992, Bornette and Amoros 1996, van der Valk 2000).

4.1.5. Competition and the Prairie Marsh

Van der Valk (2000) indicates that genesis of plant zonation patterns within a prairie marsh occurs not from any single source, but from the collective result of seed distribution, seedling recruitment, and seedling and adult mortality, further followed by ecological tolerances of species and competition. Whether subsequent competitive interactions among species do eventually affect these establishment differences, however, is unclear. Numerous studies have found evidence to support the importance of interspecific competition in shaping wetland zonation patterns (Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1985, 1986, Shipley et al. 1991), suggesting competitive displacement does influence species distribution. Marshes with naturally fluctuating water levels maintain high species diversity, low levels of monodominance (van der Valk and Davis 1980, Keddy 1989), and presumably minimized competitive interactions. Conversely, eliminating the wet-dry cycle allows dominant emergent macrophytes, no longer held "in check" by flood-drawdown events, to spread rapidly. As a result, distinct vegetation patterns develop decreasing plant species diversity, which Grace and Wetzel (1981) have attributed to competitive species eliminating poorer competitors. Nevertheless, the underlying processes and significance of competitive interactions among emergent species in determining their position along such gradients remains unclear (Shipley et al. 1991, van der Valk 2000).

4.2. Objectives

The principle objective of this study is to examine the effects of long-term water-level stabilization (i.e., absence of disturbance from water level fluctuations) on prairie marsh vegetation. Chapter 3 examined patterns of vegetation change, and development of plant zonation following a stable water-level state. Ecological processes that drive such changes, however, are incompletely understood. Emphasis of this chapter is placed on species' responses to a natural elevation gradient, and processes involved in further shaping these

vegetation patterns. Factors examined are water depth, salinity and the influence of interspecific competition. It is hypothesized that disruption of the natural disturbance regime of a prairie marsh (i.e., flood-drought cycle) will increase competitive interactions among dominant emergent macrophytes. This heightened competition will result in elimination of competitively subdominant species, while consolidating abundance of competitive dominants. Persistence of stable water levels is expected to lead to increasingly distinct vegetation zones over time, as dominant macrophytes competitively “sort themselves out” along the water depth gradient. This study does not attempt to examine factors initially forming vegetation communities or initial zonation patterns, but rather attempts to examine factors involved in long-term persistence of these landscape-level patterns, and the robustness of dominant emergent species during a stabilized regime.

4.3. Study Area

This study was conducted in the Marsh Ecology Research Program (MERP) experimental marshes (10 continuous sand-diked marshes 5-7 ha. each), located in Delta Marsh, situated at the south end of Lake Manitoba, Canada. Historically, water levels in Lake Manitoba and those in the adjoining marsh, fluctuated within a range of 1.7m (**Figure 2.3**). Since 1961, lake levels have been artificially stabilized at a mean level of 247.55 m asl, dampening lake fluctuations to less than 60 cm. Disruption of the natural wet-dry cycle has prevented marsh regeneration, resulting in dense monodominant plant zones of low species and habitat diversity. From 1985-1989, these marshes were subject to 3 different water level regimes (**Table 2.1**). Following 1989, water levels in these marshes were left to equilibrate with the surrounding Delta Marsh, having limited water level fluctuations (i.e., no flood-drought cycle) due to association with the lake. Although 3 marshes were manipulated in the early 1990's, all marshes have been in a range of stable water level states anywhere from 5-12 years (**Table 2.2**). A full description of the study site is in Chapter 2.

4.4. Methods

4.4.1. Aerial Photography, GPS sampling, and GIS Integration

Colour infrared aerial photographs were taken of the 10 experimental and 2 control marshes (11 & 12) of the MERP complex in August 1997, following procedures in Chapter 3. Aerial photos for both 1989 and 1997 were georeferenced utilizing a Trimble Geoexplorer mapping grade GPS unit, Trimble Pathfinder software, and the mapping software MapInfo

following the procedures in Chapter 3. Additionally, UTM (Universal Transverse Mercator – zone 14, North American Datum 83) coordinates were collected with the Trimble GPS unit of 1997 and 1998 sample sites, elevation markers, and sampling transect flags. Approximately 85 and 100% of the 1997 and 1998 sample sites were georeferenced respectively, as well as key areas in and around the study area. These sample sites were overlaid on new (1997) and historical (1989 and 1980) aerial photos to examine long-term vegetation trends and patterns within the MERP marshes.

4.4.2. Vegetation Classification and Mapping

Vegetation of the MERP marshes was categorized into various dominant zones distinguished by water depth (surface water or depth to water-table) and plant community composition, represented by one or more dominant species or species associations. Generally, wetland zones are composed of several species, although usually dominated by one species (van der Valk 1992, Shay et al. 1999). Vegetation classification is based on Grosshans (in press). Vegetation maps for 1989 and 1997 were generated from the georeferenced images utilizing ArcView GIS, following procedures outlined in Chapter 3. Vegetation composition maps for each marsh from 1980 to 1989 are also available from the original MERP study (van der Valk 2000). Existing historical 1980 vegetation boundary maps were scanned using a flatbed scanner, and georeferenced with collected GPS data using the MapInfo software. Vegetation composition maps from all 3 years (newly created 1997 and 1989 maps, as well as preexisting 1980 maps) were used in combination with elevation contour maps and sample site data to examine species-elevation relations within the MERP marshes.

4.4.3. Data collection

Sampling Design

Eleven permanent East-West transects (established in 1980 to divide each marsh into 10 equal zones) were located and reestablished within the MERP marshes from historical survey maps of the MERP area. Each original transect marker stake (located along the dykes on either side of each marsh) was identified with a 3 m high colour coded flag to aid in positioning during sampling. A systematic sampling design was developed to produce a highly equitable distribution of sample points; ideal for pattern determination, gradient analysis and mapping (**Figure 4.2**). Each marsh was sampled along 10 of the East-West

transects (transects 11 were not used because of close proximity to south dykes), with eight 1½ m x 1½ m sample sites established at equal distances along each transect for a total of 80 sites per marsh, and 876 sites total. Each marsh is anywhere from 150-200 m wide, and 250-330 m long. As a result, distances between sample sites along each transect within each marsh varied. In order to accurately locate transects and sample sites on georeferenced infrared images, distances between transects were measured and GPS readings were recorded. UTM coordinates (zone 14, NAD 83) were taken at all sample sites, transect location stakes, relocated survey pins at the south end of each marsh, and the corners of each marsh. Each sample site was located (using MapInfo and ArcView software) on vegetation and elevation contour maps to ultimately determine plant composition and relative elevation (m asl) at each sample site. Additionally, the Manitoba Land Surveys permanent elevation benchmark was relocated (**Figure 4.2**), and new temporary benchmarks located along the north dyke. Water depth gauges in each experimental marsh and the main marsh were resurveyed and calibrated using these elevation benchmarks.

Field Sampling

To prevent influences from surrounding dikes (van der Valk 1994), vegetation within a 10 m area of a dike was excluded from sampling. All sample sites were surveyed with relative distance to adjacent sites and UTM coordinates recorded. The following vegetation and environmental data was collected:

- Each species in the over and understory was recorded indicating which were dominant and which were secondary, to determine species diversity and level of monodominance within vegetation zones.
- Percent cover estimates for each species (as well as open water), calculated as the proportion of the sample site occupied by a given species, was obtained to determine degree of plant dominance. Low cover values were recorded as <5%, 1% or <1 %.
- Deadfall accumulation and dead species composition was recorded at each site. Thickness of the deadfall layer was measured and its density noted.
- Water depth (within sites with standing water), measured down to the vegetation mat, or depth to the water table (sites with no standing water) was measured to the nearest cm at each sample site. Elevation of water level (m asl) was determined from water depth gauges, and this data used in conjunction with available elevation contour maps of the marshes to determine the elevation gradient. Elevation data was used to determine plant species distribution along this gradient.

- Water and/or soil samples were collected at each site dependent on whether the site was above or below water, or if ground water was present. For water, sample bottles were rinsed 3 times within the sample area, before the water sample was taken from the upper 20 cm. For soil, shallow pits were dug at each site and the soil sample taken within the plant-rooting zone (upper 5-20 cm) and stored in Ziploc® bags. All samples were kept in cold storage until processing.
- Salinity, measured as electrical conductivity (μ Siemens), and pH of water and/or soil was measured at each sample site or in the lab.
- Soil pits (60 cm x 60 cm x 60 cm) were dug at representative sites to examine organic layer thickness, and the underlying soil layers and composition.
- 243 of the 876 original sites were revisited in 1998 to confirm consistency in sample site species composition. Additionally, 85 sites were sampled in the experimental marshes along North-South transect routes (as opposed to the East-West transects) to create an independent dataset for proofing the robustness of trends and testing developed models.

Water and Soil Analysis

All water samples were processed within 2 days of collection. All soil samples were oven dried in a large sample drier at a maintained temperature of 30 °C for 1-3 days, and kept in cold storage until processing. In the lab, soil samples were crushed and sifted with a 2 mm sieve to remove large organic debris and soil conglomerates. Slurries were prepared in a 1:4 (40 g: 160 ml) soil to distilled water ratio, 1:5 (20 g: 100 ml) or 1:6 (20 g: 120 ml) if samples were of high organic content. Soil slurries were stirred 4-5 times for 30 minutes, and let stand for 30 minutes. Following the 30-minute settling period, conductivity (μ Siemens) and pH was recorded. Conductivity readings were taken in the field for water samples whenever possible, or from water and soil samples in the lab, using a YSI Model 33 S-C-T meter. Conductivity was used as a measure of salinity in terms of electrical conductance (EC). All pH readings (whether water or soil) were measured in the lab using an Orion Research Ionalyzer, model 407A. Soil analysis methods follow those by Kalra and Maynard (1991).

4.4.4. Data Analysis

Vegetation-Environment Relationships: Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (CCA) was used to quantify relationships between species, sample sites and environmental data (Ter Braak 1987). Specifically, CCA

determines the degree to which the environmental data predicts the variation in vegetation composition. In this study three environmental variables were examined: water depth or depth to water (elevation), pH (soil and/or water), and salinity as electrical conductance (soil and/or water). Emphasis was placed on six main dominant plant zones and open water patches: including the three major dominant emergents, cattail (*Typha* spp.), whitetop (*Scolochloa festucacea*), and giant reed grass (*Phragmites australis*); and low prairie species goldenrod (*Solidago canadensis*), Canada thistle (*Cirsium arvense*), and sow thistle (*Sonchus arvensis*).

Plant Composition Comparisons: physiological response curves

Realized physiological response curves (species realized as opposed to fundamental niche responses) of 1997 mean species percent cover along an elevation gradient (m asl) were produced for each of the six dominant macrophytes and open water in the 10 experimental and control marsh 11. These response curves were created by plotting mean species percent cover against mean elevation within the MERP marshes, and fitted using lowess curves. Only dominant species were examined, the remaining species and vegetation zones were omitted because of their low abundance within these marshes. Salinity profiles over the elevation range were also produced and compared to species' distributions by plotting mean salinity against mean elevation.

In addition to the response curves of 1997 mean percent cover, dominance response curves (representing proportional dominance along the elevation gradient) were produced for 1989, 1997, as well as 1980. These were used to examine the long-term effects of stable water-levels on dominant plant population distributions. These curves represent the proportion of sample sites any given species dominates within a mean elevation range. To determine whether a species was dominant, georeferenced sample site locations were overlaid onto 1989, 1997 and 1980 vegetation maps using the MapInfo software. The dominant species at each site was recorded for each year utilizing either: current vegetation data for 1997, or vegetation maps available from the MERP study (van der Valk 2000) and detailed unpublished vegetation composition maps (van der Valk unpubl. maps) for 1989 and 1980. This dominance data was converted to proportions and plotted against mean elevation, fitted using lowess curves.

Modelling the Spatio-Temporal Dynamics of Competing Populations

Vegetation, environmental and elevation data collected from the experimental marshes during 1997 were used to develop a model, termed the Prairie Marsh Stabilized Regime model, which represents a prairie marsh existing under a stabilized regime. This competition-based habitat dynamics model determines the significance of environmental tolerances and competition in shaping dominant plant distributions along a complex elevation gradient in a marsh subject to prolonged water level stabilization. This model places species within a grid of increasing salinity and increasing elevation (m asl), based on salinity and elevation range data of dominant species/vegetation zones, response curves of respective vegetation zones and Canonical Correspondence Analysis. An independently collected data set from 1998 was used to verify the assumptions of this model.

The significance of competitive influences in shaping marsh zonation patterns was further demonstrated with the GRADEX simulation model from Czarán (1989). This cell automaton model uses Monte-Carlo simulation to describe the spatial-temporal dynamics of coexistence between competing plant populations along an environmental gradient (Czarán 1992). This model utilizes Lotka-Volterra type competition principles to calculate how these competing organisms might change in population size as a function of time and population sizes of their competitors (Czarán 1989, Keddy 1989). In its present version, the model only handles two populations, but it can be used to represent multi-species situations as well. The representative area of the model consists of a rectangular grid of cells, which represent small topographical locations where the species can potentially occupy. The model uses competition responses of species along an environmental gradient (in this case elevation), and calculates species interactions within each cell over discrete units of time.

In the GRADEX model, response curves are bell-shaped (i.e. normal curves) and are defined by the distance (d) between optimum points of these curves (i.e. maximum competitive strength), and a species dependent parameter specifying the steepness of each curve, or standard deviation (s), for each population (Czarán 1992) (**Figure 4.3**). In this case, response curves for the model were fitted from 1997 species' realized responses along the elevation gradient while remaining parameters are typical of competing species (Czarán 1992) (**Figure 4.4**).

The grid area of the model consists arbitrarily of 52 columns. Optimum points of the response curves M_1 and M_2 are therefore \bullet $d/2$ sites away from the central column of 26 (Figure 4.3). Therefore:

$$M_1 = 26 - d/2, \text{ and } M_2 = 26 + d/2$$

Towards the suboptimal states, the realized competitive ability of the respective species will decrease proportionally according to the steepness of the curves (Figure 4.3). This model is fully detailed in Czarán (1989), with a technical summary in Czarán (1992).

4.5. Results

4.5.1. Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) ordinations for each of the 3 treatment groups were almost identical to CCA ordinations for all experimental marshes combined (excluding marshes 2,4 and 5) (Figure 4.5a). The ordination indicates elevation to be highly correlated with axis 1 ($r = 0.860$), while salinity is correlated with ordination axis 2 ($r = 0.510$). The placement of pH near the origin and its low correlation to either axes ($r = -0.172$, $r = 0.182$ respectively) suggests it is not significant (Figure 4.5a), at least not for the ranges of pH variability in Delta Marsh. Clear separation of species and sample sites occur along axis 1 (interpreted as a complex elevation gradient) indicating plant community composition is a good indicator of site conditions. Accordingly, dominant species characteristic of deep flooded areas such as submersed aquatics, cattail (*Typha* spp.), and bulrush (*Scirpus* spp.) occur on the left side of the ordination, whereas low prairie species occurring in dry upland areas, such as Canada goldenrod (*Solidago canadensis*), thistles (*Cirsium arvense*, *Sonchus arvensis*), and various mints occur on the right side of the ordination. Species inhabiting waterlogged or shallow water conditions occur towards the middle of the ordination. Further separation of sites and species occurs along axis 2, suggesting salinity influences plant distribution within the marsh as well. Saline species such as orache (*Atriplex patula*) and sea-blite (*Suaeda calceoliformis*), occur near the top of the ordination where higher saline sites are located near the soil water transition. Separation of the dominants whitetop and *Phragmites* is also evident along axis 2.

A CCA ordination of sites dominated by the dominant emergents cattail, whitetop and *Phragmites*, confirms suspected trends (Figure 4.5b). Elevation and salinity are again highly

correlated with axes 1 and 2 respectively ($r = 0.720$, $r = 0.434$). These 3 species are sorted along both axes with cattail-dominated sites at the wettest end and whitetop and *Phragmites*-dominated sites towards the drier end. As well, *Phragmites* and whitetop-dominated sites occur at opposite ends of the salinity gradient, suggesting water depth and salinity both influence plant distributions. This triangular shaped CCA ordination illustrates the transitional areas that exist between species, i.e. cattail-whitetop, whitetop- *Phragmites*, *Phragmites* -cattail. The few sample sites having mixed communities of all three occur in the interior of the triangle. Similar to a soil composition triangle for sand, silt and clay, knowing the abundance of two, the relative abundance of the third can be determined.

A CA ordination of sites dominated by cattail, whitetop and *Phragmites* in marsh 11 (Figure 4.6) is similar to the CCA ordination of these species in the experimental marshes (Figure 4.5b). Both ordinations are triangular shaped with sites dominated by the respective species at one of three corners. Unlike the experimental marshes, however, transition sites between cattail and whitetop are absent in marsh 11 (Figure 4.6).

4.5.2. 1997 species zonation along the elevation gradient

The elevation range of the MERP marshes covers 247.0-248.2 m asl, with the majority of this area flooded to waterlogged at or below 247.8 m asl (Figure 4.7). Mean elevations (m asl), pH, and associated mean conductivities (μS) and mean dominant species percent cover is summarized in Table 4.1, with species elevation ranges in Table 4.2. Habitat response curves (representing ranges of the elevation gradient species inhabit) of the 6 dominant plant species and open water of the MERP marshes (excluding marshes 2,4 and 5) were produced by plotting mean percent cover against elevation (Figures 4.8a). Although subject to three different water level regimes from 1985-1989 [medium: 30cm above (247.8 m asl), high: 60 cm above (248.10 m asl) normal of 247.5 m asl] (Table 2.1), similar elevation responses from the dominant species occurred, forming very distinct habitat ranges. Cattail inhabits flooded areas at 247.0 m asl (247.55 m asl present water level), with greatest abundance near 247.5 m asl, declining dramatically towards uplands to 247.8 m asl (Figure 4.8a). This elevation range covers up to 90% of the entire MERP area, providing cattail a substantial habitat range (Figure 4.7). Whitetop increases dramatically within this range, inhabiting 247.4 to 247.7 m asl, with a steady decline in abundance up to 248.1 m asl. Corresponding to where whitetop abundance decreases (247.8 m asl) *Phragmites* abundance increases. This robust marsh reed inhabits areas anywhere from 247.4 to 248.5 m asl, although primarily

inhabiting areas between 247.8 to 248.2 m asl. Low prairie species occur above 247.8 m asl (**Figure 4.8a**).

Elevation response curves were also produced for control marsh 11 (**Figure 4.9a**). Again, cattail is restricted to deeper water depths with no more than 35% average cover. *Phragmites* abundance occurs in two definite peaks, from 247.6 to 247.7, and again at 248.00 m asl. The highest average increase in whitetop abundance corresponds with this dramatic trough in *Phragmites* abundance, which decreases dramatically at 247.8 m asl, restricting whitetop to a narrow water depth region. Almost no transition region occurs between zones of whitetop and cattail, concurring with the CA ordination from marsh 11 (**Figure 4.6**). Of note, the lower elevation range of *Phragmites* (247.7 m asl) corresponds with a small peak consistently found near this elevation range within the experimental marshes (247.6 m asl, **Figure 4.8a**).

Ultimately, the habitat ranges of the dominant plant species within the MERP experimental marshes produce distinct zonation patterns along the water depth gradient, directly associated with the underlying elevation gradient. These vegetation zones progress from open water with submersed aquatics (eg. *Potamogeton pectinatus*) bordered by the emergent macrophytes cattail (*Typha* spp.) and bulrush (*Scirpus* spp.) at lower permanently flooded elevations, through giant reed grass (*Phragmites australis*), whitetop (*Scolochloa festucacea*), sedges and rushes (*Carex* spp., *Juncus* spp and *Eleocharis* spp.), at seasonally flooded elevations to low prairie grasses and forbs finally surrounded by *Phragmites* grass and willows along the dykes (**Figure 1.2b**). This progression follows a decreasing elevation-moisture gradient proceeding further away from the open water.

4.5.3. Salinity, Elevation and Species Relations

Examining salinity conditions along the elevation gradient, the highest mean salinity levels (3500 to 4800 μS) occur between 247.6 to 247.85 m asl (**Figure 4.8b**), 10 cm above the current mean water level of these marshes and typical of where salinity can accumulate. This elevation range corresponds directly with the pinnacle of whitetop abundance and the corresponding decrease in cattail abundance. Furthermore, it is also not until after salinity levels drop (3500 μS) that *Phragmites* abundance increases (**Figure 4.8a**). This is also true in marsh 11, where the highest mean conductivity levels (5000 to 7500 μS) again correspond directly with a peak in whitetop and a drop in *Phragmites* abundance (**Figure 4.9**). The lower elevation range of *Phragmites* evident in all marshes develops at the soil water

transition where salinity levels appear to be low, while the trough in *Phragmites* abundance occurs above the soil water interface where salinity levels are typically higher, suggesting salinity could be affecting long-term vegetation patterns.

Species response to salinity

Evidence from the CCA plots indicates whitetop dominated areas fall within the higher salinity higher elevation range, *Phragmites* in low salinity high elevation, and cattail lower salinity low elevation (**Figures 4.5, 4.6**). Species proportional dominance (50% + cover indicates species dominance) along a salinity gradient (**Figure 4.10**) confirms *Phragmites* typically does not dominate areas of higher salinity within the MERP marshes, dropping in abundance at 2000 μS , and decreasing in dominance with increased salt levels. Cattail is fairly salt tolerant dominating within moderate to high saline areas. Whitetop dominance clearly increases with increased salinity, suggesting whitetop is much more salt tolerant, dominating these higher saline areas.

Expressing 1997 elevation response curves as mean salinity rather than mean percent cover, determines mean salinity of areas dominated along the elevation range by the respective dominant macrophytes (**Figure 4.11**). This confirms whitetop-dominated areas examined in the elevation response curves consistently have the highest salinity levels (**Figure 4.11**), averaging up to 6500 μS (**Table 4.2**), whereas Cattail and *Phragmites*-dominated areas average up to 4500 μS and 2800 μS respectively. A fair amount of overlap does occur in the 247.6 to 248.0 m asl range, due to local slope variations in the landscape. Nevertheless, these data indicate where *Phragmites* does occur within this elevation range, these areas consistently on average have lower salinity levels, while whitetop dominated areas within this range have the highest salinity levels (**Figure 4.11**).

Dominant species mean height

Height was used as a measure of biomass and species performance along the elevation gradient. Mean plant height was measured for cattail, whitetop and *Phragmites* within areas dominated by these respective species (**Figure 4.12**). Cattail performs quite well in areas dominated by its own, as well as in upland areas dominated by *Phragmites*. F-tests indicate on average cattail grows slightly shorter in whitetop-dominated areas ($p = 0.0018$). Whitetop mean height, however, is not statistically different ($p = 0.0557$), and is consistently similar in height throughout its habitat range. *Phragmites* grows quite well in waterlogged regions it

dominates as well as in flooded cattail-dominated areas. Within whitetop-dominated areas, however, the mean height of *Phragmites* plants is considerably shorter ($p = < 0.0001$). As previously discussed, these areas are where salinity levels are on average higher, suggesting salinity is inhibiting *Phragmites* growth and not water depth.

4.5.4. Long-term changes in plant zonation patterns with water-level stabilization

Stabilization from 1989 to 1997

Infrared photos (**Figure 3.2**) and vegetation maps (**Figure 3.1**) from 1989 and 1997 show dramatic changes in the vegetation community with a substantial increase in the amount of cattail cover and a corresponding decrease in open water. Total number of sample sites ($n = 555$) dominated by respective species during 1989, 1997 and 1980 is illustrated in **Figure 4.13**. Proportional dominance of species in 1989 and 1997 is illustrated as elevation response curves for the treatment groups and all marshes combined (excluding marshes 2,4 and 5) in **Figures 4.14a-c** and **d** respectively, with frequency of species present within elevation ranges summarized in **Table 4.3**. As a consequence of the changing water level regime, elevation along the X-axis was a constant that could be compared between years, representing the global effects of the water depth gradient. In each treatment group during 1989 and 1997, species are sorted along the elevation gradient according to tolerance to water depth: cattail in deeper water habitats, whitetop at the soil water transition, *Phragmites* higher upslope, and grasses and forbs upland (**Figures 4.14a-d**). Marshes 6 and 10, which were flooded higher than normal until 1989 (high: 60 cm above normal of 247.5 m asl) experienced a slight shift of species downslope up to 1997 as water levels receded (**Figures 4.14a**), as did the medium treatment marshes 1 and 9 (medium: 30 cm above normal of 247.5 m asl) to a lesser extent (**Figures 4.14b**). Dominance ranges of species in marshes 3, 7, and 8 (mean water level of 247.5 m asl since 1985) are already fairly segregated in 1989 (**Figures 4.14c**), with *Phragmites*' lower habitat range more prominent in these marshes in 1989 and 1997.

Combining all marshes (**Figure 4.14d**), species had a fairly wide overlapping distribution along the elevation gradient during 1989, due in part to the water level treatments. Regardless of water levels experienced in 1989, similar global changes are evident in all marshes demonstrating robustness of vegetation trends. MERP marshes in 1989 consist of almost 60% open water in areas up to 247.6 m asl, representing some 70% of the total MERP area (**Figure 4.6**), with cattail dominating flooded areas from 247.0 to 248.0 m asl (**Figure**

4.14d), the higher range a result of high treatment marshes 6 and 10 (Figure 4.14a). *Phragmites* dominates primarily above 247.7 m asl, as well as 5% of areas at its lower range near 247.4-247.5 m asl. Whitetop dominates primarily from 247.4 to 247.9 m asl in 1989, with peripheral higher and lower ranges as a result of treatment level (Figure 4.14a,b and c). Following stabilization up to 1997, species dominance elevation ranges narrowed to similar ranges in all marshes regardless of past water level regime. Most dramatic is a substantial increase in cattail and corresponding decrease in open water cover within all marshes (Figure 4.14a-d). Cattail now dominates a high proportion of area from 247.0 to 247.7 m asl, while open water occurs below 247.5 m asl (Figure 4.14d). *Phragmites* now persists more in uplands above 247.8 m asl, while still persisting near the current water level of 247.5 m asl (Figure 4.14d). Whitetop has narrowed its range along the gradient by 1997 in all marshes regardless of past water level regime (Figure 4.14a-d). Peripheral higher and lower ranges in 1989 have disappeared by 1997, restricted to a range above the soil-water transition between cattail and *Phragmites*. This range, which also corresponds to a trough in *Phragmites* abundance, corresponds to the range of highest salinity. At the peripheral ranges, flooded bulrush areas from 1989 have almost disappeared persisting only near open water borders at 247.5 m asl while upland low prairie species are narrowed to a range above 247.9 m asl (Figure 4.14d). Ultimately, species habitat ranges have narrowed while subject to the long-term stable water-level regime.

1980 response curves

Similar species dominance along the elevation gradient existed in 1980 (Figure 4.15) as occurs in 1997 (Figure 4.14d). Following almost 20 years of stabilized water levels in 1980 (since 1961 stabilization of the lake and adjoining Delta Marsh) species were distinctly segregated along the elevation gradient, with definite zonation from open water, bulrush, cattail, whitetop, *Phragmites*, to grasses/forbs. Cattail dominated the flooded areas, *Phragmites* dominated uplands, while whitetop was restricted to a region above the soil water transition (247.60-247.80 m asl, 0.10 to -0.10 m water depth). *Phragmites*' lower elevation range at the soil-water interface (present in all 1997 marshes) corresponds with a much larger peak in 1980, which has a greater degree of overlap with whitetop. Marsh 11 (Figure 4.8), stabilized with the rest of Delta Marsh since 1961, presently exhibits these similar vegetation patterns as the MERP marshes did in 1980 (Figure 4.15).

4.5.5. The GRADEX model - modelling the dynamics of competing populations

In utilizing the GRADEX model to examine the coexistence of cattail and *Phragmites* (the two dominant species of the MERP marshes), elevation response curves for these two species were fitted utilizing the program NORMAL (Kenkel unpubl.) from their 1997 realized responses along the elevation gradient (Figure 4.4). The grid area of the GRADEX model consists arbitrarily of 52 columns, which places these curves 40 columns apart. The optimum points, therefore, of the cattail and *Phragmites* response curves M_1 (cattail) and M_2 (*Phragmites*) are $\pm d/2$ sites away from the central column of 26 (Figure 4.4). Therefore:

$$\begin{array}{lcl} M_1 = 26 - 40/2 & & M_2 = 26 + 40/2 \\ = 6 & \text{and,} & = 46 \end{array}$$

A species dependent parameter specifying the steepness of each curve, or standard deviation (s), for each population was calculated by the GRADEX program to be a value of 12, calculated from the steepness of the fitted 1997 response curves. Since the present study did not directly examine the remaining parameters used with the model, parameters were used which are typical of competing species as determined by Czarán (1992) (Figure 4.4).

4.6. Discussion

4.6.1. Current Plant Composition in the Stabilized Regime.

Within the stabilized regime of the MERP marshes, extremely dense homogenous vegetation zones have developed, with little to no species diversity. No longer suppressed by fluctuating water levels, cattail and *Phragmites* grew uninhibited to produce dense monodominant stands with heavy deadfall accumulations. In 1997, these stands often contained so much deadfall that few other understory species (eg. mints; stinging nettle, *Urtica dioica*; or thistles, *Cirsium arvense*, *Sonchus arvensis*) occurred. Deadfall accumulation and monodominance in MERP control marsh 11 was even higher than the experimental marshes, with often more deadfall than live standing crop. Day et al. (1988), also found a decrease in species richness with increased standing crop and litter accumulation. Additionally, in the absence of fluctuating water levels wet meadow and low prairie areas no longer receive inundations of water. Consequently, previously whitetop patches are converting to low prairie vegetation, while large herbaceous forbs, such as Canada goldenrod and thistle, continue to overgrow low prairies. This dense vegetation

ingrowth that occurs during a stabilized regime would not occur to such an extent in a naturally fluctuating marsh environment where high and low water periods effectively knock vegetation back, maintaining open vegetation stands and species diversity.

Marsh level stabilization also has an effect on plant decomposition, and the build up of organic matter and sediment in a marsh system (van der Valk and Davis 1978, Wrubleski et al. 1997). Soils in flooded and waterlogged areas of the MERP marshes are poorly drained layers of organic muck and peat overlying a high content of silt and sand. These soil layers vary in thickness between and within vegetation zones and communities dependent on organic matter buildup. Organic layers within cattail and whitetop communities (10.0-20.0 cm thick), for example, are on average 2-3 times thicker than those within *Phragmites* communities (3.0-12.0 cm thick). As a result of long term stabilization for the past 36 years, organic matter layers in *Phragmites* patches of control marsh 11 are extremely thin, averaging only 6.0 cm in thickness above silt and sand layers. In the absence of fluctuating water levels in these marshes, deadfall builds up and organic matter does not accumulate.

The three MERP marshes managed early in the 1990's (marshes 2,4 and 5; water levels drawdown, vegetation cut and/or burned, then reflooded to normal levels) can be considered the youngest marshes in the MERP succession, in essence being stabilized for only five years. These marshes have not overgrown to the extent of the other experimental marshes, and possess more open patchy areas of vegetation cover, intermixed areas of open water, and submersed aquatics. As a result they offer much more suitable waterfowl habitat and consequently contain greater numbers of waterfowl than those marshes untouched since 1989. These marshes also contain greater numbers of understory species of mints, stinging nettle, and thistles, as well as open areas dominated by bulrush, whitetop and *Phragmites*, which could eventually be invaded by cattail.

4.6.2. Habitat Changes with Prolonged Periods of Stabilized Water Levels.

No boundaries, a return to stabilization: 1989 to 1997

Prior to 1989 stabilization, all of the MERP marshes experienced an initial flooding and drawdown between 1981 and 1985 to reset all marshes to the same condition (Murkin et al. 2000). Following this all 10 marshes were reflooded to 3 different randomly assigned treatment water levels (normal, medium 30cm above normal, and high 60 cm above normal, Table 2.1), maintained and monitored for the next 5 years (1985-1989). With the onset of

1989 stabilization at levels comparable to the surrounding Delta Marsh, each marsh contained a significant amount of open water. Vegetation zones at this time would have been much more open and diverse than in 1997 (van der Valk et al. 1994), possessing some species overlap as they began sorting themselves along the water depth gradient (**Figure 4.16a**). Despite being flooded, species persisted within their global elevation range in water depths deeper than they would normally be found (Squires and van der Valk 1992), residual from where highest concentration of plants would have been present following drawdown (van der Valk et al. (2000). Van der Valk et al. (1994) found there to be a lag time of species movement following initial flooding in 1985, and that these species did not dramatically migrate upslope. Sessile organisms such as these marsh emergents typically show a 3-year lag time in their response to a new water level (Miller 1973, van der Valk and Davis 1980, van der Valk and Squires 1992, van der Valk et al. 1994, van der Valk 2000). These robust marsh emergents are very resilient, and once established it takes a long time for them to be eradicated from an area.

Due in part to the three different water-level treatment groups, species had a wider elevation range in 1989. Dominant species arranged themselves at a different elevation range globally, although arranging themselves locally at similar water depths. Whitetop, for example, is typically found near the soil-water interface, occurring within this region in both 1989 and 1997 bordered on either side by cattail and *Phragmites*. Following 8-years of stabilized water levels from 1989 to 1997, dominant species continued to “sort-themselves-out” along the water depth gradient narrowing their habitat range (**Figure 4.16b**). Although globally different in 1989, resultant vegetation patterns in 1997 end up the same in all marshes. Typically, this was not a case of cattail or *Phragmites* moving down the water depth gradient to invade previously other species-dominated areas. Rather, local environmental conditions changed enough after 1989 to favour these two dominants, allowing their abundance to increase substantially. In 1997, cattail and *Phragmites* continue to dominate flooded and upslope water-logged areas respectively, while whitetop is restricted to an area between them. In any case, all 7 treatment marshes in 1997 have migrated to the same final vegetation pattern, indicating the robustness of these vegetation trends.

Consistent within all treatment marshes in 1997 was the development of the secondary elevation range peak in *Phragmites* near the soil-water interface. It never completely occupies but can persist within this water-depth range (**Figure 4.16b**). This seems to occur within a stable regime, where there is an absence of water level fluctuations to knock *Phragmites* growth back. Without these disturbances *Phragmites* abundance within this

habitat range increases with prolonged water level stability. This lower range was also evident in 1980 and control marsh 11, where a much larger peak has expanded to encompass whitetop's habitat range. de Swart et al. (1994) and van der Valk (2000), who also examined 1980 distribution of emergent species within the MERP experimental marshes, found this distinct secondary peak in *Phragmites* abundance as well. Greater overlap of *Phragmites* and whitetop at this range occurs in 1980 due in part to local variations within the landscape (local conditions more favorable to either species), as well as restricting data to a 2-dimensional plot (i.e. constraining multivariate elevation gradient to a 2-axis chart). In any event, the smaller dominance range of *Phragmites* in 1997 within this lower range could eventually expand to the same extent in control marsh 11 and MERP marshes of 1980.

In accordance with the lower peak in the habitat range of *Phragmites* is a corresponding decrease in *Phragmites* dominance within the 247.6 to 247.8 m asl elevation range. This range corresponds with the region where whitetop is dominant, and where soil salinity levels are typically highest. Persistent water levels allow for the accumulation of salts near the soil-water transition, where surface evaporation leaves rising salts behind (Brady 1990). Without fluctuating water levels to effectively flush away these dissolved salts (Neill 1993), salinity levels build up and persist. Lissner and Schierup (1997) and Lissner et al. (1999) have found salt tolerance to vary in *Phragmites* due to clonal variations. Salinity responses from this study suggest the Delta Marsh clonal variety of *Phragmites* has a low salt tolerance. Conceivably, high salinity could be affecting its growth, simultaneously aiding whitetop from being completely excluded from these marsh habitats (**Figure 4.16b**). Modeling by de Swart et al. (1994) and van der Valk (2000) supports this suggesting water depth alone may not be sufficient to predict the distribution of whitetop, implying other environmental factors might affect its distribution. Salinity appears to become a significant factor during prolonged periods of water level stability.

A window to the Future: Comparison to 1980 Vegetation Communities

Based on current conditions of control marsh 11 and past 1980 plant communities, the vegetation stands of the MERP marshes will continue to become overgrown within the stabilized regime (**Figure 4.16c**). Following almost 20 years of stabilization in 1980, distinct species segregation occurs; cattail and *Phragmites* almost completely dominate flooded and water-logged areas respectively, while whitetop is really restricted to the range of highest salinities near the soil-water interface. As well, the lower secondary range in *Phragmites* dominance has continued to persist and expand below the soil-water interface, a region where

salt levels are lower than those slightly upslope. This suggests *Phragmites* is able to take advantage of these low saline areas, moving into this habitat range (Figure 4.16c).

In comparison between 1980 (Figure 4.15) and 1997 (Figure 4.14d) species responses along the elevation gradient in the MERP marshes, the 1997 vegetation community has almost reached a similar stage as in 1980. A significant difference, however, is that there was a substantial amount of bulrush present in 1980 (its niche in the deeper range between open water and cattail), which is absent in 1997. The elevation responses of the dominant species confirm trends shown in chapter 3. Cattail, for example, expanded to encompass the range once inhabited by bulrush. This expansion observed by Grosshans (in press) in the whole of Delta Marsh, was attributed to the dramatic increase in the abundance of hybrid cattail, *T. x glauca*, as well as nutrient enrichment of the marsh from agricultural runoff. Also confirmed from chapter 3 is that with prolonged stabilization previously whitetop-dominated meadows have indeed been slowly invaded by *Phragmites* and grasses/forbs in the range at the soil water interface, and slightly upslope respectively. In 1997 whitetop still inhabited previously *Phragmites*-dominated as well as low prairie areas from 1980, areas which could still be lost to these species as stabilization of water levels persist.

4.6.3. The Underlying Processes

Water depth is considered the primary determinant of plant zonation patterns in prairie marshes, during both a natural disturbance regime and periods of water level stability (Stewart and Kantrud 1972, Spence 1982). Nevertheless, Day et al. (1988) expressed that water depth is only one part of the complex gradient of elevation, which combines a series of physical factors ultimately affecting plant position in a prairie marsh. This study confirms that secondary factors further affect the exact position of plant species along this gradient, one factor of which is salinity. Nevertheless, although the influence of such factors is evident, the exact mechanisms involved in affecting plant zonation are often unclear (Shipley and Keddy 1987). The influence of competitive mechanisms in shaping plant distribution patterns in wetlands has been supported (Harris and Marshall 1963, Weller and Spatcher 1965, Grace and Wetzel 1981, van der Valk 1981, Keddy 1983, Snow and Vince 1984, Wilson and Keddy 1986b, Shipley et al. 1991, Kenkel 1992, van der Valk 2000) suggesting the habitat ranges of the dominant MERP species may be reduced when grown in the presence of one another. Typically in natural systems, sessile plant species compete for available space (Keddy 1989), and those more tolerant of an area's environmental conditions will persist. Whether subsequent interactions among these species (i.e., competition)

eventually will decrease or eliminate initial establishment differences, however, is often unclear (Shiple et al. 1991, van der Valk 2000). Evidence from the present study is supported by Grace and Wetzel (1981), who suggest competition among emergent species helps determine their position along a water-depth gradient.

4.6.4. Competition evidence within the MERP marshes

Resource partitioning models are often used to explain stable coexistence within plant communities, being less important in communities exposed to recurrent periods of disturbance (Keddy 1989). Resource response patterns of the dominant macrophytes from the present study show the arrangement of species along a natural elevation-moisture gradient, with evidence from their coexistence suggesting there could indeed be competition occurring. Whitetop, for example, appears to be outcompeted on either side from cattail and *Phragmites*, while at the same time excluding them from its own habitat range above the soil-water transition.

Flood tolerance: Man the life boats, they might be drowning!

Results from this study agree with the competitive hierarchy model, which states resource use patterns develop as a consequence of interspecific interactions (Wisheu and Keddy 1992). Essentially, if competition is indeed occurring then fundamental niches of species are wider than realized niches, narrowed as a direct result of competitive interactions for resources or space. In experimental trials Squires and van der Valk (1992) demonstrated the dominant macrophytes in Delta Marsh do in fact have wider fundamental niches than realized niches. They determined the water depth distribution ranges of these species overlapped more when grown in monoculture than when found in the marsh, and were capable of inhabiting a wide habitat range along the water depth gradient without the presence of neighbour species. In comparison, these fundamental ranges were wider than those determined from the present study (**Figures 4.14d**). In addition, Smith (1972) found whitetop in uplands (water table to 0.5 m) to flooded areas 1.5 m deep, while Grace and Wetzel (1981) found cattail in waterlogged (water table to 0.15 m) to flooded areas 2 m deep. Grace and Wetzel (1981) also determined that species had a wider fundamental niche than their realized niche, and attributed this to competition actively influencing habitat ranges and zonation patterns. Pederson (1981) adds further evidence to support the influence of competition from the seed bank of Delta Marsh. Seeds typically accumulate along the elevation gradient where species are normally found (van der Valk and Welling 1988), and

Pederson (1981) found dominant species located in a wide range along the gradient. van der Valk and Welling (1988) also found the initial population emerging in the MERP marshes after drought also showed these wide patterns along the landscape and then narrowed sorting themselves along the water depth gradient following flooding.

These studies all provide evidence to support the influence of interspecific competition in shaping vegetation communities during the prolonged stabilized water-level period of the MERP marshes. This suggests water depth ranges of the dominant species are suppressed when grown in the presence of one another. Fundamentally, cattail, *Phragmites*, and whitetop all have some overlapping habitat, suggesting their habitat ranges in the MERP marshes are narrowed by competitive interactions. Additionally, competitive tolerances to additional environmental stresses, such as salinity buildup, brought about during the stabilized regime may affect species locations as well.

Salinity, an underestimated long-term influence?

Many experimental studies have described the combined causal influences of physiological tolerances and interspecific competition on plant zonation in various ecosystems (Reader and Best 1989, Sharitz and McCormick 1973, Grace and Wetzel 1981, Wilson and Keddy 1985, 1986, Wilson and Tilman 1991), more specifically the combined influences of salt tolerance and competition (Barbour 1978, Snow and Vince 1984, Badger and Unger 1990, Kenkel et al. 1991). Kenkel et al. (1991), for example, showed that greater salt-tolerant species grown in monoculture perform better at the lower end of the salinity gradient, and are only excluded from lower and restricted to higher saline areas due to competitive exclusion. These species shift to the higher end of the gradient as a result of being suppressed by more competitive species at the lower end (Kenkel et al. 1991, Snow and Vince 1984), suggesting they are facultative rather than obligate halophytes (Kenkel et al. 1991, Glenn 1995).

The present study indicates that in the absence of flood inundations during the stable water level regime of the MERP marshes, salinity indeed appears to have significantly influenced plant distribution patterns in these prairie wetlands. Salinity typically remains highest near the soil-water transition (-5 to -10 cm depth to water table range) and under the stable water level regime of the MERP marshes salts have accumulated and persisted. As previously discussed, this range of higher salinity along the elevation gradient corresponds to where whitetop abundance is high and *Phragmites* abundance is low, inhabiting ranges on either side of whitetop away from the influence of salinity. Neckles et al. (1985) describes

whitetop as comparatively salt tolerant to cattail and *Phragmites*, inhabiting flooded and waterlogged saline soils of up to 14 700 μS . Cattail's deep-water preference in the MERP marshes provides it with mainly freshwater habitats, although also inhabiting saline waters of up to 9000 μS . This is supported by Glenn (1995) who found cattail in waters up to 8500 μS . Like cattail, *Phragmites* prefers freshwaters in the MERP marshes, although also found dominating saline areas when in the absence of competition with whitetop. Shay and Shay (1986) have also found it quite salt tolerant for the moderate salinity levels found across prairie marshes, although not as tolerant or competitive as reported in coastal salt marshes of the southeastern US (Rice et al. 2000). Lissner and Schierup (1997) and Lissner et al. (1999) indicate the variation in *Phragmites* salt tolerance and competitive ability is related to its clonal variety, with the clone at Delta Marsh described as a fairly noncompetitive variety (J. Lissner pers. comm.).

Evidence indicates that within the stable water level regime of the MERP marshes, salinity appears to be aiding whitetop from being completely excluded from these marshes, aiding its competitive dominance over *Phragmites* and cattail. Height was used as a measure of biomass, and how successful these species are performing (Waters and Shay 1990) and can be used as a measure of competitive ability within these habitats. The negative effects on *Phragmites* growth within whitetop-dominated areas regardless of salinity levels suggest competition is occurring between these species. Whitetop is dominant in relatively high saline areas of the MERP marshes not because it is physiologically adapted to grow better at these extremes (Neill 1993), nor because it is the only species that can survive there (Glenn 1995) (suggesting competition would not occur for this space). Rather, its salt tolerance combined with its preference for this water depth range make it a better competitor for this habitat during prolonged periods of water-level stability. It is often suggested that there is a physiological tradeoff between environmental tolerance and competitive ability (Kenkel et al. 1991), and that species having higher tolerance to extreme levels are usually less competitive at moderate levels. Whitetop may be less competitive at the lower end, but is much more tolerant of the higher end of the salinity gradient. Conversely, *Phragmites* sacrifices salt-tolerance in exchange for higher competitive ability in lower saline areas. Although this study does not directly examine interspecific competition, effects from its influence are consistent with results from competitive studies (Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1985, 1986, Reader and Best 1989, Badger and Unger 1990, Kenkel et al. 1991, Wisheu and Keddy 1992).

Marsh 11 evidence for competition

MERP control marsh 11 has been in a stable water level state for almost 40 years, and in the absence of fluctuating water levels macrophyte species have experienced increasing competitive interactions. The cattail-whiteweed transition range present in the treatment marshes (Figures 4.5, 4.7) has all but disappeared in marsh 11 (Figures 4.5, 4.8a). Within this range *Phragmites* has dramatically increased in abundance, competitively restricting whiteweed to a very narrow region of water depth. Like cattail, *Phragmites* is less competitive during natural water level fluctuations where changes in water depth controls its vegetative spread. They are both excellent competitors, however, in the absence of water level fluctuations and rapidly spread by vegetative clonal growth (Cross and Fleming 1989). Within lower saline areas near the soil-water transition, *Phragmites* has slowly invaded this range to ultimately exclude whiteweed, while restricting it to higher saline habitats. Whiteweed cannot be eliminated from this system, however, due to its greater competitive ability in saline areas. Invasion of this range is evident throughout the experimental marshes, suggesting the cattail-whiteweed transition will disappear with prolonged stabilization.

4.6.5. Fluctuating vs. a Stabilized Regime - Modeling Marsh Dynamics

From Disturbance to Competition: A paradigm shift

Evidence indicates that the degree in water level fluctuations affects the relative competitive ability of the three main dominants, cattail, whiteweed, and *Phragmites*, along the elevation gradient (Figure 4.17a). As previously described, cattail and *Phragmites* are less competitive during natural water level fluctuations where changes in water depth controls their vegetative spread (Cross and Fleming 1989). With fluctuating levels, environmental conditions in an area change from season to season, and so no one species is favoured. In year 1 we may have flooding conditions in a given area A where environmental conditions favour cattail growth, while this same area A in year 2 may experience dry conditions favouring *Phragmites* growth (Figure 4.17a). In this cyclical disturbance driven environment, considerable changes in vegetation composition occur as these water levels fluctuate (i.e. high species turnover), resulting in considerable species overlap, high species diversity, and high habitat complexity (Figure 4.18a). This is primarily a result of physiological tolerances (i.e. water depth), as well as stochastic effects (i.e. the seed bank). Accordingly, seed reserves play a critical role in the initial formation and perpetuation of prairie marsh zonation patterns. Ultimately, these flood drought disturbances are essential to

maintaining habitat diversity of prairie marshes (Weller and Spatcher 1965; van der Valk and Davis 1976b, 1978; van der Valk 1981; Pederson and van der Valk 1984; Kenkel 1992; Bornette and Amoros 1996).

Conversely, with prolonged water level stabilization environmental conditions in a given area remain the same from year to year, allowing competitive species to persist and dominate (**Figure 4.17b**). With minor water level fluctuations not enough to cause major vegetation changes, area A, for example, will remain dominated by whitetop, while in permanently flooded and drier areas cattail and *Phragmites* will persist respectively. Grace (1987) found that the initial seed density between competing species strongly influenced the early outcome of competition. In the stable-state environment vegetative spread and competitive displacement by cattail and *Phragmites* have overcome these initial effects of spatial and temporal preemption (Grace 1987) to ultimately exclude whitetop from mutual habitats. Cattail and *Phragmites* are excellent competitors in this absence of water level fluctuations, rapidly spreading by vegetative clonal growth (Cross and Fleming 1989). With stabilization, these highly competitive emergent macrophytes are no longer held 'in check' by flood-drought events, resulting in distinct species segregation along the elevation gradient (**Figure 4.18b**) as these species spread uninhibited to form dense monodominant plant zones. Further stabilization prevents elimination and regeneration of marsh vegetation, while simultaneously increasing the influence of interspecific competition among plant species. Under the stabilized regime periodic disturbance events are eliminated causing a paradigm shift from a disturbance to a competition driven environment.

The above patterns of proportional dominance that develop along the elevation gradient under these water level regimes, are similar to patterns of fundamental and realized responses (occur in the absence and presence of neighbour competition respectively) (**Figure 4.18**). For competition to be occurring realized must be narrower than fundamental response patterns, as they are in 1997 compared to 1989. Certainly, 1989 dominance patterns are not fundamental responses, but are nevertheless more similar than those observed from 1997 or even 1980. Considerable species overlap does occur in 1997 and 1980, due primarily to local variation, but also because in reality these species are not sorted along a 2-dimensional, but rather a multi-dimensional plane. As previously discussed, elevation is a complex environmental gradient made up of many factors, which here includes salinity (Barbour 1978, Snow and Vince 1984b, Kenkel et al. 1991) as well as competition (Grace and Wetzel 1981). Ultimately, tolerance for factors such as flooding, salinity, shading, pH, all affect the

competitive ability of these species and therefore where they will be located along the environmental gradient.

Modelling the Spatio-Temporal Dynamics of Competing Populations

Czaran (1989) demonstrated that if the response curves of two competing species along an environmental gradient are different enough, the regional coexistence of these two populations is possible provided that this gradient is sufficiently steep within this region. Parameters determined from 1997 species responses along the elevation gradient within the MERP marshes were utilized with the GRADEX simulation model of Czaran (1989) (**Figure 4.4**), further proving the influences of competition in shaping these marsh zonation patterns. The model was run with various changes to these parameters with the only major resulting difference being the time it takes to reach these zonation patterns. This model demonstrates that in a naturally fluctuating environment (i.e. a prairie marsh) species diversity is maintained by regular disturbances (i.e. flooding and drought) that periodically reset these vegetation communities. In this case, this “resetting” will maintain an open diverse marsh system with a mosaic of vegetation communities (**Figure 4.19a**). When these periodic disturbances are removed, species continue to expand uninhibited along this environmental gradient, dominating within their competitive range. The gradient determines the direction these species are sorted, being able to exclude each other locally while coexisting regionally (Czaran 1989). Within the stabilized regime of a prairie marsh, dominants such as cattail and *Phragmites* persist, forming dense monodominant plant zones with low species diversity (**Figure 4.19d**). Although the GRADEX model only demonstrates a 2-species situation along a simple gradient, a region between the dominant ranges of cattail and *Phragmites* is evident (**Figure 4.19d**). This region clearly demonstrates the range along the elevation gradient whitetop dominates, and where influences of salinity affect the relative competitive ability of cattail and *Phragmites*. Salinity would allow whitetop to competitively dominate within this region. Without salinity, it is conceivable that over a long-term period of stabilization whitetop could eventually be completely eliminated.

4.6.6. The Prairie Marsh Stabilized Regime Model

This study further expands the idea of centrifugal organization of Wisheu and Keddy (1992) to arrange species along various environmental gradients. (Day et al. 1988) described elevation as a complex gradient combining a series of environmental factors, such as spring flooding, growing season water depth and fluctuations, litter accumulation, and organic

matter content, which ultimately affect plant position and zonation within a prairie marsh. Within a marsh system undergoing natural cyclical water changes the three dominant plant species, cattail, *Phragmites* and whitetop, will primarily "sort-themselves" according to water depth. When these fluctuations, however, are removed and the marsh system is subject to prolonged water level stabilization, the influence of other factors, not normally playing as large a role in a naturally fluctuating environment, become much more significant. In the stabilized regime of the MERP marshes, the dominant plant species continued to not only sort-themselves along the elevation gradient, primarily according to flood tolerance, but are further arranged according to salinity (**Figure 4.20**). Elevation during a stabilized regime is a multidimensional complex environmental gradient combining not only water depth and salinity, but oxygen availability, deadfall accumulation and rhizome/seed bank composition. With prolonged periods of water level stabilization the influence of these factors increases, with the result that interspecific competition becomes a major driving force in shaping vegetation patterns. As indicated, with water level stabilization there is a paradigm shift from a disturbance-driven environment subject to natural water level fluctuations, to a competition-driven environment, which develops during this stabilized regime.

Cattail, *Phragmites*, and whitetop, are all extremely resilient marsh species. Consequently, "who gets there first" is still a major factor in determining future concentrations of dominant species. Czaran's (1989) model demonstrates that when a species is established, they can persist for numerous generations. Ultimately, results indicate that long-term stabilization from 1989 to 1997 has led to increasingly distinct vegetation patterns, which we attribute to competitively dominant species "sorting-themselves-out" along a complex elevation gradient (**Figure 4.20**). If elevation were a simple gradient of water depth, or if mean salinity levels in the MERP marshes were relatively low (below 5.0 μS) the Stabilized Regime model indicates that whitetop could eventually be eliminated or reduced to very low abundance (**Figure 4.20**). This study indicates that during a stable water level environment the effects of other environmental factors, such as salinity, clearly become much more significant than they would normally be in a fluctuating regime. As a result, it is the combined influences of water depth (a consequence of elevation), salinity (associated with water depth) and competitive interactions (due to the stabilized regime) which ultimately affect the position of these plant species along this gradient.

4.6.7. Management implications: Disturbance or competition driven, so what?

This study indicates that with water level stabilization, there has been a paradigm shift from a disturbance-driven ecosystem to a competition-driven one. But how does this actually affect the inhabitants or users of wetland environments? Prairie marsh ecosystems are highly dynamic systems. As a consequence of annual variations in spring runoff, precipitation, and evapotranspiration, these marshes normally experience significant annual and seasonal fluctuations in water levels (van der Valk and Davis 1978). This maintains plant species diversity, and provides a mosaic of wildlife habitats (Harris and Marshall 1963, Weller and Spatcher 1965; van der Valk and Davis 1976a, 1978; van der Valk 1981; Kenkel 1992; Bornette and Amoros 1996). When this cycle of disturbances is disrupted with long-term periods of human-induced stabilization, extensive dense monocultures of emergent macrophytes rapidly develop as more competitive species eliminate poorer competitors (Kantrud et al. 1989a). As these dominant species spread, there is a dramatic accumulation of standing deadfall filling these marsh environments, closing open vegetation patches, and further inhibiting the growth of understory plant species (van der Valk 1986, Jurik et al. 1994). This leads to increasingly distinct vegetation patterns within this landscape, with greatly reduced species diversity, resulting in a loss of valuable wildlife habitat (Kadlec and Smith 1992) and reduced access to these marsh environments. In the absence of flushing water levels there is also a buildup of salts above the soil-water transition. This can further lead to salinity problems in agricultural areas surrounding the marsh environment (Milne and Rapp 1968). With stabilization there is also a lower rate of decomposition in areas that no longer receive inundations of water, resulting in a loss of soil organic matter accumulation, and a loss of gradually sloping marsh shorelines (Grosshans in press). With no disturbance to rejuvenate the marsh from the seed bank, or eliminate accumulated litter, this community will enter a state of stagnation (i.e. a very homogenous marsh system).

The ecological processes that drive vegetation changes in prairie marshes, i.e. fluctuating water levels, stabilization and competitive interactions, are complex and often unclear. By examining long-term vegetation data, which is not normally available for natural systems, this study contributes further to our knowledge of the effects of stabilizing water levels on the structure, composition and habitat diversity in prairie marsh ecosystems. Observed patterns in the landscape are often evident, nevertheless, long-term studies of the underlying processes forming these patterns are lacking. Ultimately, if wetlands are to be protected and effectively managed, a more complete knowledge of the mechanisms that drive successional dynamics is required.

Cyclical Disturbance

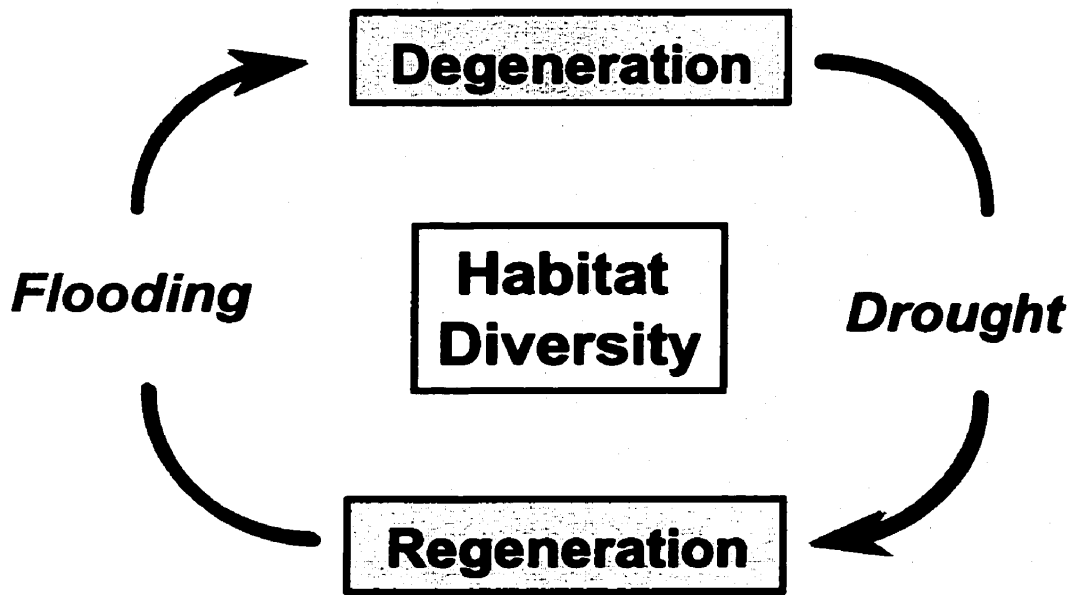


Figure 4.1. Cyclical marsh plant succession can be summarized into 2 general stages of degeneration and regeneration. Degeneration is a result of persistent water levels and prolonged flooding which eliminates standing vegetation, whereas regeneration occurs during droughts, which allows species to reestablish by recruitment from underground reserves (i.e. seeds and rhizomes). It is recognized these periodic cycles of disturbances (i.e. degeneration and regeneration) are essential in maintaining species and habitat diversity in prairie marshes

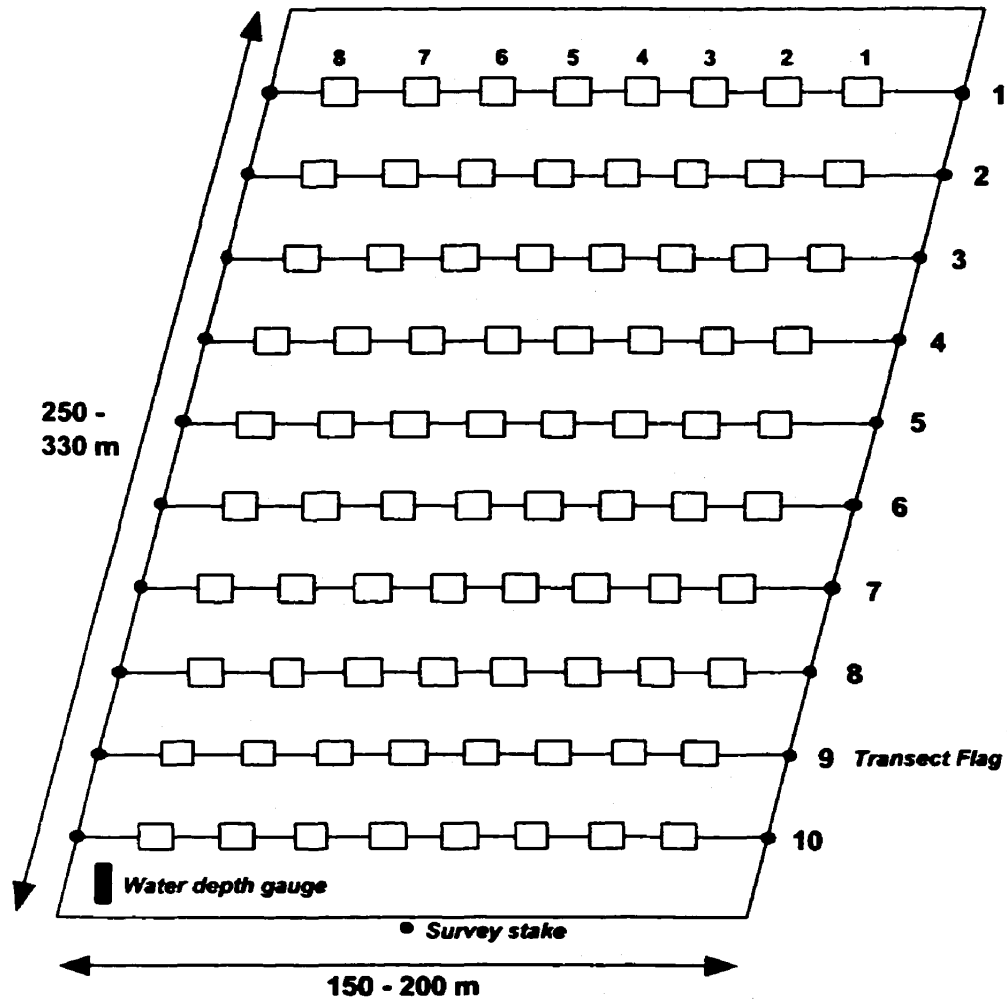
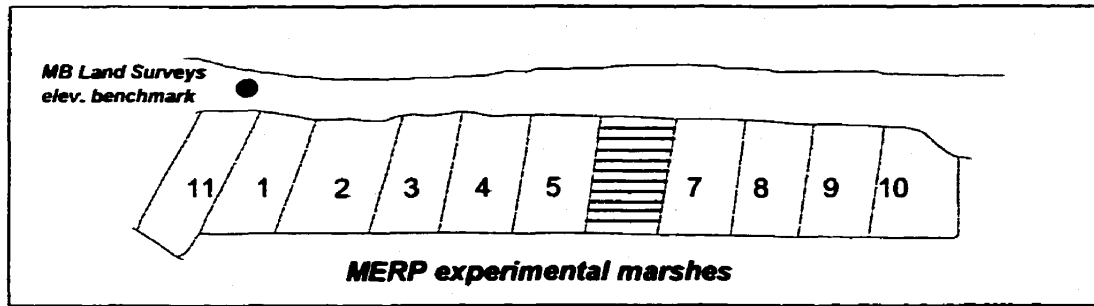


Figure 4.2. A systematic sampling design was used for a highly equitable distribution of sample points; ideal for pattern determination, gradient analysis and mapping. Each marsh was sampled along 10 East-West transects, with eight $1\frac{1}{2}$ m x $1\frac{1}{2}$ m sample sites established at equal distances for a total of 876 sample sites. Each marsh is anywhere from 150-200 m wide and 250-330 m long. Water depth gauges and survey stakes are located at the south west corner and south central dyke of each marsh respectively.

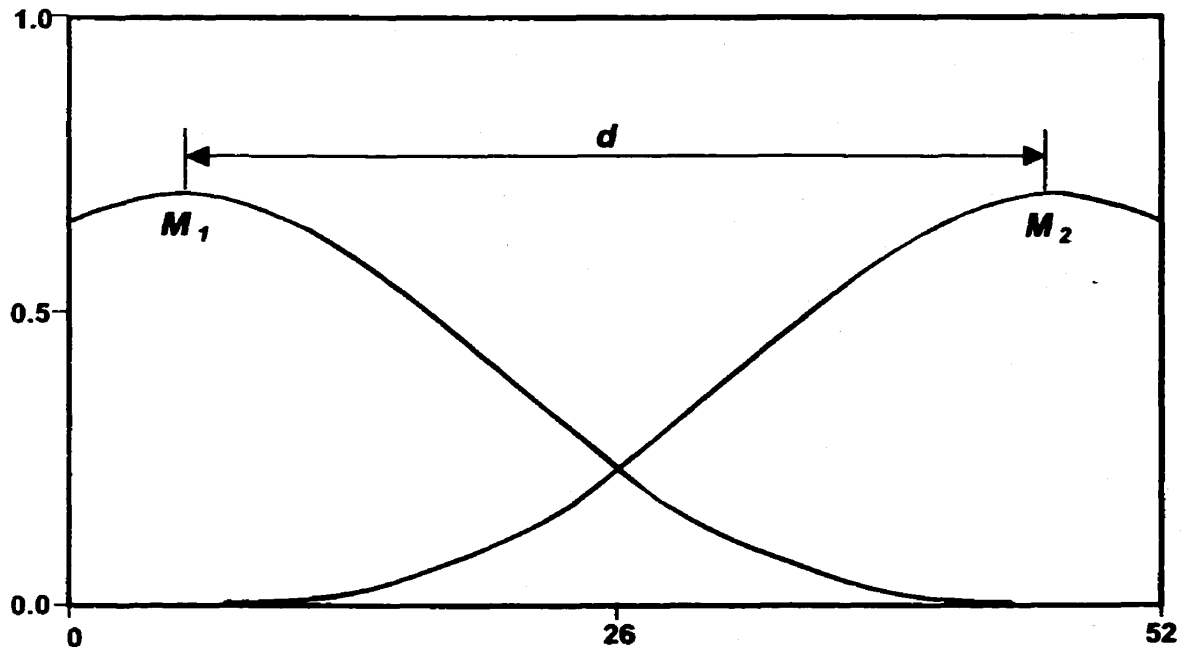
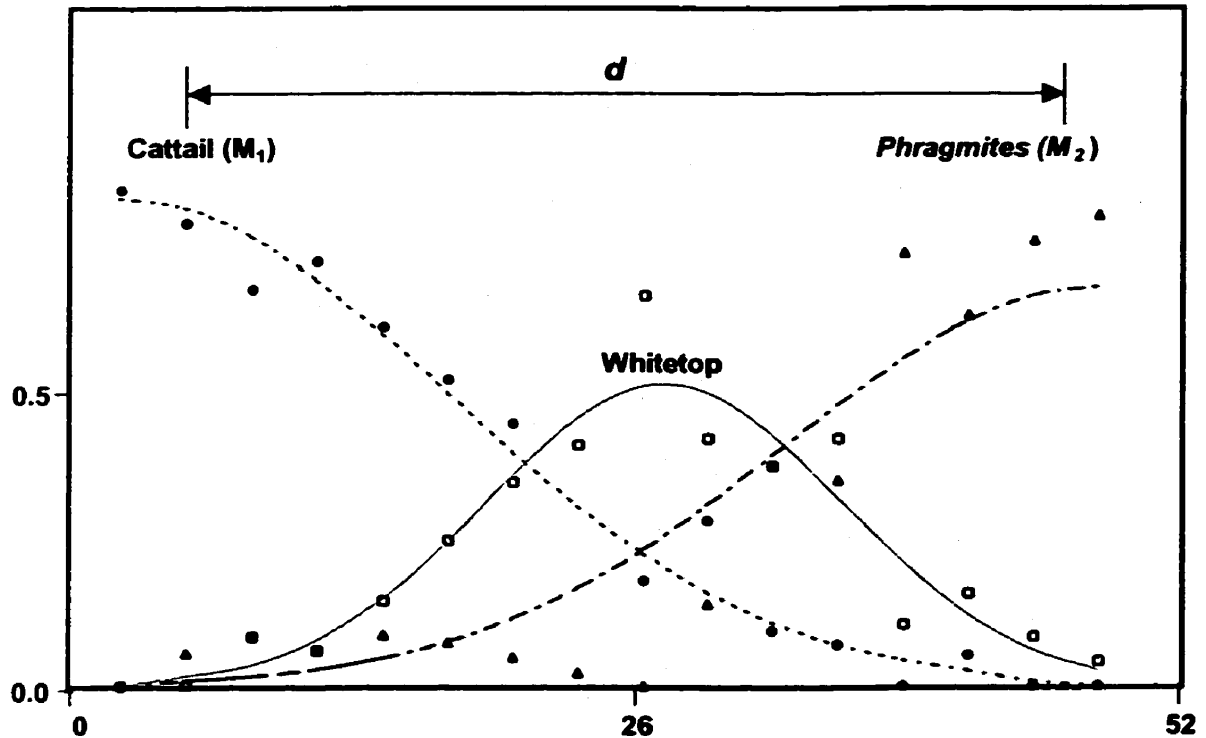


Figure 4.3. In the GRADEX simulation model, response curves are bell-shaped (i.e. normal curves) and are defined by the distance (d) between optimum points of these curves (i.e. maximum competitive strength), and a species dependent parameter specifying the steepness of each curve, or standard deviation (s), for each population (Czaran 1992). The grid area of the model consists arbitrarily of 52 columns. Optimum points of the response curves M_1 and M_2 are therefore $d/2$ sites away from the central column of 26



Input parameters for the GRADEX (Czaran 1992) simulation model of competing plant populations along an elevation gradient.

Distance of means of response curves	$d = 40$
Deviation parameter of response curves	$s = 12$
Interspecific competition coefficients	$a_1 = 1.0$ $a_2 = 1.0$
Carrying capacity of sites	$k = 3$
Fecundities for each population	$f_1 = 5$ $f_2 = 5$
Chances of dispersing outside cell	$p_1 = 0.5$ $p_2 = 0.5$
Initial number of individuals	$N_1 = 1000$ $N_2 = 1000$

Figure 4.4. Fitted response curves of the competing populations cattail, *Phragmites* and whitetop in the MERP experimental marshes. Cattail (species 1) and *Phragmites* (species 2) curves were utilized with the GRADEX simulation model of Czaran (1992). Distance (d) and deviation (s) of curves were determined from 1997 realized responses along the elevation gradient, while remaining input parameters are typical of competing species along an environmental gradient as determined by Czaran (1992).

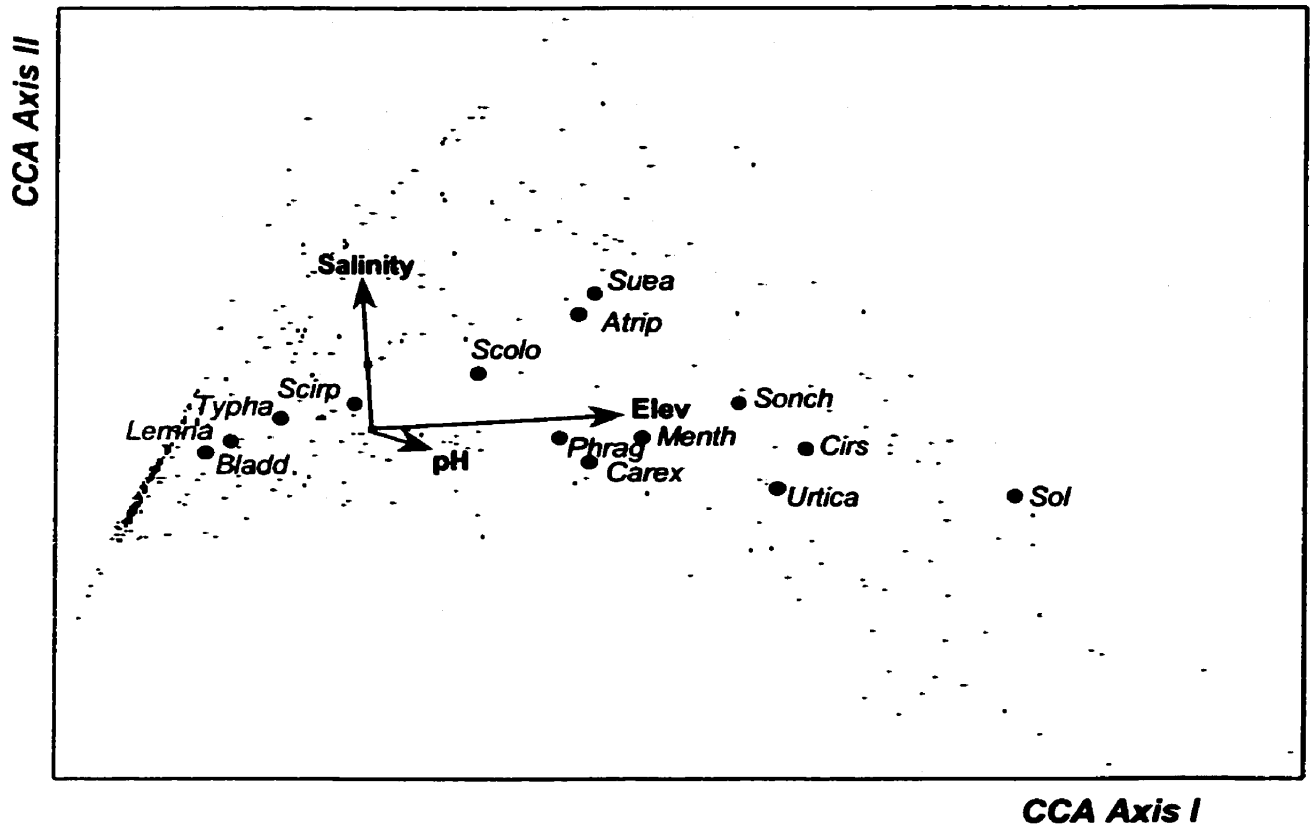


Figure 4.5a. Canonical correspondence (CCA) ordination of 690 sample sites (small dots) in the MERP experimental marshes, based on plant species cover and constrained by 3 environmental variables. Dominant macrophytes (large dots) include cattail (*Typha*), whitetop (*Scolo*), *Phragmites* (*Phrag*), Canada goldenrod (*Sol*), Canada thistle (*Cirs*) and sow thistle (*Sonch*). Minor plant species include bulrush (*Scirp*), duckweed (*Lemna*), bladderwort (*Bladd*), sedge (*Carex*), mint (*Menth*), stinging nettle (*Urtica*), orache (*Atrip*), and sea-blite (*Suea*). Environmental variables (vectors) include Salinity, pH and water depth (Elev). Eigenvalues: 1 = 0.563, 2 = 0.131. Species-environment correlations: axis 1 = 0.867, axis 2 = 0.575. Redundancy (ratio of canonical to unconstrained eigenvalues) = 0.768/4.165 = 18.4%.

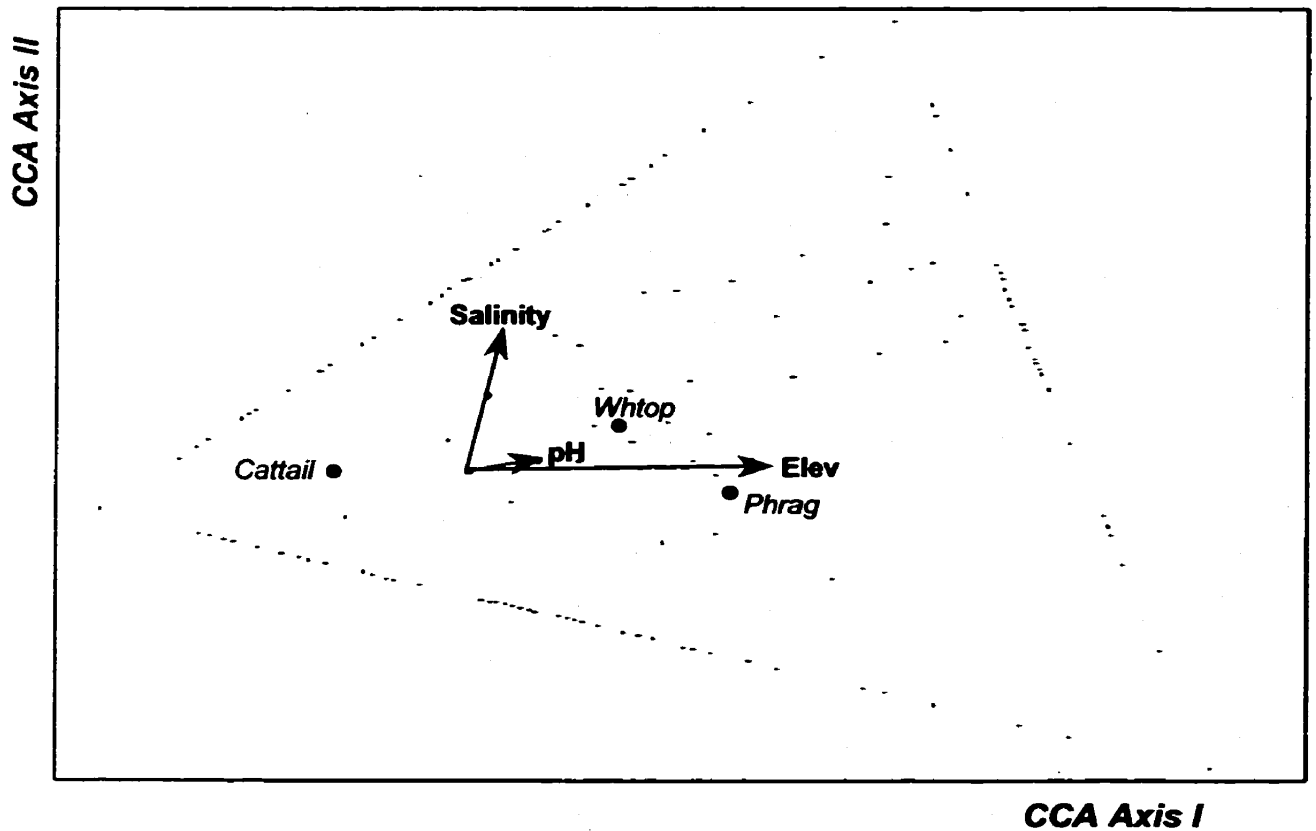


Figure 4.5b. Canonical correspondence (CCA) ordination of 690 sample sites (small dots) in the MERP experimental marshes, based on plant species cover and constrained by 3 environmental variables. The 3 dominant macrophytes (large dots) include cattail, whitetop (*Whtop*), and *Phragmites* (*Phrag*). Environmental variables (vectors) include salinity, pH and water depth (Elev). Eigenvalues: 1 = 0.356, 2 = 0.092. Species-environment correlations: axis 1 = 0.726, axis 2 = 0.435. Redundancy (ratio of canonical to unconstrained eigenvalues) $0.448/1.158 = 38.7\%$.

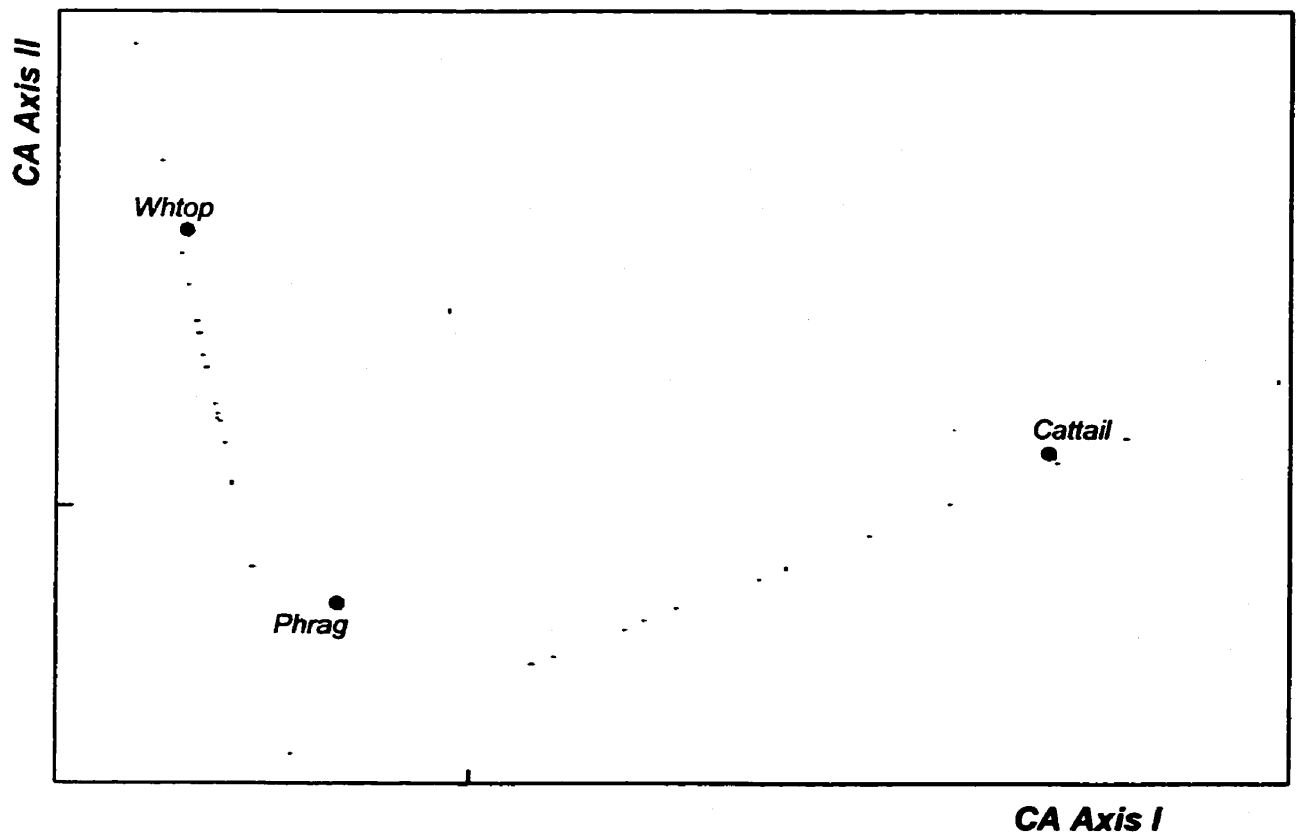
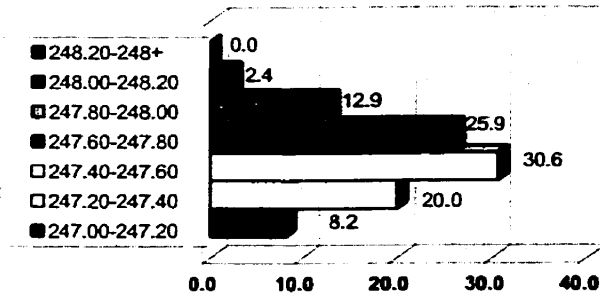
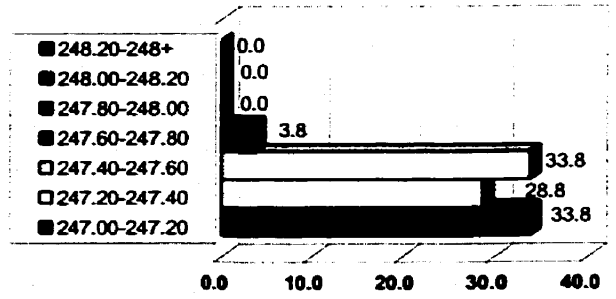


Figure 4.6. Correspondence analysis (CA) ordination of the 77 plots in MERP control marsh 11, based on species composition. The three dominant macrophytes (large dots) are cattail, whitetop (*Whitop*), and *Phragmites* (*Phrag*). Eigenvalues: 1 = 0.722 (64.4%), 2 = 0.399 (35.6%).

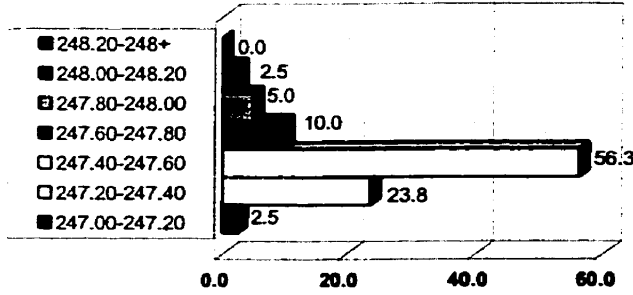
a. Marsh 1 (med)



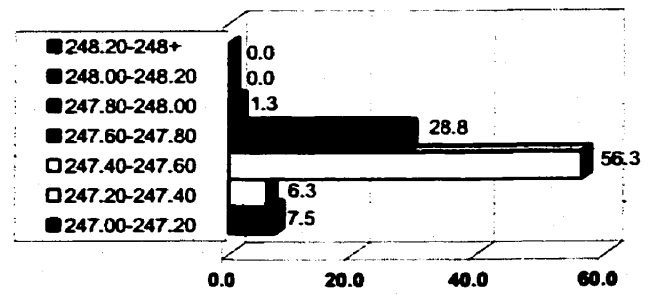
e. Marsh 3 (norm)



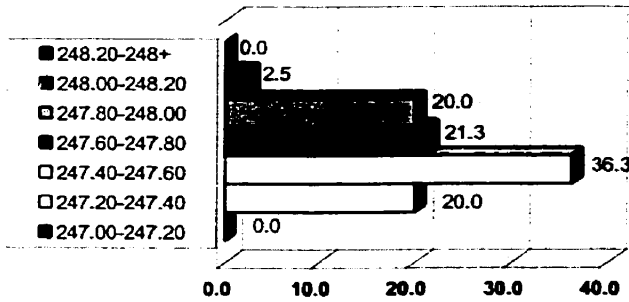
b. Marsh 9 (med)



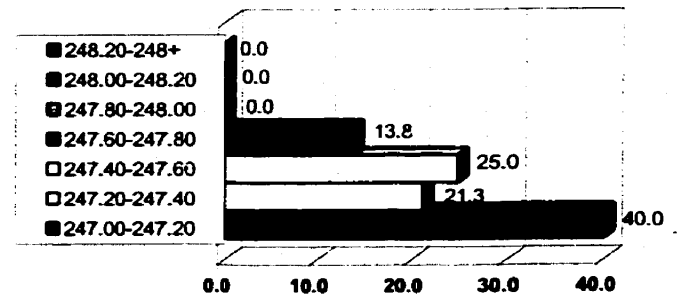
f. Marsh 7 (norm)



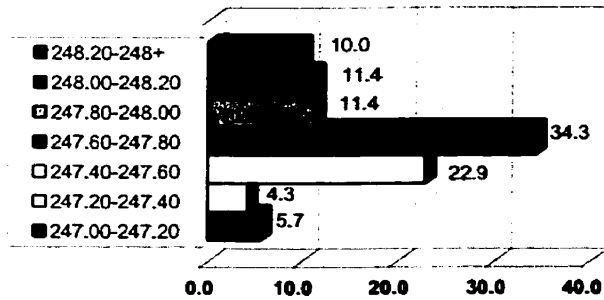
c. Marsh 6 (high)



g. Marsh 8 (norm)



d. Marsh 10 (high)



h. All marshes combined

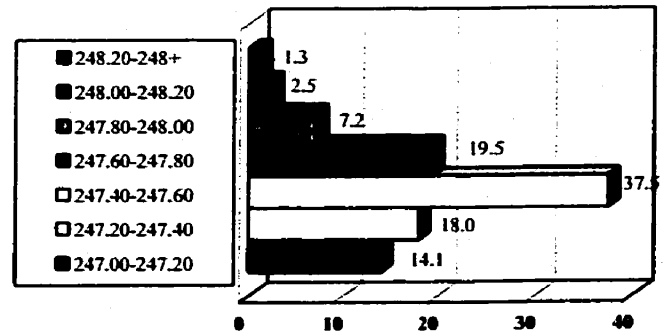


Figure 4.7. Proportional elevation range of sample sites in the MERP marshes, for all individual marshes and all marshes combined. Treatment marshes are identified; medium = med, high, normal = norm.

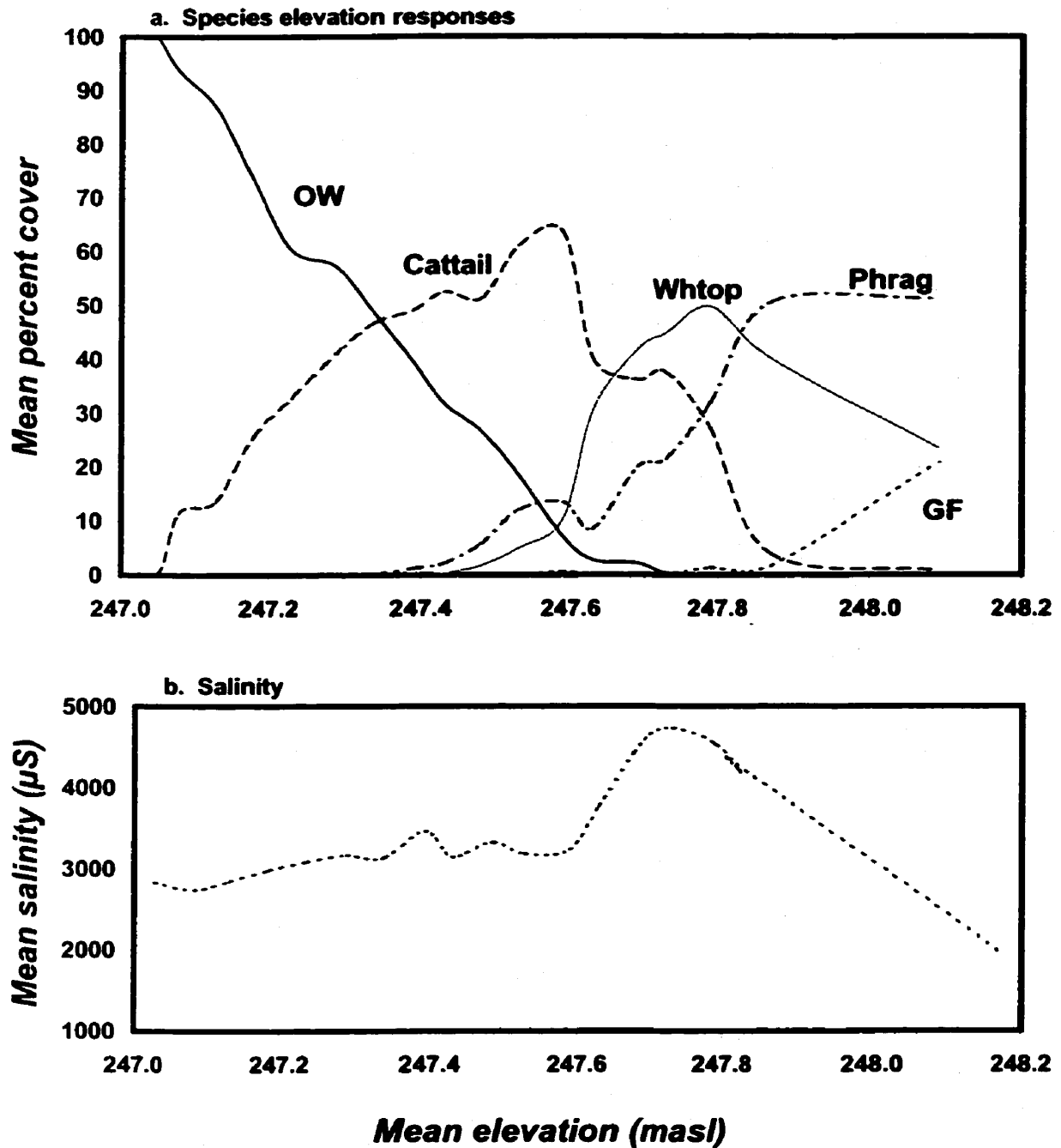


Figure 4.8. a. Realized elevation response curves of the dominant macrophytes in the MERP experimental marshes (excluding marshes 2, 4 and 5). Dominant zones include open water (OW), cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Data fitted using loess curves. **b.** Mean salinity measured as conductance (μS) over the elevation range (masl) is also given.

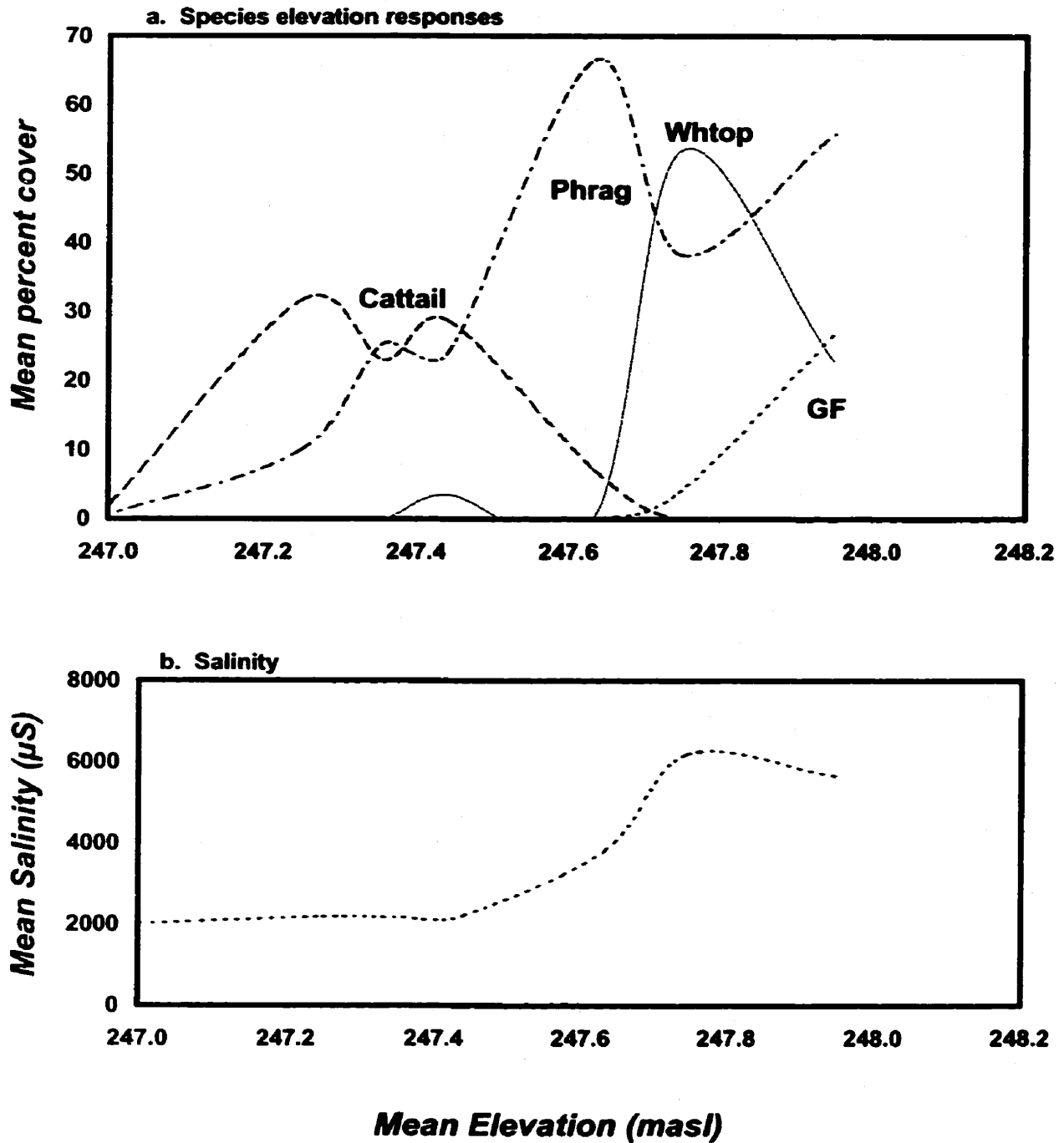


Figure 4.9. a. Realized elevation response curves of the dominant macrophytes in the MERP control marsh 11. Dominant zones include open water (OW), cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Data fitted using lowess curves. **b.** Mean salinity measured as conductance (μS) over the elevation range (masl) is also given.

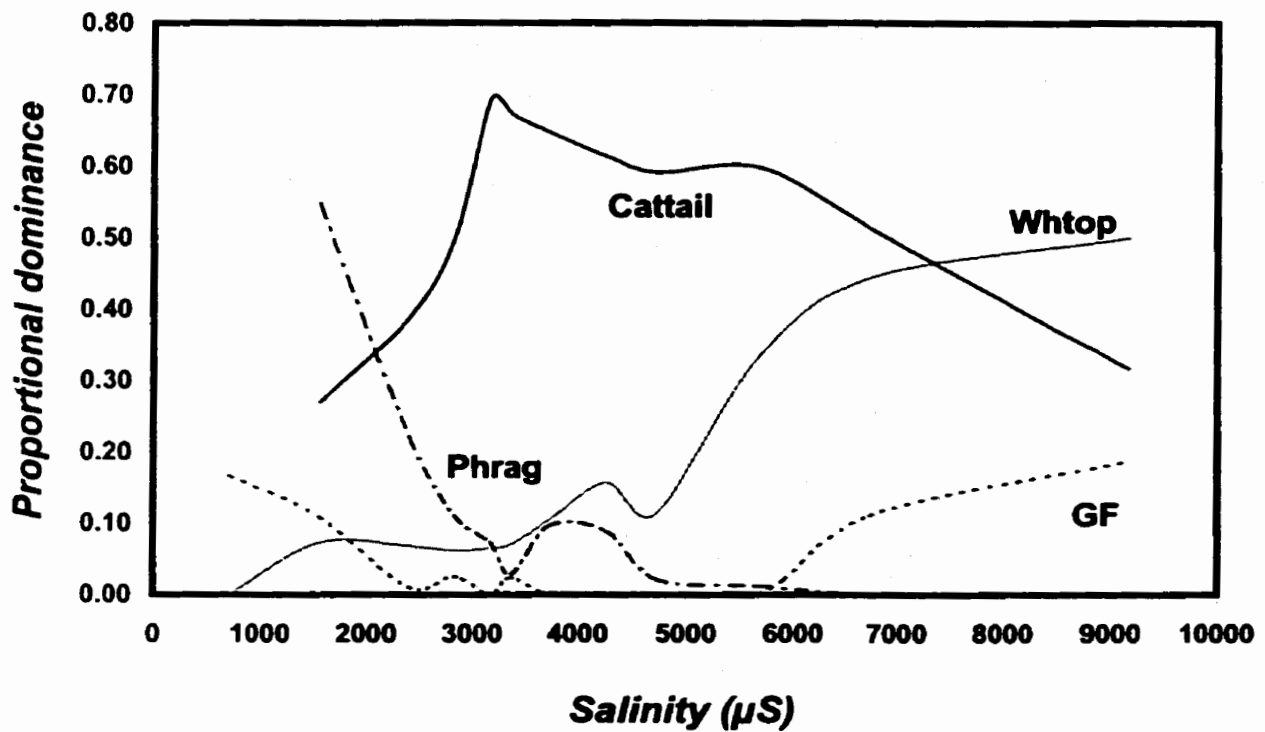


Figure 4.10. 1997 realized salinity response curves of the dominant macrophytes in the MERP experimental marshes, given as proportional species dominance at a given salinity range by the respective species, for all marshes combined (excluding marshes 2, 4 and 5). Dominant species include cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Data fitted using lowess curves.

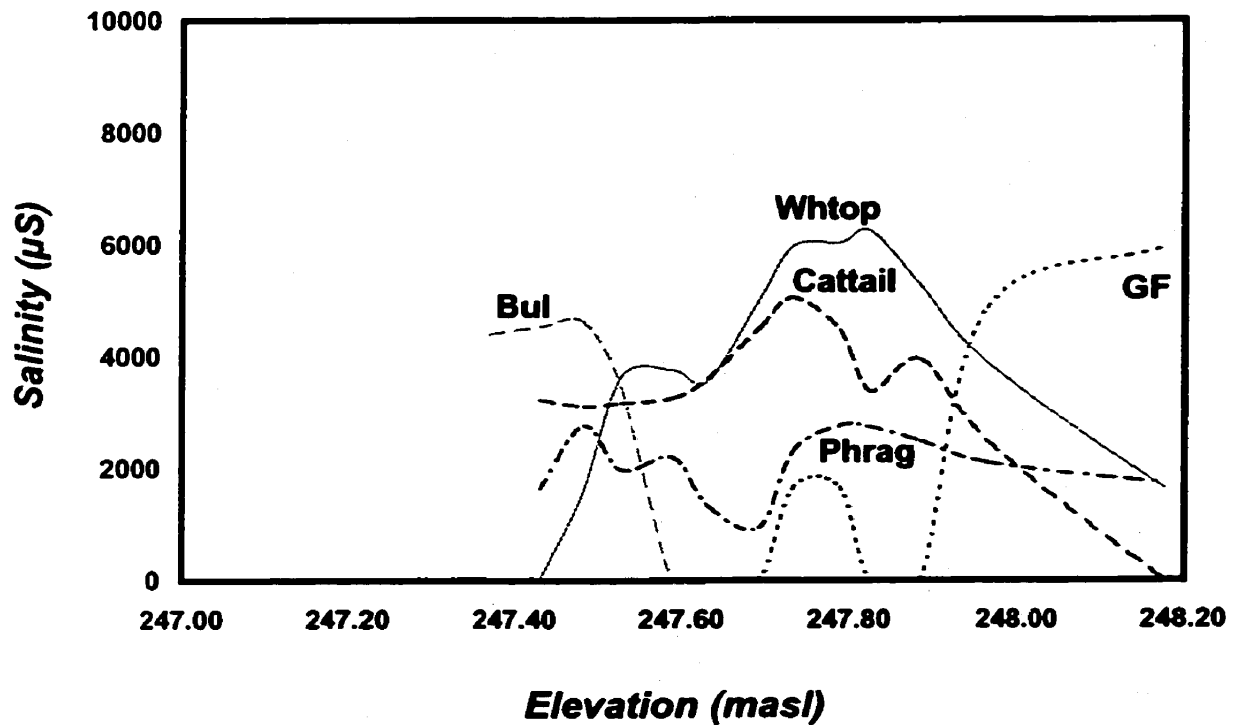


Figure 4.11. 1997 species realized elevation response curves expressed as mean salinity to determine mean salinity of areas dominated by respective dominant macrophytes of the MERP experimental marshes, for all marshes combined (excluding marshes 2, 4 and 5). Dominant species include cattail, bulrush (Bul), whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Data fitted using lowess curves.

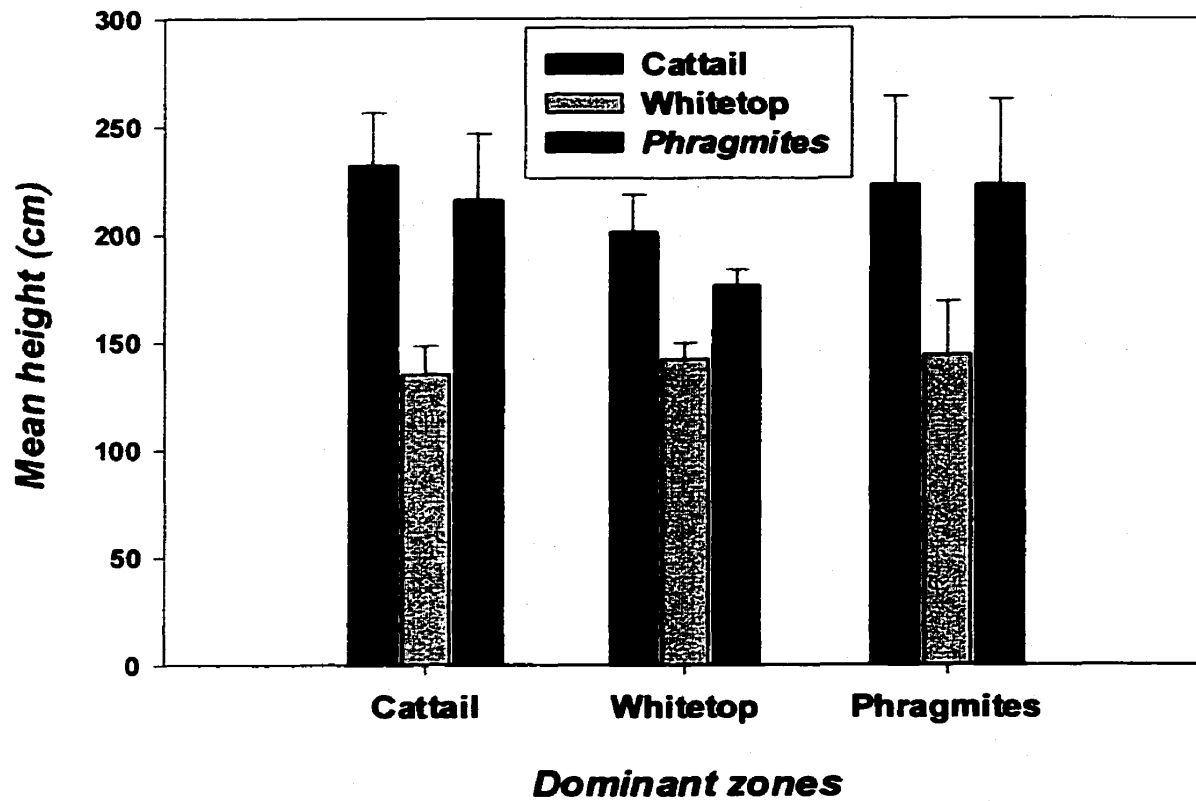


Figure 4.12. Mean plant height (+/- s.e.) of the three dominant macrophytes cattail (n = 43, 10, 13) Whitetop (n = 13, 46, 17) and *Phragmites* (n = 21, 30, 19) in areas dominated by these species respectively.

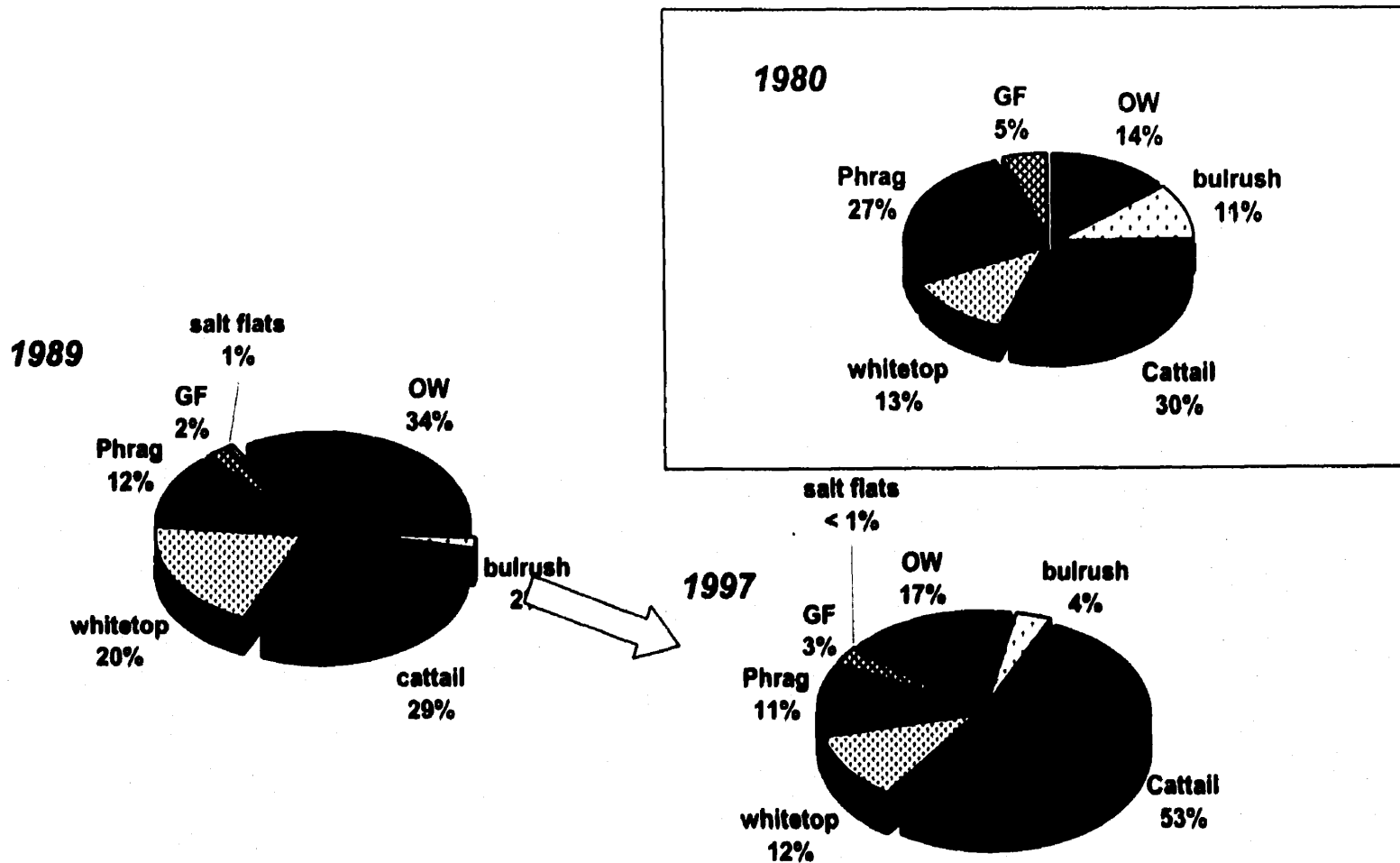


Figure 4.13. Change in percentage of sample sites (n=555, excluding marshes 2,4 and 5) dominated by respective species/ vegetation zones in the Marsh Ecology Research Program experimental marshes, subject to prolonged water level stabilization from 1989-1997. Percent of sample sites dominated by respective species in 1980 is also given. Dominant zones include cattail, open water (OW), whitetop, *Phragmites* (Phrag), grasses and forbs (GF), bulrush, sedges (car), and salt flats.

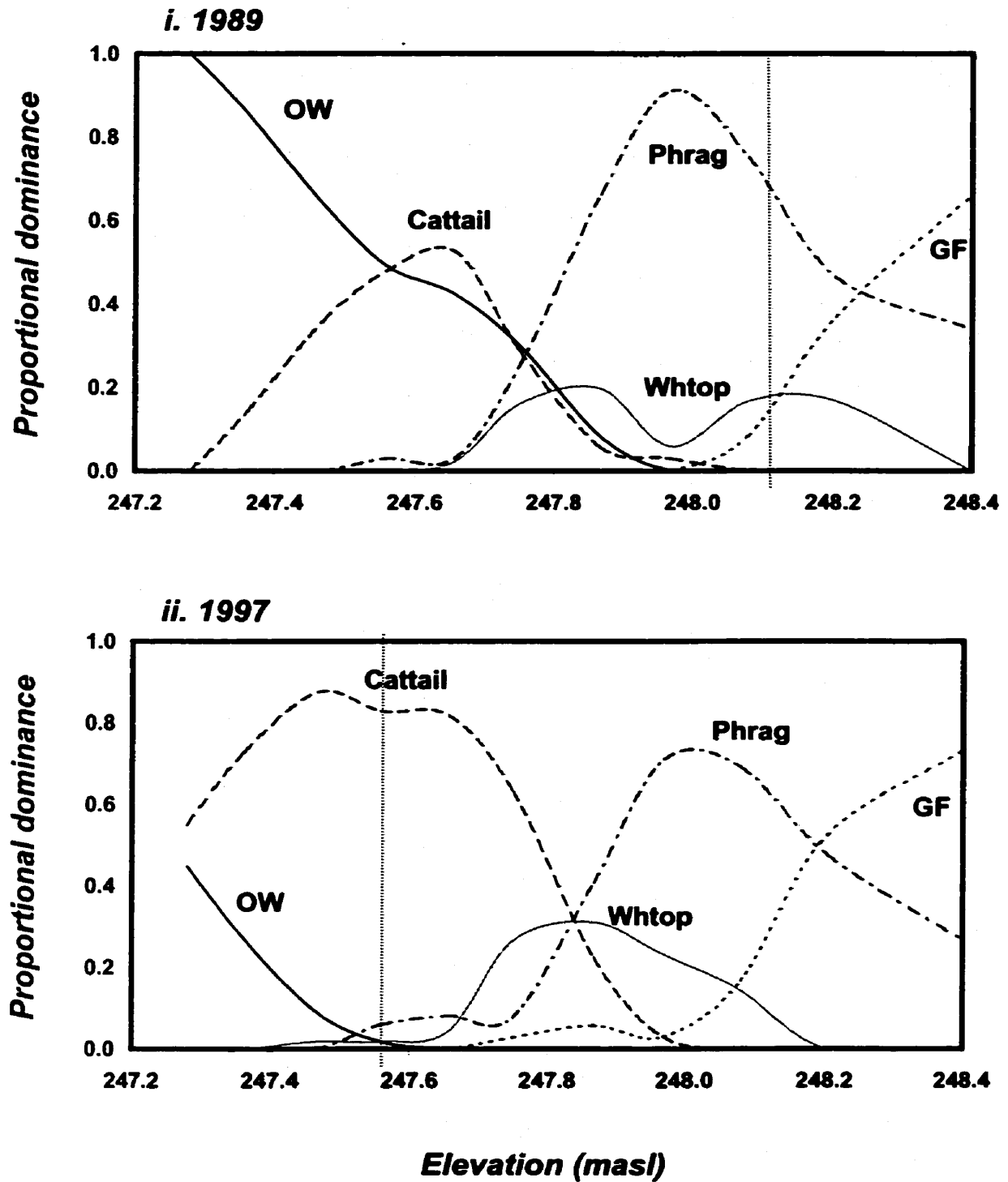


Figure 4.14.a. High treatment group (marshes 6 and 10) proportional species dominance in the MERP experimental marshes given as the proportion of sample sites dominated at a given elevation range by the respective species or vegetation zone in i. 1989, and ii. 1997. Dominant zones include open water (OW), cattail, whitetop (Whitop), *Phragmites* (Phrag), and grasses/forbs (GF). Vertical line indicates period mean water level. Data fitted using lowess curves.

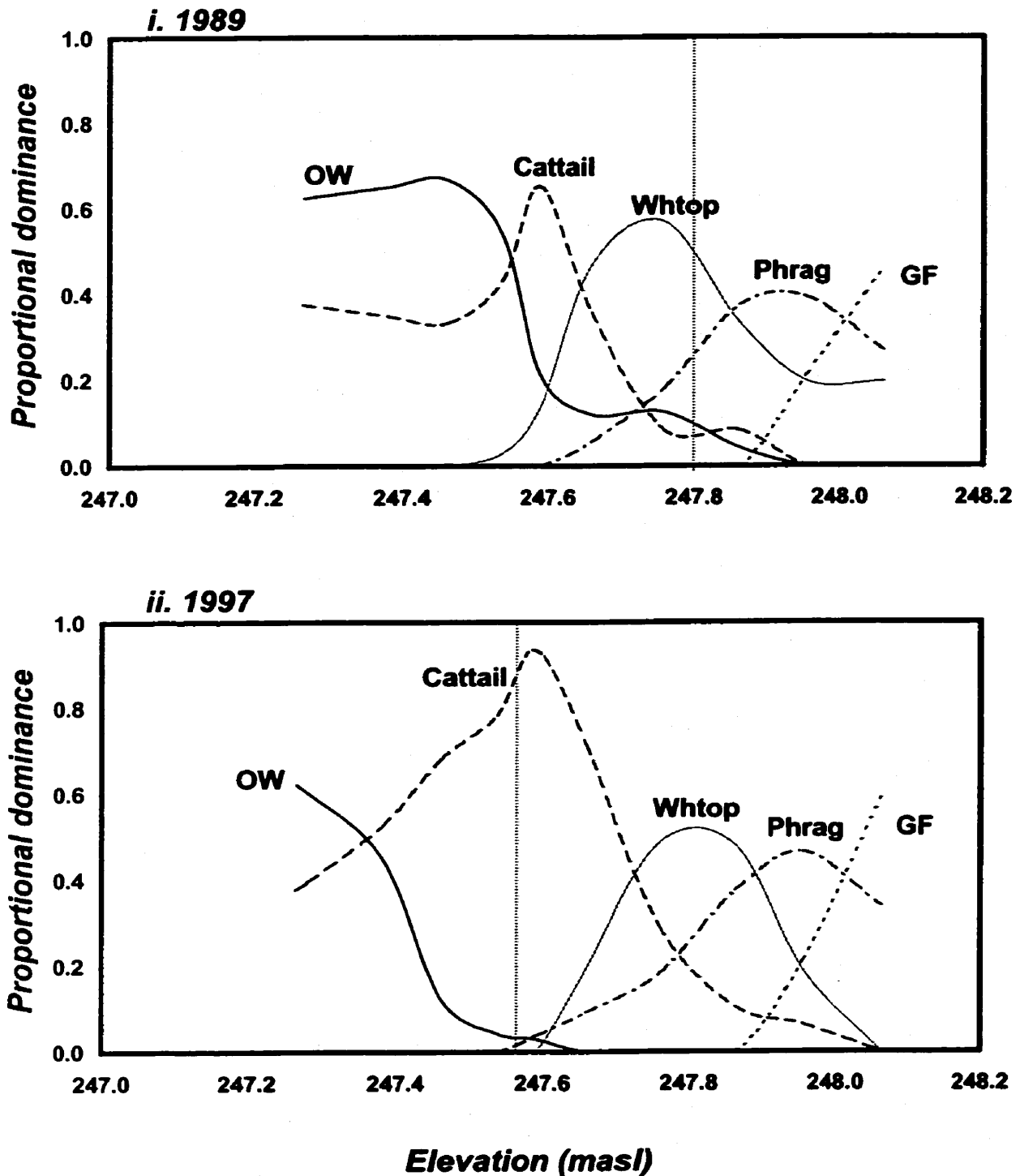


Figure 4.14.b. Medium treatment group (marshes 1 and 9) proportional species dominance in the MERP experimental marshes, given as the proportion of sample sites dominated at a given elevation range by the respective species or vegetation zone in i. 1989, and ii. 1997. Dominant zones include open water (OW), cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Vertical line indicates period mean water level. Data fitted using lowest curves.

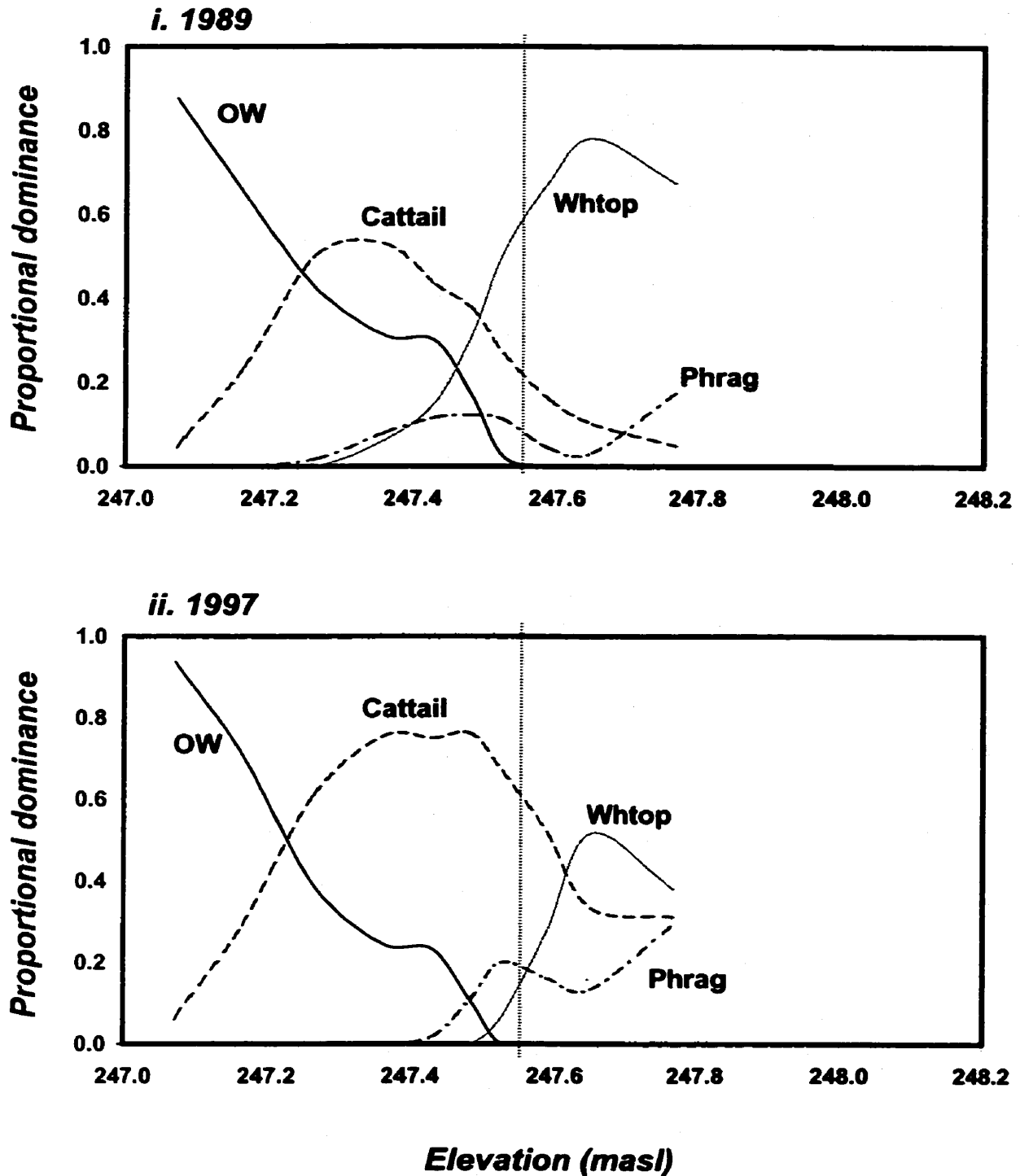


Figure 4.14.c. Normal treatment group (marshes 3,7 and 8) proportional species dominance in the MERP experimental marshes, given as the proportion of sample sites dominated at a given elevation range by the respective species or vegetation zone in i. 1989, and ii. 1997. Dominant zones include open water (OW), cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Vertical line indicates period mean water level. Data fitted using lowess curves.

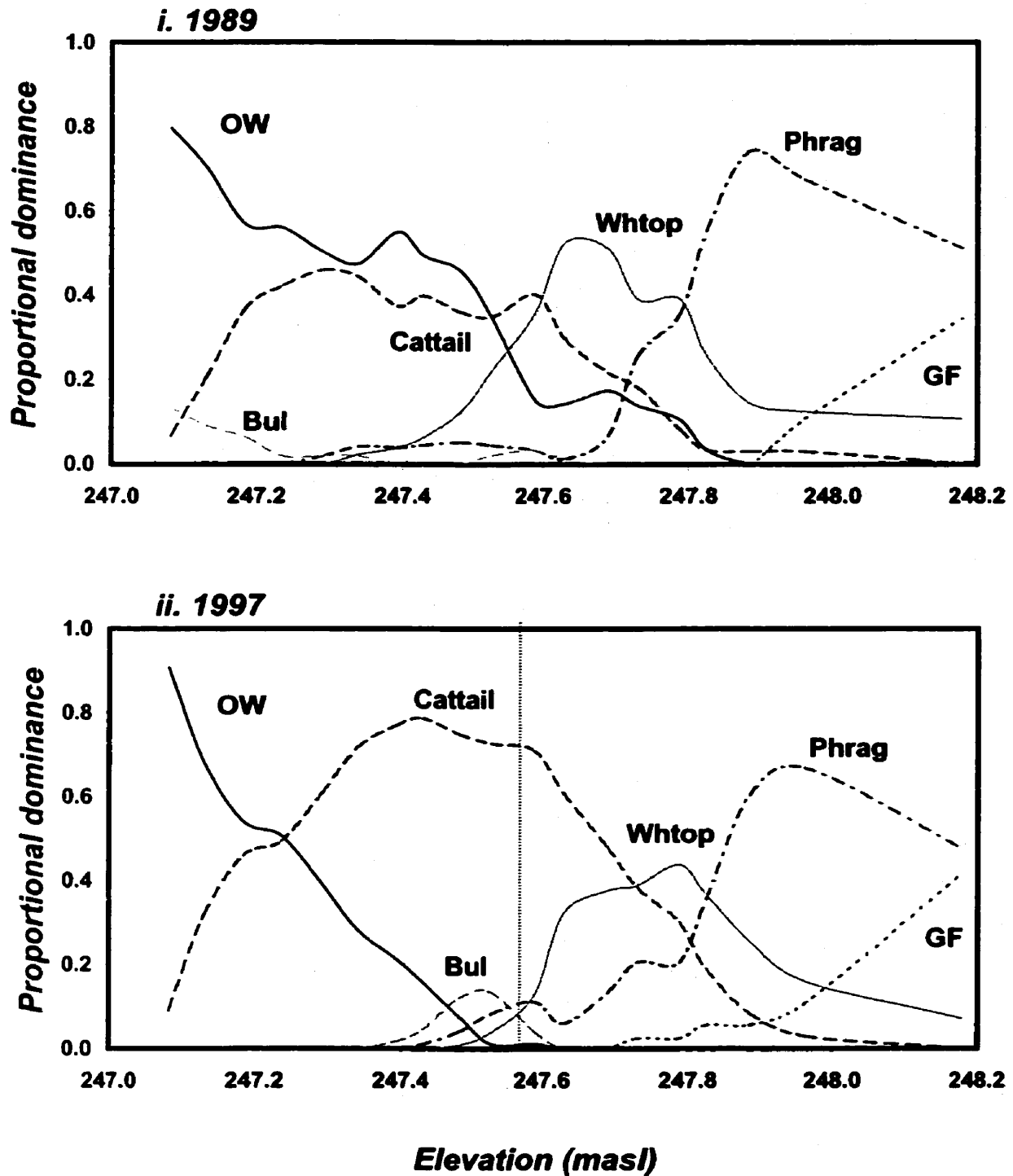


Figure 4.14.d. Proportional species dominance in the MERP experimental marshes for all marshes combined (excluding 2, 4 and 5), given as the proportion of sample sites dominated at a given elevation range by the respective species or vegetation zone in i. 1989, and ii. 1997. Dominant zones include open water (OW), bulrush (Bul) cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Vertical line indicates period mean water level. Data fitted using lowest curves.

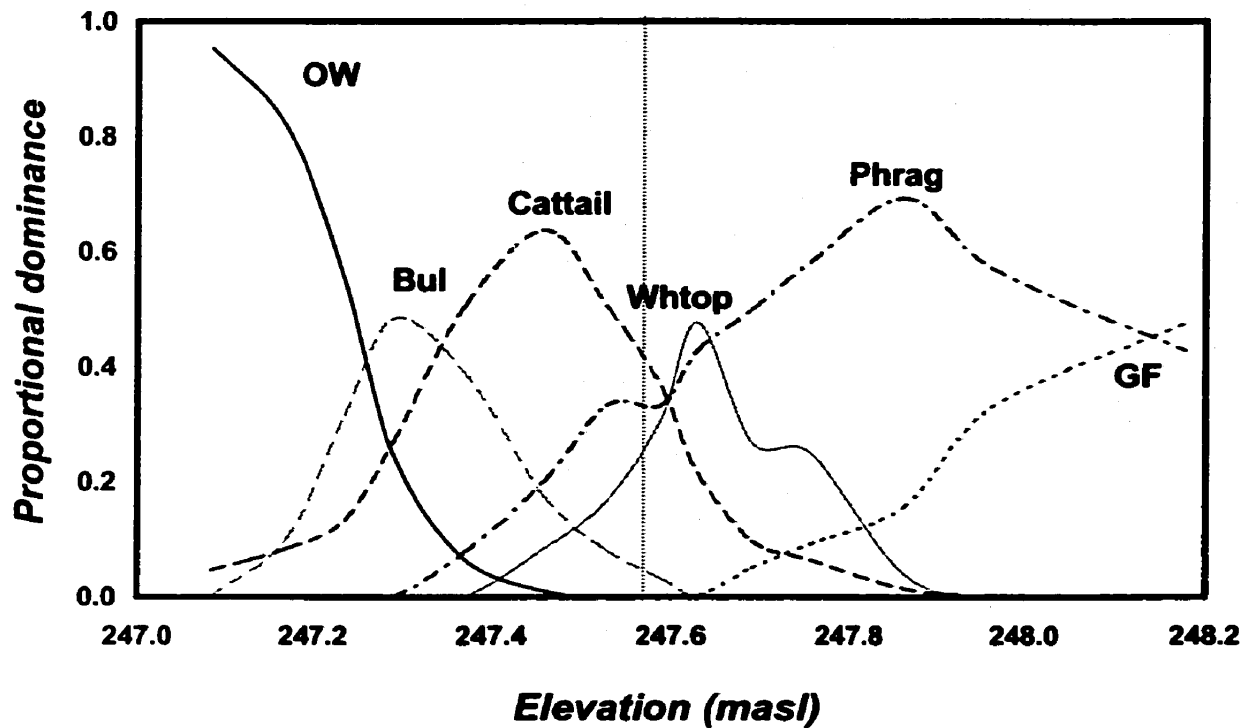
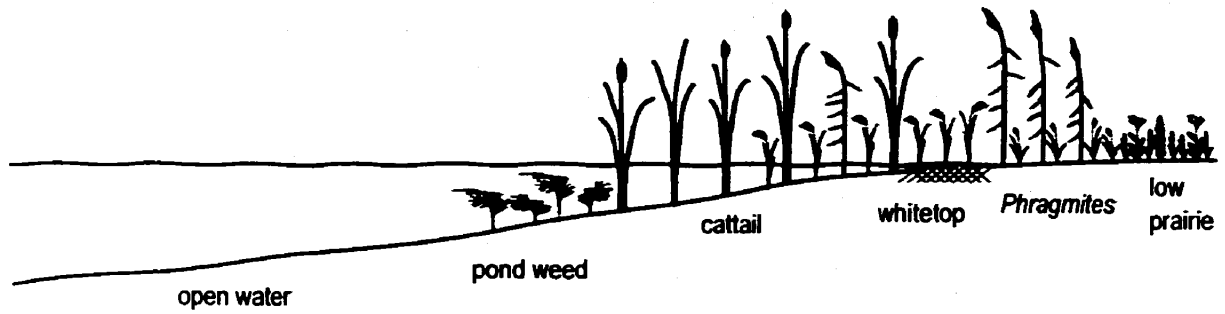
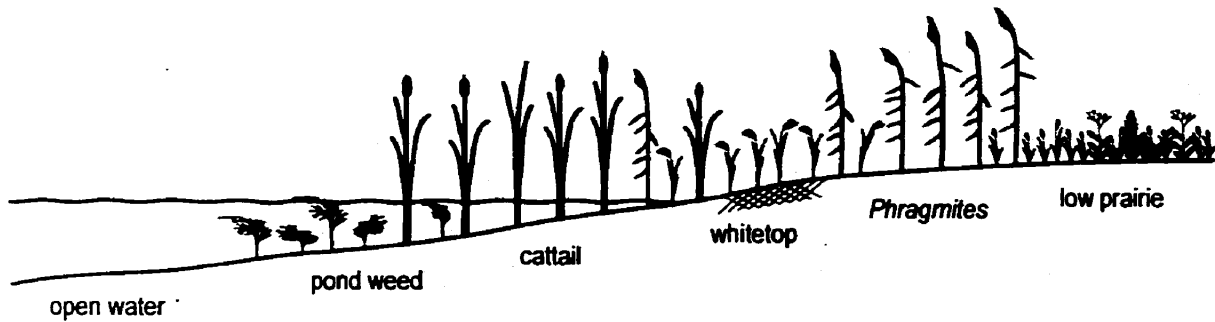


Figure 4.15. 1980 proportional species dominance in the MERP experimental marshes for all marshes combined (excluding marshes 2, 4 and 5), given as the proportion of sample sites dominated at a given elevation range by the respective species or vegetation zone. Dominant zones include open water (OW), bulrush (Bul) cattail, whitetop (Whtop), *Phragmites* (Phrag), and grasses/forbs (GF). Vertical line indicates period mean water level.

a. 5 years post-disturbance (1989).



b. 8 years following initial stabilization of water levels (1989-1997).



c. 20 years following initial stabilization of water levels (1961-1981).

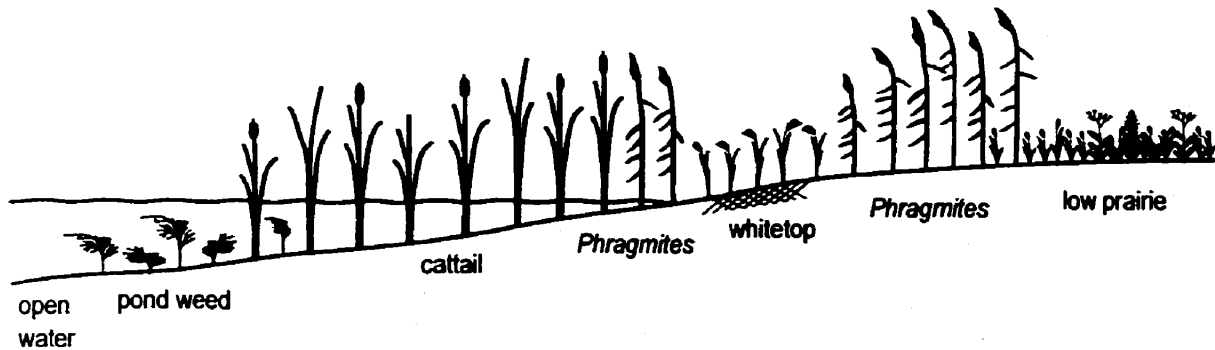


Figure 4.16. Vegetation zonation in a prairie marsh subject to prolonged waterlevel stabilization. **a.** 5 years following disturbance (i.e. flood, drought), **b.** 8 years of stabilized water levels and **c.** 20 years of stabilization. Areas of salt accumulation are illustrated by cross-hatchings.

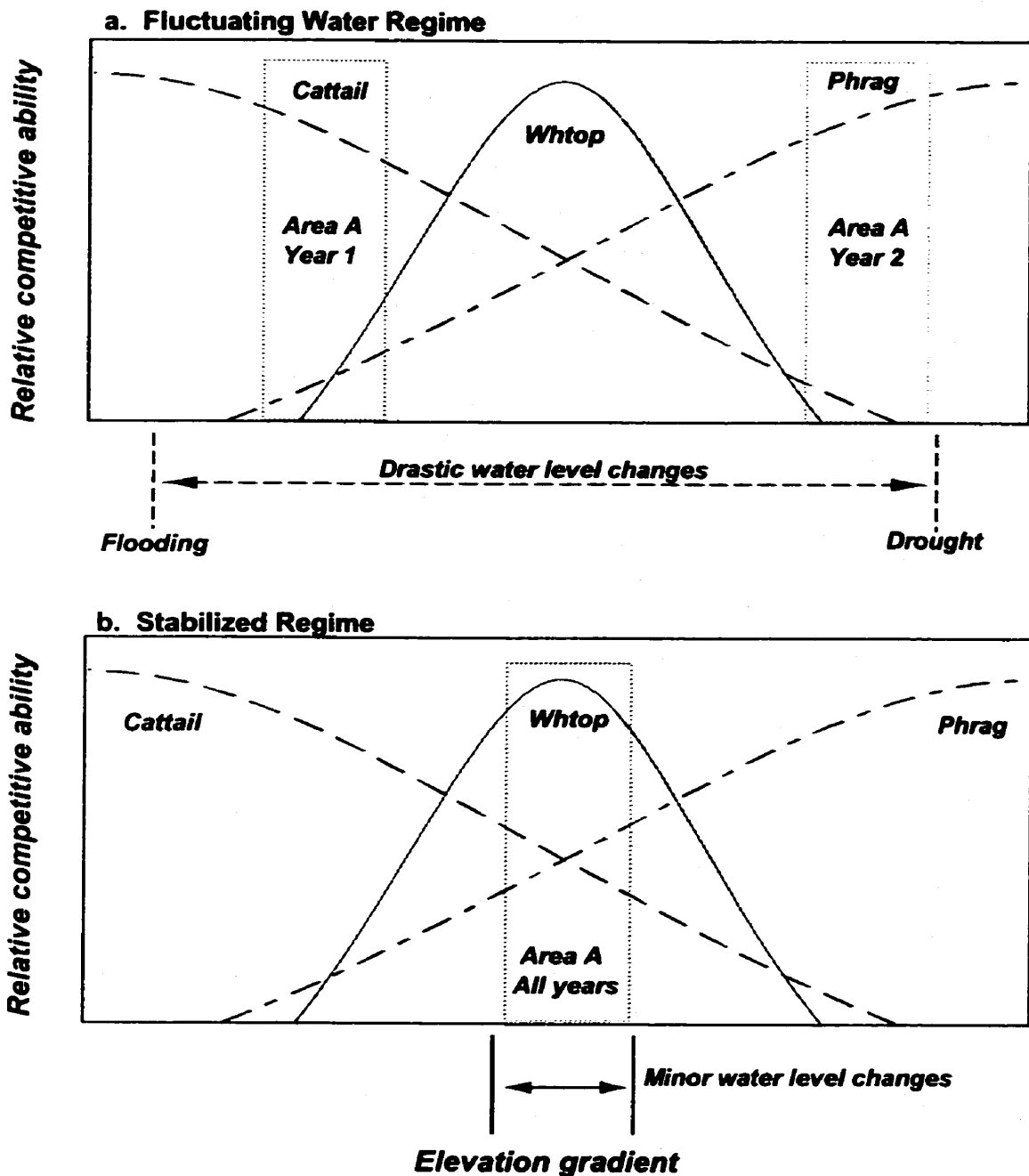


Figure 4.17. a. With fluctuating water levels, environmental conditions in an area change season to season, allowing no one species to be favoured. Year 1 may have flood conditions in a given area A where environmental conditions favour cattail growth. This same area A in year 2 may experience dry conditions favouring *Phragmites* growth. b. With prolonged water stabilization, conditions of a given area remain the same from year to year, allowing species to persist and dominate. With minor water level fluctuations not enough to cause major vegetation changes, area A will remain dominated by whitetop, while in permanently flooded and drier areas cattail and *Phragmites* persist respectively.

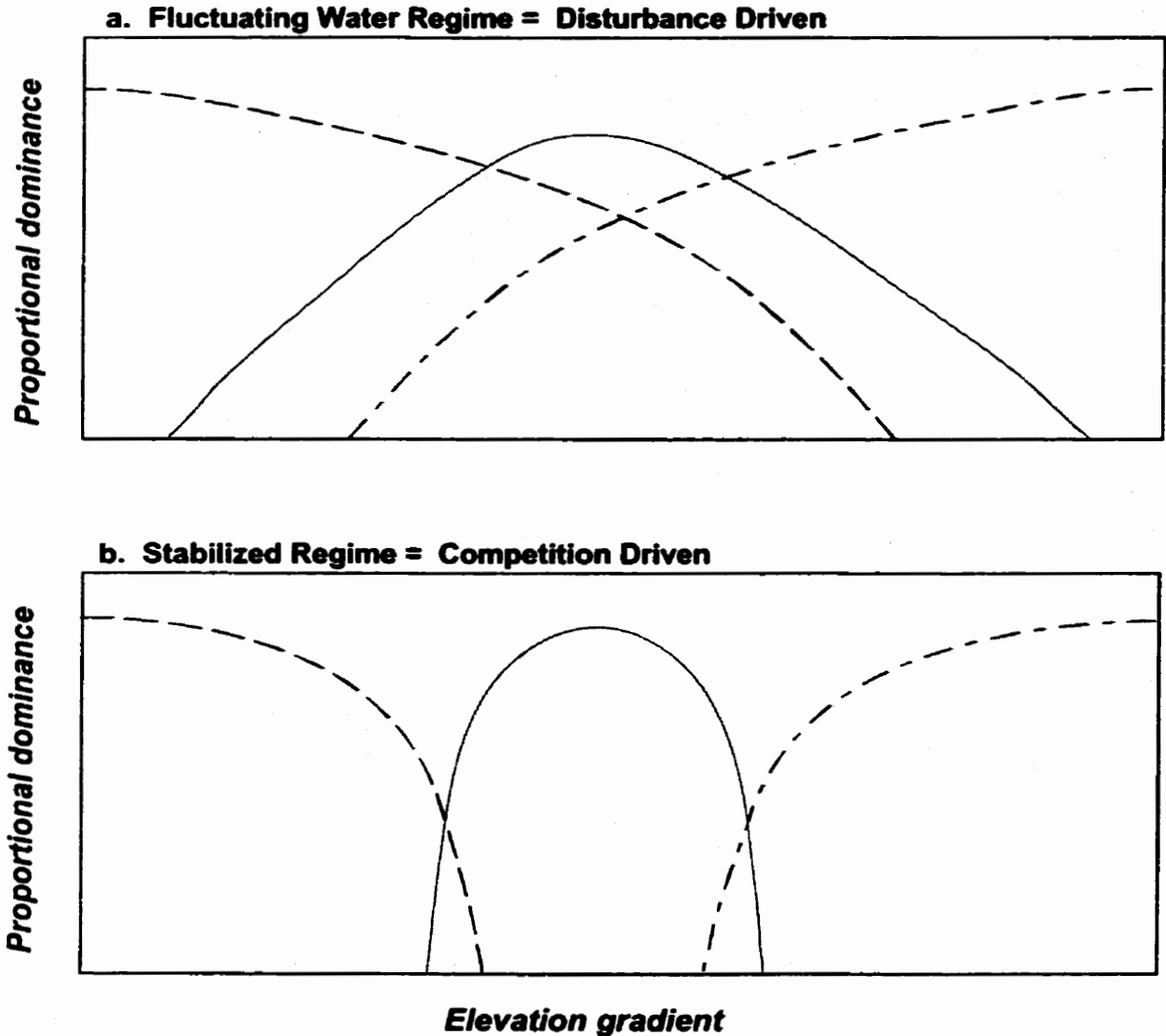


Figure 4.18. **a.** In a fluctuating water regime significant changes in vegetation composition occurs (i.e. high species turnover), resulting in considerable species overlap and diversity. **b.** Without fluctuating water levels dense monodominant plant zones develop, forming distinct species segregation along the elevation gradient. Patterns of proportional dominance developing along the elevation gradient under these water level regimes are similar to fundamental (**a.**) and realized responses (**b.**). Fundamental resource-use patterns occur in the absence of competition from neighbours, whereas realized resource-use patterns occur with competition. For competition to be occurring realized responses must be narrower than fundamental responses.

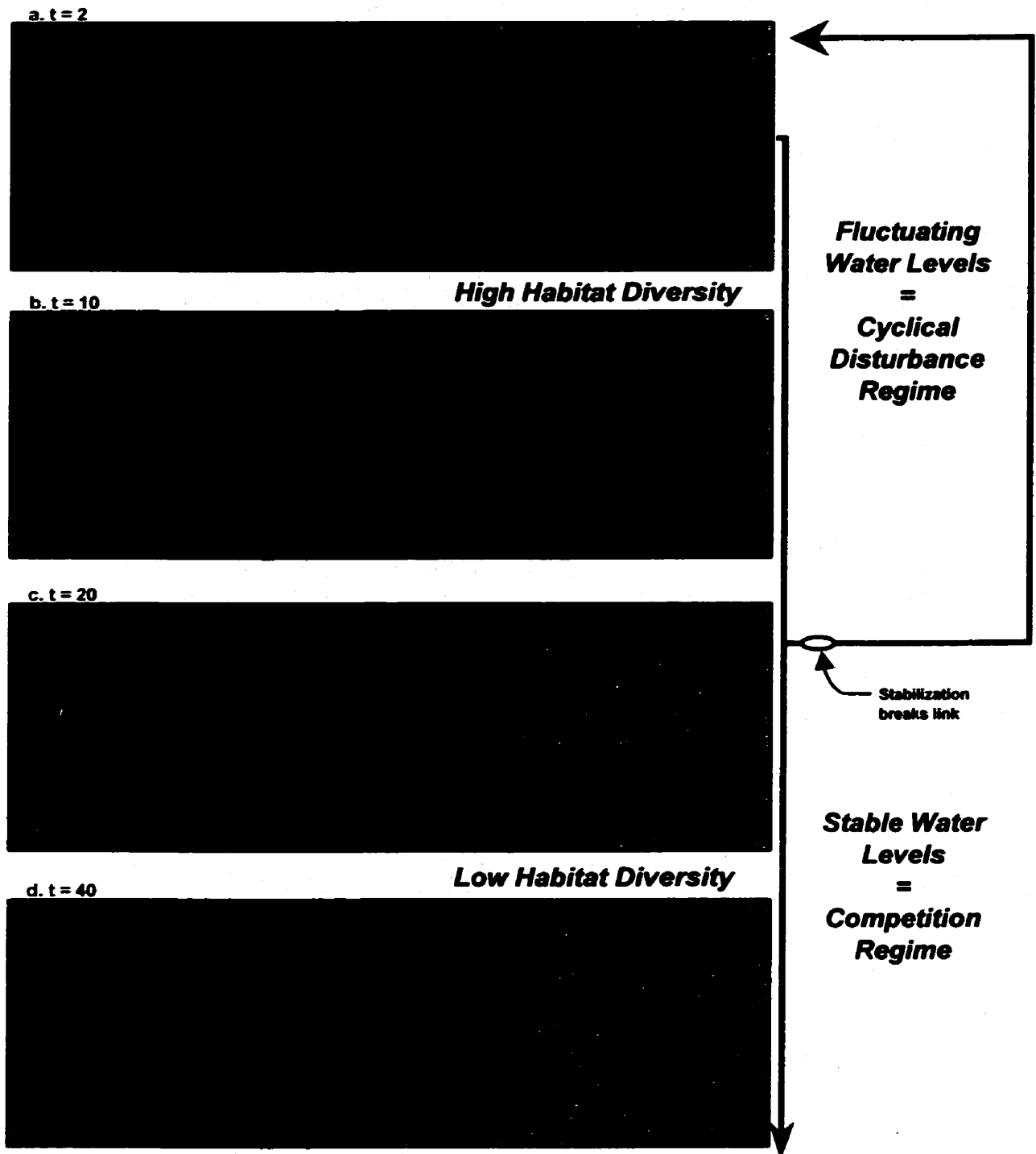


Figure 4.19. Spatial patterns of competing species along an environmental gradient after a. 2, b. 10, c. 20, and d. 40 generations respectively. Drk grey: sp. 1, lt. grey sp. 2, black: transition zone between sp. 1 and 2. With regards to the MERP marshes, the environmental gradient represents elevation with cattail (sp. 1) at flooded and *Phragmites* (sp. 2) at waterlogged areas respectively. The transition zone represents elevation range where whitetop could potentially inhabit due to the secondary factor of salinity buildup.

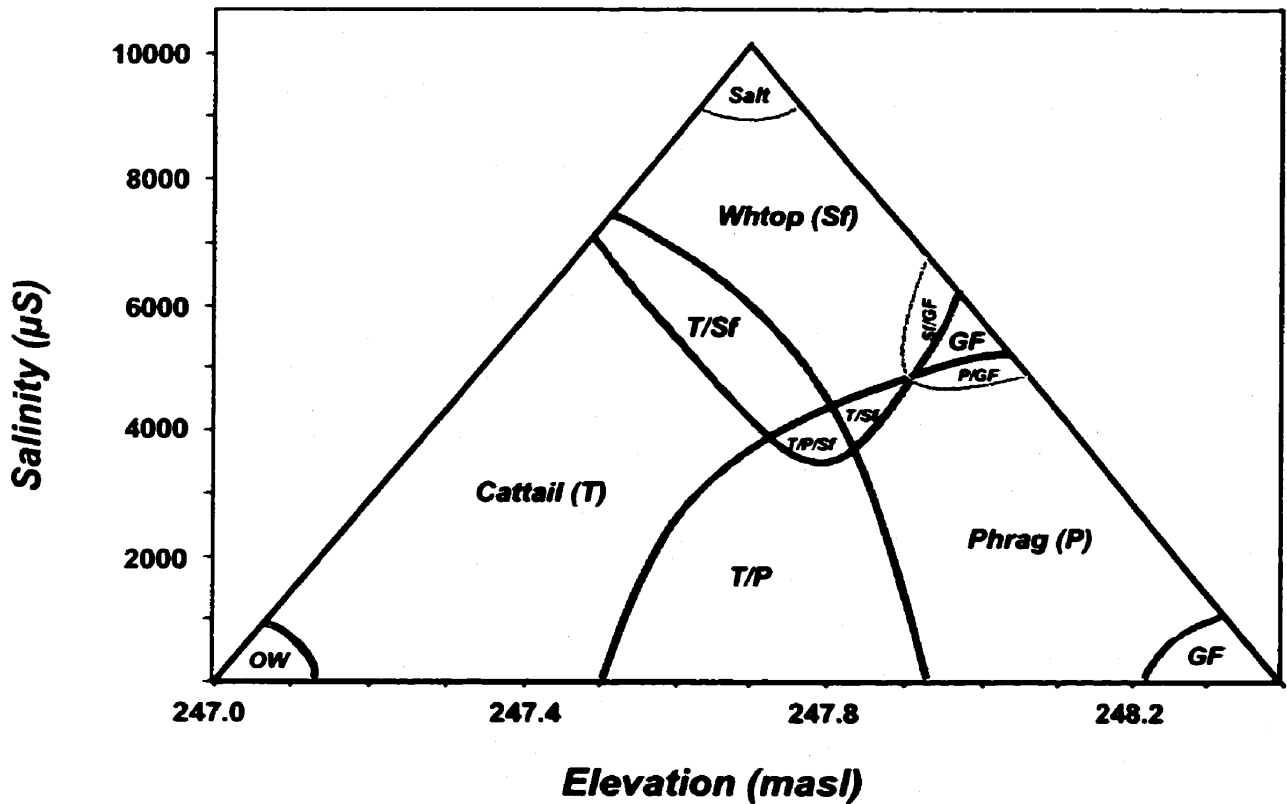


Figure 4.20. The Prairie Marsh Stabilized Regime model indicates that in the stabilized regime of the MERP marshes, dominant plants not only sort themselves out along the elevation gradient (primarily flood tolerance) but further sort themselves according to salinity. With prolonged stabilization this influence increases, with interspecific competition becoming a major driving force in shaping vegetation patterns. Dominant plant zones include open water (OW), cattail (T, Typha), whitotop (Sf, Whtop), *Phragmites* (P, Phrag), grasses/forbs (GF) as well as highly saline areas (Salt). The highest Salt zone includes salt flat species such as foxtail (*Hordeum jubatum*) and orache (*Atriplex patula*). The upper GF zone located at 248.0 m asl includes species associated with wetter slightly saline areas, such as stinging nettle (*Urtica dioica*) and various mint, whereas the lower GF zone above 248.2 m asl includes low prairie species such as Canada thistle (*Cirsium arvense*) and Canada goldenrod (*Solidago canadensis*).

Table 4.1. Mean elevation ranges (m asl) and associated mean conductivities (μ Siemens), mean water depth (cm), mean pH, and average percent cover of the dominant macrophytes in the MERP experimental marshes. Highest abundance range of each species is indicated.

Elev (m asl)	Cond. (μ S)	pH	Water depth (cm)	Sago pondweed <i>Potamogeton pectinatus</i>	Cattail <i>Typha spp.</i>	Whitetop <i>Scolochloa festucea</i>	Giant reed grass <i>Phragmites australis</i>	Canada goldenrod <i>Solidago canadensis</i>	Canada thistle <i>Cirsium arvense</i>	Sow thistle <i>Sonchus arvensis</i>
246.99	2500.0	8.5	56 cm	75.00	0	0	0	0	0	0
247.05	3009.1	8.2	50 cm	28.64	0	0	0	0	0	0
247.08	2765.0	8.1	47 cm	40.75	11.50	0	0	0	0	0
247.13	2863.6	8.1	42 cm	30.00	13.64	0	0	0	0	0
247.18	2963.3	8.0	37 cm	23.17	25.83	0	0	0	0	0
247.23	3014.3	8.0	32 cm	17.14	32.86	0	0	0	0	0
247.29	3173.1	7.9	26 cm	15.19	41.08	0	0	0	0	0
247.34	3118.0	7.6	21 cm	13.00	46.80	0	0.08	0	0	0
247.39	3342.0	7.6	16 cm	7.20	49.20	0	1.20	0	0	0
247.43	3201.9	7.5	12 cm	5.00	52.55	0.47	2.11	0	0	0
247.48	3309.9	7.5	7 cm	0.28	51.35	2.92	5.75	0	0	0
247.53	3058.7	7.2	2 cm	0.11	61.13	6.96	12.02	0	0	0
247.59	3234.4	7.2	-4 cm	0	63.47	13.88	13.51	0.58	0.47	0.23
247.63	4005.0	7.3	-8 cm	0	40.15	47.22	8.52	0	0	1.09
247.69	4624.8	7.5	-14 cm	0	36.25	36.64	20.04	0.04	0.36	1.79
247.73	4393.2	7.9	-18 cm	0	37.64	53.23	21.59	0	5.23	5.50
247.79	4660.0	7.5	-24 cm	0	27.13	46.33	32.00	1.33	5.33	7.33
247.87	3573.0	7.8	-32 cm	0	3.96	34.00	50.68	1.60	8.88	5.16
248.09	2982.8	7.9	-54 cm	0	0.74	12.91	51.26	20.88	28.32	28.12

Table 4.2. Dominant species-environment relations. Given is highest mean conductivity (μS), mean elevation (masl), and the conductivity and elevation ranges of sites dominated by respective species.

Species/Vegetation zone	Highest mean cond. ($\mu\text{Siemens}$)	Conductivity range ($\mu\text{Siemens}$)	Mean elevation (masl)	Elevation range (masl)
Open water	4600.0	2100 - 4600	247.19	246.98 - 247.53
Bulrush (<i>Scirpus</i> spp.)	4616.7	3000 - 5500	247.48	247.40 - 247.51
Cattail (<i>Typha</i> spp.)	5050.0	950 - 9000	247.46	247.07 - 247.90
Whitetop (<i>Scolochloa festucacea</i>)	6466.7	1200 - 10500	247.71	247.50 - 247.95
Phragmites (<i>Phragmites australis</i>)	3300.0	420 - 4600	247.82	247.45 - 248.50
Grasses/forbs	5900.0	410 - 11500	247.99	247.72 - 248.40

Table 4.3. Frequency of occurrence of dominant vegetation zones within elevation ranges (masl) of the MERP experimental marshes for **a.** 1989 and **b.** 1997. Vegetation zones include open water (OW), submergents (subs), bulrush (bul), alkali bulrush (sm), cattail (T), whitetop (Sf), *Phragmites* (P), grasses/forbs (GF), and foxtail/saline flats (Hj/salt). Dead patches are indicated by "D" followed by the species (i.e. DT = dead cattail).

a. 1989 frequency of occurrence of vegetation zones within the MERP marshes.

Elev. (masl)	1989 OW	1989 subs	1989 bul	1989 sm	1989 T	1989 DT	1989 Sf	1989 DSf	1989 car	1989 P	1989 DP	1989 GF	1989 salt	1989 total
247.03	0.74	0.00	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.08	0.60	0.00	0.20	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.13	0.50	0.00	0.19	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.19	0.38	0.00	0.20	0.00	0.35	0.00	0.00	0.03	0.00	0.05	0.00	0.00	0.00	1.00
247.24	0.41	0.00	0.21	0.00	0.31	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	1.00
247.29	0.28	0.00	0.15	0.00	0.41	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	1.00
247.34	0.41	0.00	0.06	0.00	0.31	0.00	0.03	0.00	0.00	0.19	0.00	0.00	0.00	1.00
247.39	0.47	0.00	0.05	0.00	0.34	0.00	0.03	0.00	0.00	0.11	0.00	0.00	0.00	1.00
247.43	0.39	0.00	0.11	0.00	0.25	0.00	0.06	0.02	0.00	0.17	0.00	0.00	0.00	1.00
247.48	0.30	0.00	0.05	0.01	0.33	0.00	0.10	0.02	0.01	0.17	0.00	0.00	0.00	1.00
247.53	0.17	0.00	0.07	0.06	0.31	0.00	0.20	0.05	0.01	0.12	0.00	0.00	0.00	1.00
247.59	0.10	0.01	0.01	0.03	0.30	0.00	0.28	0.06	0.03	0.13	0.00	0.00	0.04	1.00
247.63	0.22	0.03	0.00	0.00	0.11	0.00	0.36	0.10	0.01	0.08	0.00	0.01	0.07	1.00
247.69	0.18	0.00	0.00	0.00	0.18	0.00	0.27	0.00	0.04	0.18	0.00	0.09	0.05	1.00
247.76	0.16	0.00	0.02	0.03	0.06	0.00	0.30	0.02	0.03	0.30	0.00	0.05	0.05	1.00
247.86	0.04	0.00	0.00	0.04	0.14	0.00	0.18	0.02	0.00	0.39	0.00	0.14	0.04	1.00
247.96	0.00	0.00	0.00	0.00	0.08	0.00	0.12	0.00	0.00	0.50	0.08	0.15	0.08	1.00
248.18	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00	0.16	0.29	0.04	0.38	0.00	1.00

b. 1997 frequency of occurrence of vegetation zones within the MERP marshes.

Elev. (masl)	1997 OW	1997 subs	1997 bul	1997 sm	1997 T	1997 DT	1997 Sf	1997 DSf	1997 car	1997 P	1997 DP	1997 GF	1997 salt	1997 total
247.03	0.74	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.08	0.58	0.26	0.00	0.00	0.13	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.13	0.35	0.24	0.00	0.00	0.29	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.19	0.41	0.03	0.00	0.00	0.35	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.24	0.28	0.06	0.00	0.00	0.42	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.29	0.23	0.00	0.00	0.00	0.45	0.30	0.00	0.00	0.00	0.00	0.03	0.00	0.00	1.00
247.34	0.26	0.06	0.00	0.00	0.49	0.17	0.00	0.00	0.00	0.00	0.03	0.00	0.00	1.00
247.39	0.16	0.05	0.05	0.00	0.56	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
247.43	0.14	0.00	0.08	0.00	0.59	0.14	0.00	0.00	0.00	0.04	0.01	0.00	0.00	1.00
247.48	0.03	0.00	0.14	0.00	0.52	0.16	0.04	0.00	0.01	0.09	0.01	0.00	0.00	1.00
247.53	0.04	0.00	0.06	0.00	0.56	0.06	0.07	0.00	0.00	0.19	0.03	0.00	0.00	1.00
247.59	0.00	0.00	0.01	0.00	0.49	0.03	0.16	0.00	0.03	0.25	0.01	0.00	0.00	1.00
247.63	0.00	0.00	0.05	0.00	0.39	0.02	0.39	0.00	0.03	0.13	0.00	0.00	0.00	1.00
247.69	0.00	0.00	0.00	0.00	0.33	0.04	0.25	0.00	0.00	0.30	0.04	0.05	0.00	1.00
247.76	0.00	0.00	0.01	0.00	0.24	0.00	0.35	0.00	0.01	0.32	0.01	0.06	0.00	1.00
247.86	0.00	0.00	0.00	0.00	0.07	0.00	0.24	0.00	0.00	0.51	0.02	0.13	0.02	1.00
247.96	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.55	0.00	0.27	0.05	1.00
248.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.46	0.00	0.54	0.00	1.00

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Appendix I. Vegetation Classification Descriptions of the MERP marshes

1. Non-vegetated (no emergent macrophytes)

1A. Open water (no emergents, often submergents)

Permanent open water areas devoid of emergent vegetation. Water depth averages <1 metre but can reach a maximum depth of up to 3 metres within the borrow pits. Deeper areas typically have no vegetation whereas shallow areas support beds of submersed plants, typically pondweed (*Potamogeton* spp.) and coontail (*Ceratophyllum demersum*).

1B. Submergents and free floating

Dominant submersed species include pondweed (*Potamogeton* spp.), coontail (*Ceratophyllum demersum*), water milfoil (*Myriophyllum sibiricum*), and bladderwort (*Utricularia macrorhiza*). Dense mats of duckweed (*Lemna minor*, *L. trisulca*) may also be found in sheltered areas.

2. Emergent Vegetation (permanently-seasonally flooded)

2A. Bulrush (*Scirpus*)

Monodominant stands of bulrush (*Scirpus* spp.) including the taller round stemmed hard- and soft-stem bulrush (*S. acutus* and *S. tabernaemontani*) as well as the coarser three-sided alkali bulrush (*S. maritimus*). Hard- and soft-stem bulrush grow mainly along permanent open water borders and tolerate deeper water habitats, while Alkali bulrush tends to grow in shallower disturbed locations and areas where soils are slightly more saline. Submersed species are often present, including bladderwort (*Utricularia macrorhiza*), pondweed (*Potamogeton* spp.) and water milfoil (*Myriophyllum sibiricum*) as well as the free-floating duckweeds (*Lemna minor*, *L. trisulca*). Very few bulrush stands remain within the MERP marshes.

2B. Cattail (*Typha*)

Dense, monodominant stands of cattail (*Typha* spp.) are composed largely of a hybrid (*Typha* x *glauca*) between *T. latifolia* and *T. angustifolia* in varying characteristic degrees towards either parental species. Stands are typically dense with an extremely thick understory of fallen and standing deadfall. Cattail within the MERP marshes grows up to 2 metres in

height and survives a range of water depths from 0 to 2 metres. It is extremely widespread throughout the MERP marshes, also forming dense floating mats or islands in deeper waters. Cattail usually borders open water and forms transition areas with whitetop (*Scolochloa festucacea*) and giant reed (*Phragmites australis*). Understory species include whitetop, awned sedge (*Carex atherodes*), cursed crowfoot (*Ranunculus sceleratus*) and aquatic mosses. Submersed vegetation is often present in standing water, primarily bladderwort (*Utricularia macrorhiza*), as well as free floating duckweeds (*Lemna minor*, *L. trisulca*). Cattail is an aggressive, competitive species dominant throughout the MERP marshes.

2C. Giant reed grass (*Phragmites australis*)

Monodominant stands of giant reed grass (*Phragmites australis*) can be found in standing water, but typically grow in water-logged organic soils above the water table. These stands have also accumulated extremely dense layers of fallen and standing deadfall. Average height of *Phragmites* is around 2 metres, often reaching heights up to 3 metres. Reeds often form transition areas with cattail (*Typha* spp.) or whitetop (*Scolochloa festucacea*), and form borders along the dykes surrounding the MERP marshes. Understory dominants include Canada thistle (*Cirsium arvense*), sow thistle (*Sonchus arvensis*), water hemlock (*Cicuta maculata*), stinging nettle (*Urtica dioica*) and a variety of mints (*Teucrium canadense*, *Mentha canadensis*, *Lycopus asper*, *Stachys palustris*, *Scutellaria galericulata*) depending on soil moisture. Other representative species found in lower abundance are hedge bindweed (*Calystegia sepium*), wild cucumber (*Echinocystis lobata*) and black bindweed (*Polygonum convolvulus*).

3. Wet meadow (seasonally-temporarily flooded)

3A. Sedges and rushes (*Carex*, *Eleocharis*, *Juncus*)

These areas are characterized by flooding for a few weeks in the spring, with 0 to 0.3 metres of surface water persisting until early-summer. Soil water usually remains within the rooting zone throughout the growing season. Sedges and rushes typically occur near or within wet meadows of class 3B, as well as bordering patches of class 2B and 2C. These patches are mostly dominated by dense stands of awned sedge (*Carex atherodes*) and beaked sedge (*C. retrorsa*). Those areas found adjacent to zones 3B and 3C and those near zone 4, are typically dominated by fine textured rushes and sedges (**Table 3.3**). Characteristic taxa include sedges (*Carex* spp.), spike rushes (*Eleocharis* spp.), rushes (*Juncus* spp.) and alkali

bulrush (*Scirpus maritimus*), with lower abundance of whitetop (*Scolochloa festucacea*) and crowfoot (*Ranunculus* spp.).

3B. Whitetop (*Scolochloa festucacea*)

These dense monodominant patches of whitetop (*Scolochloa festucacea*) are usually inundated for a few weeks in the spring, with 0 to 0.3 metres of surface water persisting until mid-summer. Soil in the rooting zone remains saturated throughout the growing season. Whitetop typically grows in dense stands on the margins of zones 2B and 2C, as well as bordering zones 3 and 4. This marsh grass, which typically inhabits areas of higher soil salinity, reaches heights from 1 –1.4 metres. Whitetop is the typical wet meadow transition between marsh emergents and low prairie vegetation. Understory species (**Table 3.3**) include awned sedge (*Carex atherodes*), various mints (*Teucrium canadense*, *Mentha canadensis*, *Lycopus asper*, *Stachys palustris*), sow thistle (*Sonchus arvensis*), Canada thistle (*Cirsium arvense*), water hemlock (*Cicuta maculata*), smartweed (*Polygonum* spp.) and foxtail (*Hordeum jubatum*), all dependent on standing water or soil moisture.

3C. Foxtail/salt flat species (*Hordeum*, *Puccinellia*, *Suaeda*)

These are poorly drained areas where soils are more saline. Found where the water table is at or near the soil surface, these areas are often waterlogged in the early spring. As water levels fall, salts are brought to the surface by capillarity and are concentrated through surface evaporation (Brady 1990). Small patches occur throughout the MERP marshes (usually associated with zones 3B, and 4, however, the only significant patches occur within marshes I and II). Characteristic dominant species (**Table 3.3**) are foxtail (*Hordeum jubatum*), salt meadow grass (*Puccinellia nuttalliana*), sea-blite (*Suaeda calceoliformis*), orache (*Atriplex patula*), lamb's quarters (*Chenopodium album*) and sow thistle (*Sonchus arvensis*), with lower abundance of couch grass (*Elytrigia repens*), rayless aster (*Brachyactis ciliata*) and red samphire (*Salicornia rubra*). Other representative species found in low abundance are Canada thistle (*Cirsium arvense*) and whitetop (*Scolochloa festucacea*).

4. Grasses and forbs (i.e. low prairie, temporary to no flooding)

These areas are typical grassy patches, characterized by varying proportions of grasses and forbs. Typically throughout the MERP marshes, these patches are characterized by > 50% grass and < 50% forb cover. These areas may experience brief flooding to saturated soil

conditions in the early spring, rapidly lost to evapotranspiration and seepage, with soil moisture varying throughout the growing season. They are typically dominated by low to intermediate grasses and forbs including blue grass (*Poa* spp.), sow thistle (*Sonchus arvensis*), Canada thistle (*Cirsium arvense*), Canada goldenrod (*Solidago canadensis*), blue lettuce (*Lactuca tatarica*) and asters (*Aster* spp.). Less abundant species include couch grass (*Elytrigia repens*), salt meadow grass (*Puccinellia nuttalliana*), foxtail (*Hordeum jubatum*), awnless brome (*Bromus inermis*), sedges (*Carex* spp.), germander (*Teucrium canadense*), and common mint (*Mentha canadensis*). Patches found at slightly higher elevations, within marshes 10 and 11, are dominated primarily by mixed upland grasses, forbs and shrubs, characterized by > 50% forb and < 50% grass cover. Dominant species include awnless brome (*Bromus inermis*), blue grass (*Poa* spp.), Canada thistle (*Cirsium arvense*), sow thistle (*Sonchus arvensis*), Canada goldenrod (*Solidago canadensis*), asters (*Aster* spp.), blue lettuce (*Lactuca tatarica*), and snowberry (*Symphoricarpus occidentalis*). Species of lower abundance are couch grass (*Elytrigia repens*), Canada wild rye (*Elymus canadensis*), foxtail (*Hordeum jubatum*), and redtop (*Agrostis stolonifera*).

5. Trees (i.e. tree and shrub cover, little to no flooding)

These areas include trees, willows and tall shrub cover where slightly higher elevations along the dykes and ridge road enable these species to grow. Dense deciduous tree and shrub cover characterizes the forested beach ridge north of the MERP marshes, separating Delta marsh from Lake Manitoba. Representative trees of the ridge include Manitoba maple, or boxelder (*Acer negundo*), hackberry (*Celtis occidentalis*), green ash (*Fraxinus pennsylvanica*), plains cottonwood (*Populus deltoides*), chokecherry (*Prunus virginiana*) and American elm (*Ulmus americana*). Understory species include dogwood (*Cornus sericea*), stinging nettle (*Urtica dioica*), wild sarsaparilla (*Aralia nudicaulis*), Virginia creeper (*Parthenocissus quinquefolia*), Joe Pye Weed (*Eupatorium maculatum*), awnless brome (*Bromus inermis*), blue grass (*Poa* spp.), Canada thistle (*Cirsium arvense*), Canada goldenrod (*Solidago canadensis*), hedge bindweed (*Calystegia sepium*), black bindweed (*Polygonum convolvulus*), wild cucumber (*Echinocystis lobata*) and poison ivy (*Toxicodendron radicans*). Generally, only willow thickets (*Salix* spp.) and chokecherry bluffs occur along the northern edges of the MERP marshes themselves.

Appendix II. Microsoft Excel Prairie Marsh Transition Matrix Macro.

Dim TransMatrix, PropArray, MyOut As Range

Dim TempProp As Double

,

' **Macro2 Macro**

' **Macro recorded 3/11/99 by N. Kenkel**

,

' **Keyboard Shortcut: Option+Cmd+h**

,

Sub Macro2()

Set TransMatrix = Application.InputBox(Prompt:="Select the Transition Matrix:",
Title:="Matrix Input" _ , Type:=8)

Set PropArray = Application.InputBox(Prompt:="Select the initial species proportions" _
Title:="Proportions Input", Type:=8)

PropArray.Offset(1, 0).Select

Set MyOut = Selection

NumSpecies = PropArray.Columns.Count

For reps = 1 To 100

For j = 1 To NumSpecies

TempProp = 0

For i = 1 To NumSpecies

TempProp = PropArray.Cells(1, i).Value * TransMatrix.Cells(i, j).Value + TempProp

Next

MyOut.Cells(1, j).Value = TempProp

Next

Set PropArray = MyOut

Set MyOut = MyOut.Offset(1, 0)

Next

MyOut.Select

End Sub

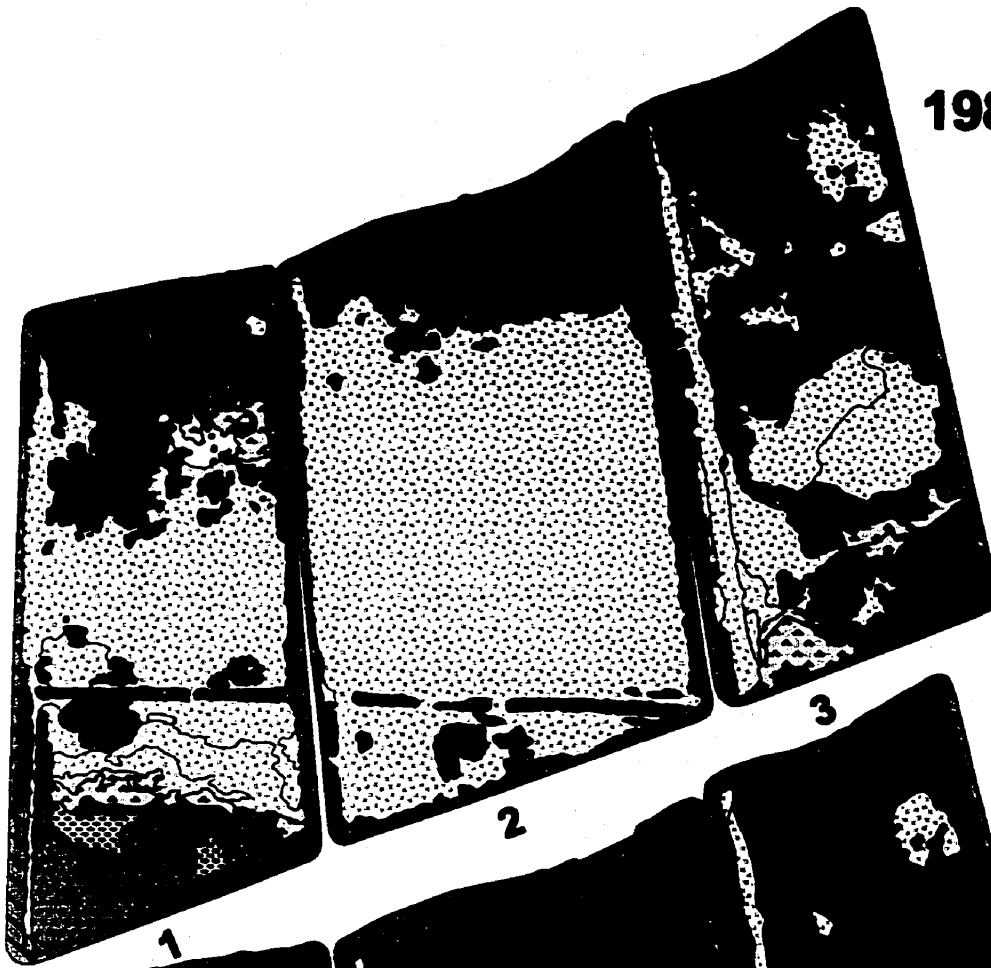
Appendix III. Plant species list for the MERP experimental marshes. Species listed alphabetically by scientific name from Kartesz (1994), with more familiar names from Scoggans (1979) also listed. Also listed are common names, taxonomic Family (both scientific and common name), forms of the plant (tree, shrub, grass, forb, carex, submerged, emergent (present in standing to wet/moist soil conditions) or aquatic (free floating on water). Given is abundance (dominant, common, uncommon or rare), distribution of the plants (zones these are plants are mostly found). Listed is also if the plant is ubiquitous throughout the MERP marshes or limited to certain areas.

NAME	Scientific (Kartesz 1994)	(Scoggans 1979)	Common	Family Scientific	Common	FORM ABUNDANCE DISTRIBUTION		
	<i>Atriplex patula</i>		orache, sparsely	Chenopodiaceae	Goosefoot	forb	dominant	foxtail/salt flat, sow thistle, grass/forbs - ubiquitous
	<i>Brachyactis ciliaris</i> ssp. <i>Angusta</i>		rayless aster	Asteraceae	Asters	forb	rare, local	mudflats
	<i>Bromus inermis</i>		awnless brome	Poaceae (Graminae)	Grass	grass	rare, local	grass/forbs
	<i>Calystegia sepium</i>		morning glory, hedge bindweed	Convolvulaceae	Morning-glory	forb	common	Phragmites
	<i>Carex asinibolensis</i>		sedge	Cyperaceae	Sedge	car	common	carex, whitetop, catail
	<i>Carex altherodes</i>		awned sedge	Cyperaceae	Sedge	car	common	carex, whitetop, catail, phragmites
	<i>Carex retrorsa</i>		sedge	Cyperaceae	Sedge	car	common	carex, whitetop, catail, phragmites
	<i>Ceratophyllum demersum</i>		coontail	Ceratophyllaceae	Hornwort	sub	uncommon	bulrush, typha, open water
	<i>Chenopodium album</i>		lamb's quarters	Chenopodiaceae	Goosefoot	forb	uncommon	mudflats, muskrat mounds
	<i>Cleista maculata</i>		water hemlock, spotted cowbane	Umbelliferae	Parley	erect	common	Phragmites, catail, whitetop
	<i>Cirsium arvense</i>		Canada thistle	Asteraceae	Asters	forb	dominant	grass/forbs, disturbed, whitetop, Phragmites - ubiquitous
	<i>Cuscuta gronovii</i>		viny berry, dodder	Convolvulaceae	Morning-glory	forb	rare, local	Phragmites
	<i>Echinocystis lobata</i>		wild cucumber	Cucurbitaceae	Cucumber	forb	common	Phragmites
	<i>Eleocharis acicularis</i>		spike rush	Cyperaceae	Sedge	car	common	carex, whitetop, catail
	<i>Elymus trachycalus</i> ssp. <i>subsecundus</i>		slender wheatgrass, couch-grass	Poaceae (Graminae)	Grass	grass	dominant	grass/forb, foxtail/salt flat - ubiquitous
	<i>Elytrigia repens</i>		quackgrass, couch-grass	Poaceae (Graminae)	Grass	grass	dominant	grass/forb, foxtail/salt flat - ubiquitous
	<i>Eupatorium maculatum</i>		Joe-Pye-Weed	Asteraceae	Asters	forb	rare, local	grass/forbs, ridge road
	<i>Hordeum jubatum</i>		foxtail, wild barley, equine-tail grass	Poaceae (Graminae)	Grass	grass	dominant	foxtail/salt flat, whitetop, sow thistle - ubiquitous
	<i>Juncus balticus</i> var. <i>littoralis</i>		bulbic rush	Juncaceae	Rush	car	common	carex, whitetop, catail
	<i>Lactuca tatarica</i>		blue lettuce	Asteraceae	Asters	forb	common	grass/forb, Phragmites
	<i>Lemna minor</i>		lesser duckweed	Lemnaceae	Duckweed	aqua	v. common	catail, phragmites, whitetop, open water - ubiquitous in standing water
	<i>Lemna trisulca</i>		star duckweed	Lemnaceae	Duckweed	aqua	v. common	catail, phragmites, whitetop, open water - ubiquitous in standing water
	<i>Lycopus asper</i>		western water horehound	Labiatae	Mint	forb	dominant	Phragmites, grass/forb, whitetop
	<i>Mentha canadensis</i>		common mint	Labiatae	Mint	forb	dominant	Phragmites, grass/forb, whitetop
	<i>Myriophyllum sibiricum</i>		water milfoil	Haloragaceae	Water-milfoil	sub	uncommon	open water
	<i>Phragmites australis</i>		Phragmites, cane reed	Poaceae (Graminae)	Grass	erect	dominant	Phragmites, catail, whitetop, sow thistle - ubiquitous
	<i>Poa palustris</i>		foxt blue grass, foxt meadow-grass	Poaceae (Graminae)	Grass	grass	dominant	grass/forb, phragmites, dyke
	<i>Poa pratensis</i>		Kentucky blue-grass	Poaceae (Graminae)	Grass	grass	dominant	grass/forb, phragmites, dyke
	<i>Polygonum amphibium</i> var. <i>emersum</i>		smartweed, swamp persicaria	Polygonaceae	Buckwheat	forb	uncommon	whitetop, carex

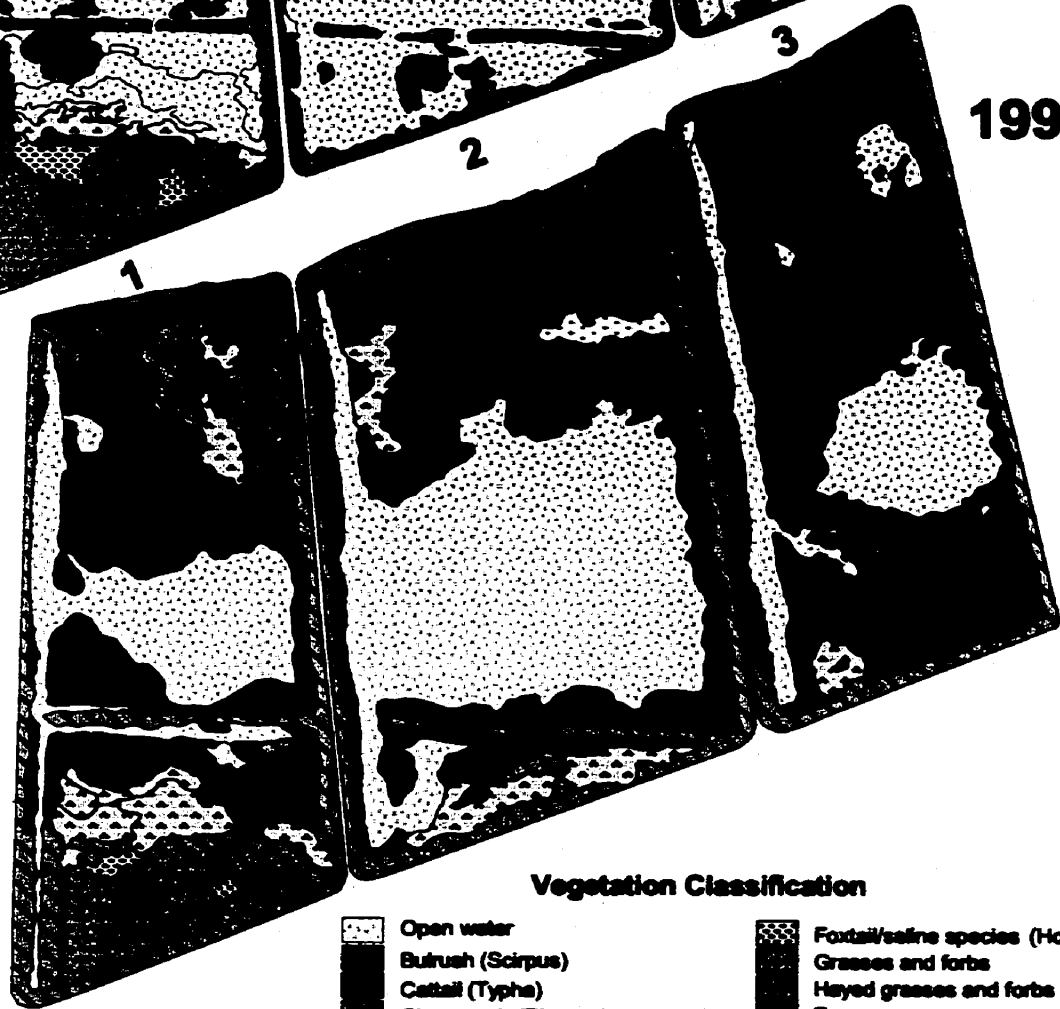
Appendix III. Cont'd. Plant species list for the MERP experimental marshes.

NAME Scientific (Kartesz 1994)	(Scoggans 1979)	Common	FAMILY Scientific	Common	FORM	ABUNDANCE	LOCATION
<i>Polygonum convolvulus</i>	<i>Polygonum convolvulus</i>	black bindweed, wild buckwheat	Polygonaceae	Buckwheat	forb	uncommon	Phragmites
<i>Potamogeton</i> sp.	<i>Potamogeton</i> sp.	pondweed	Zosteraceae	Pondweed	sub	dominant	open water
<i>Prunus virginiana</i>	<i>Prunus virginiana</i>	chokecherry	Rosaceae	Rose	shrub	rare, local	ridge road, dykes
<i>Puccinellia nuttalliana</i>	<i>Puccinellia nuttalliana</i>	salt meadow grass, alkali grass	Poaceae (Graminae)	Grass	grass	v. common	grass/forbs, foxtail/salt flats
<i>Ranunculus cymbalaria</i>	<i>Ranunculus cymbalaria</i>	seaside crowfoot	Ranunculaceae	Crowfoot	forb	rare, local	cattail, mudflats, whitetop
<i>Rosa arkansana</i>	<i>Rosa arkansana</i>	low prairie rose	Rosaceae	Rose	forb	rare, local	grass/forb, dykes
<i>Rumex aquaticus</i> var. <i>fenestratus</i>	<i>Rumex occidentalis</i>	western dock	Polygonaceae	Buckwheat	forb	rare, local	grass/forbs
<i>Salicornia rubra</i>	<i>Salicornia rubra</i>	red samphire	Chenopodiaceae	Goosefoot	forb	rare, local	foxtail/saline, roads
<i>Salix</i> spp.	<i>Salix</i> spp.	willow	Salicaceae	willow	tree	uncommon	dykes, Phragmites
<i>Scirpus acutus</i>	<i>Scirpus acutus</i>	hardstem bulrush	Cyperaceae	Sedge	emer	dominant	cattail, open water, bulrush
<i>Scirpus maritimus</i>	<i>Scirpus maritimus</i>	alkali bulrush	Cyperaceae	Sedge	emer	common	cattail, bulrush, carex, foxtail/saline
<i>Scirpus pungens</i>	<i>Scirpus americanus</i>	three square bulrush	Cyperaceae	Sedge	car	common	cattail, bulrush, carex, foxtail/saline
<i>Scirpus tabernaemontani</i>	<i>Scirpus validus</i>	softstem, great bulrush	Cyperaceae	Sedge	emer	dominant	cattail, open water, bulrush
<i>Scolochloa festucacea</i>	<i>Scolochloa festucacea</i>	whitetop, spangle-top	Poaceae (Graminae)	Grass	grass	dominant	whitetop, cattail, Phragmites, carex, fen grasses, grass/forbs
<i>Scutellaria galericularia</i>	<i>Scutellaria galericularia</i>	marsh skullcap, common skullcap	Labiatae	Mint	forb	common	Phragmites, grass/forbs, whitetop
<i>Solidago canadensis</i> var. <i>gilvocanescens</i>	<i>Solidago canadensis</i>	Canada goldenrod	Asteraceae	Asters	forb	dominant	grass/forbs, Phragmites, sow thistle - ubiquitous
<i>Sonchus arvensis</i> ssp. <i>ulliginosus</i>	<i>Sonchus arvensis</i>	sowthistle, field-sowthistle	Asteraceae	Asters	forb	dominant	grass/forbs, disturbed, whitetop, Phragmites, foxtail/saline - ubiquitous
<i>Spartina pectinata</i>	<i>Spartina pectinata</i>	alkali cord grass	Poaceae (Graminae)	Grass	grass	rare, local	whitetop, grass/forbs
<i>Stachys palustris</i> ssp. <i>pilosa</i>	<i>Stachys palustris</i>	marsh hedge-nettle, woundwort	Labiatae	Mint	forb	uncommon	Phragmites, whitetop, grass/forb
<i>Stellaria longifolia</i>	<i>Stellaria longifolia</i>	long-leaved chickweed	Caryophyllaceae	Pink	forb	rare, local	Phragmites
<i>Suaeda calceoliformis</i>	<i>Suaeda depressa</i>	sea-blite	Chenopodiaceae	Goosefoot	forb	dominant	foxtail/saline
<i>Symphoricarpos occidentalis</i>	<i>Symphoricarpos occidentalis</i>	snowberry	Caprifoliaceae	Honey-suckle	forb	common	grass/forbs, Phragmites
<i>Teucrium canadense</i> var. <i>occidentale</i>	<i>Teucrium occidentale</i>	mint, germander	Labiatae	Mint	forb	dominant	Phragmites, grass/forbs, whitop
<i>Typha angustifolia</i>	<i>Typha angustifolia</i>	narrow leaved cattail	Typhaceae	Cattail	emer	dominant	cattail, open water, bulrush, phragmites, mudflats, whitetop, carex - ubiquitous
<i>Typha latifolia</i>	<i>Typha latifolia</i>	common cattail	Typhaceae	Cattail	emer	dominant	cattail, open water, bulrush, phragmites, mudflats, whitetop, carex - ubiquitous
<i>Typha x glauca</i>	<i>Typha x glauca</i>	hybrid cattail	Typhaceae	Cattail	emer	dominant	cattail, open water, bulrush, phragmites, mudflats, whitetop, carex - ubiquitous
<i>Ulmus americana</i>	<i>Ulmus americana</i>	American elm	Ulmaceae	Elm	tree	rare	grass/forbs, dykes
<i>Urtica dioica</i> ssp. <i>gracilis</i>	<i>Urtica dioica</i>	stinging nettle	Urticaceae	Nettle	forb	dominant	Phragmites, grass/forb
<i>Utricularia macrothiza</i>	<i>Utricularia vulgaris</i>	common bladderwort	Lentibulariaceae	Bladderwort	sub	dominant	open water, cattail, phragmites

1989



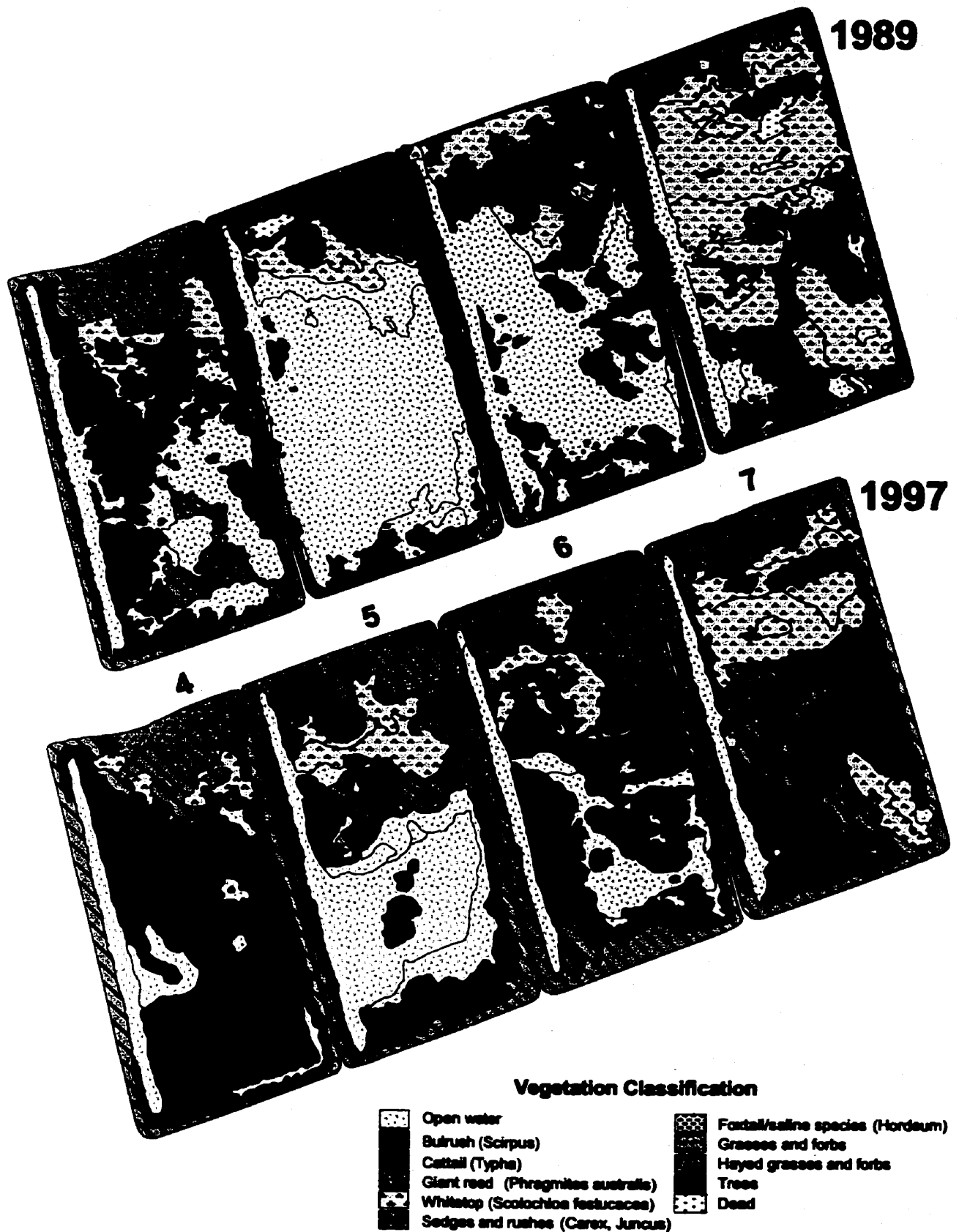
1997



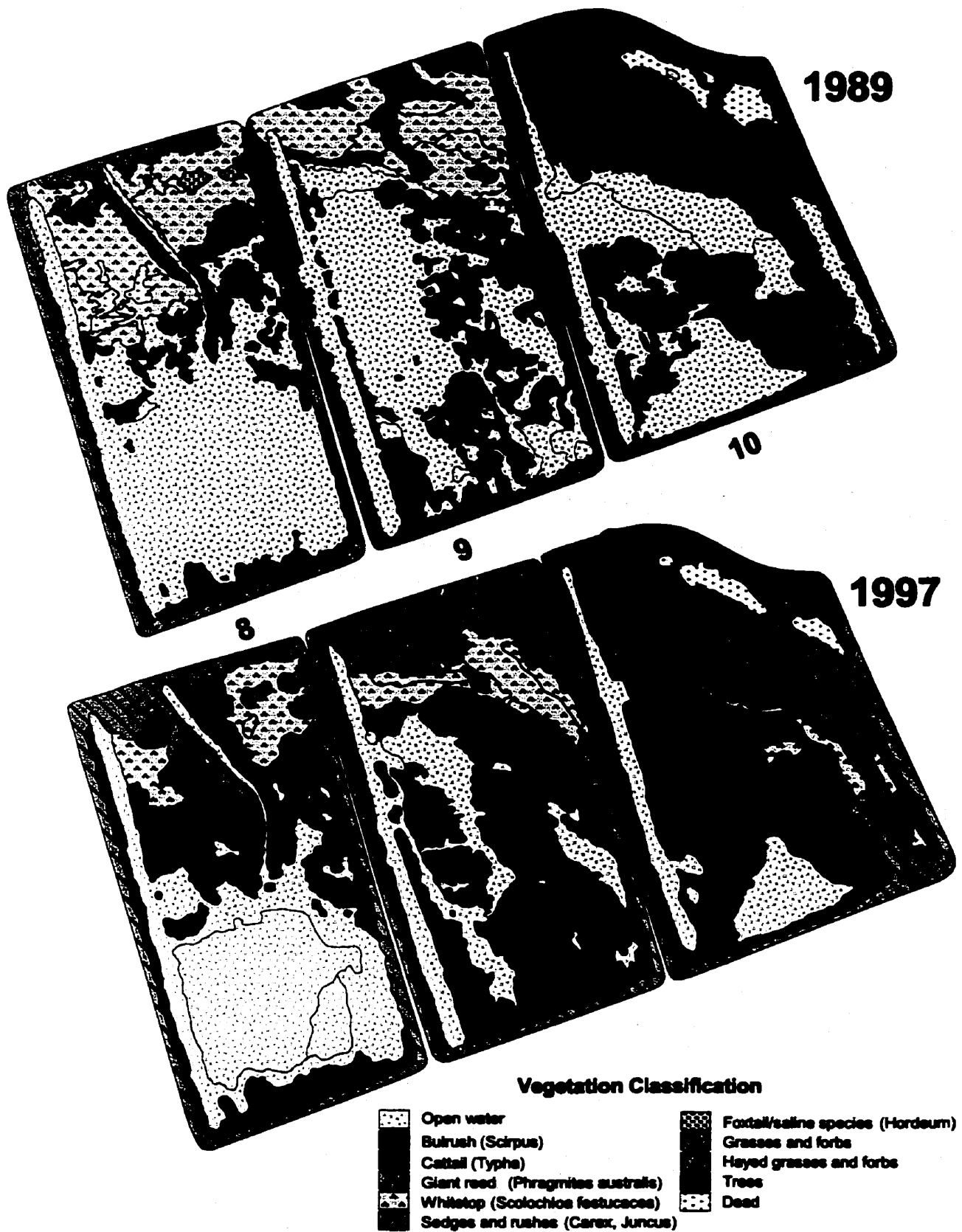
Vegetation Classification

	Open water		Foxtail/saline species (<i>Hordeum</i>)
	Bulrush (<i>Scirpus</i>)		Grasses and forbs
	Cattail (<i>Typha</i>)		Mixed grasses and forbs
	Giant reed (<i>Phragmites australis</i>)		Trees
	Whiteweed (<i>Scolochloa festucacea</i>)		Dead
	Sedges and rushes (<i>Carex, Juncus</i>)		

Appendix IVa. Vegetation classification of marshes 1, 2, and 3 of the MERP experimental marshes, Delta Marsh, Manitoba, Canada, showing vegetation zone composition. Within zone boundaries indicate subzones with differences in composition of secondary species and/or presence of open water.

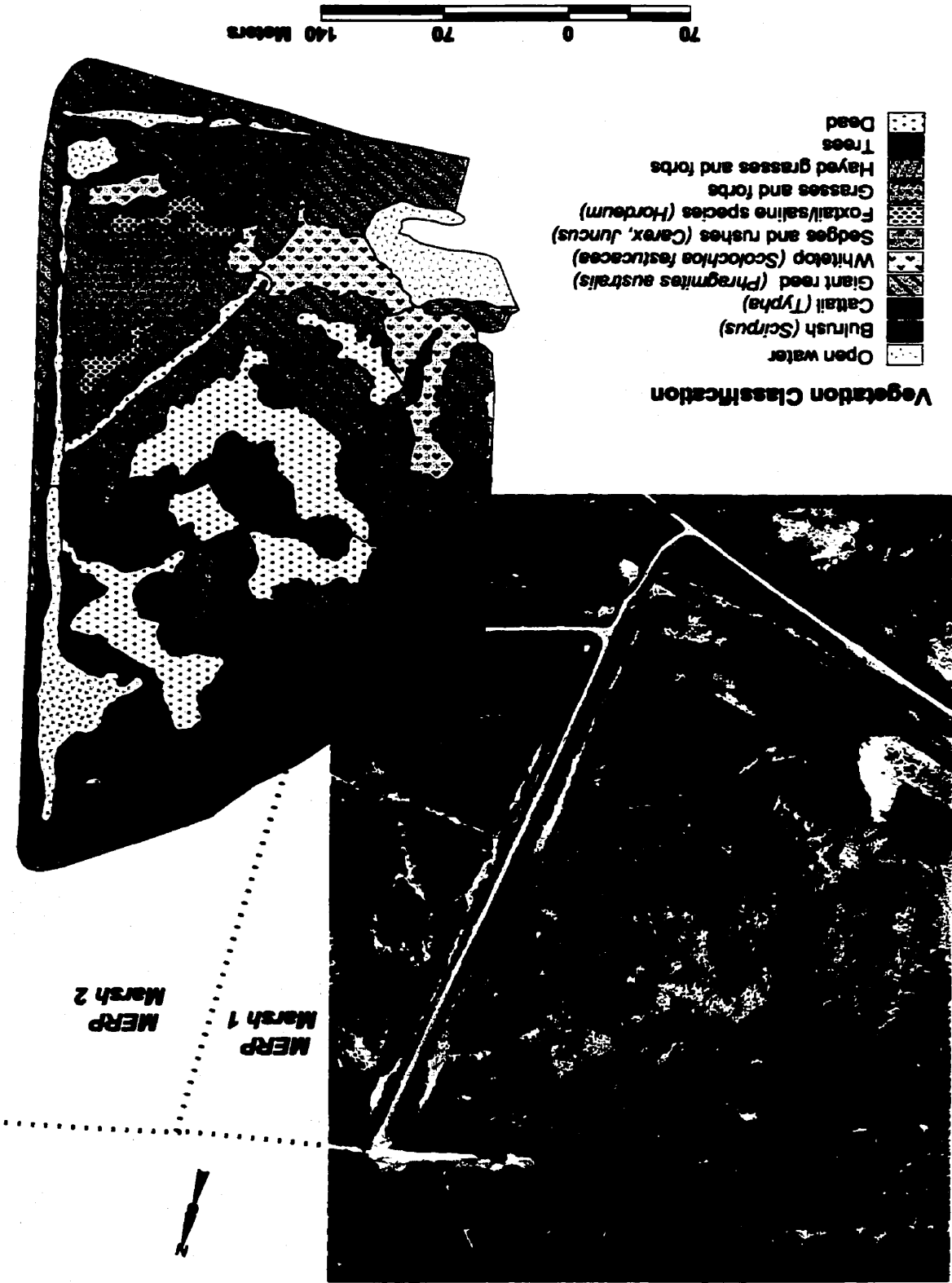


Appendix IVb. Vegetation classification of marshes 4, 5, 6, and 7 of the MERP experimental marshes, Delta Marsh, Manitoba, Canada, showing vegetation zone composition. Within zone boundaries indicate subzones with differences in composition of secondary species and/or presence of open water.



Appendix IVc. Vegetation classification of marshes 8, 9, and 10 of the MERP experimental marshes, Delta Marsh, Manitoba, Canada, showing vegetation zone composition. Within zone boundaries indicate subzones with differences in composition of secondary species and/or presence of open water.

Appendix IVd. 1997 Vegetation classification of MERP control marsh 11, located to the west of the experimental marshes in Delta Marsh, Manitoba, Canada, showing vegetation zone composition.



Vegetation Classification

- Open water
- Bulrush (*Scirpus*)
- Cattail (*Typha*)
- Giant reed (*Phragmites australis*)
- Whiteweed (*Scotocloa fastuosa*)
- Sedges and rushes (*Carex, Juncus*)
- Forb/saline species (*Hordeum*)
- Grasses and forbs
- Hayed grasses and forbs
- Trees
- Dead

Appendix V. Mean percent cover of all species within mean elevation ranges (masl) of the MERP experimental marshes. Low percent cover of species indicates their low abundance within the experimental marshes. Dead vegetation patches are indicated by "D" followed by species name (i.e. D Cat = dead cattail). Species abbreviations are listed in appendix V.

Elev. (masl)	Cond. (μ S)	pH	OW	Meta	Pwd	CoonT	Mil	Bladw	L Trl	L Min	Bul	Cat	Whtop	Phrag	Car	Sm
246.99	2500.0	8.5	100.0	100.0	75.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.05	3009.1	8.2	100.0	28.4	28.6	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.08	2765.0	8.14	87.3	45.4	40.8	5.0	0.0	18.5	11.0	12.0	0.0	11.5	0.0	0.0	0.0	0.0
247.13	2863.6	8.14	86.4	46.4	30.0	9.1	0.0	23.2	19.1	19.1	0.0	13.6	0.0	0.0	0.0	0.0
247.18	2963.3	8.04	60.0	25.8	23.2	3.0	0.0	25.8	7.0	5.2	0.0	25.8	0.0	0.0	0.2	0.0
247.23	3014.3	8.03	60.7	16.9	17.1	0.0	0.0	24.5	0.2	0.1	0.0	32.9	0.0	0.0	0.0	0.0
247.29	3173.1	7.94	53.9	4.4	15.2	0.0	0.0	26.0	7.9	9.2	0.0	41.1	0.0	0.0	0.0	0.0
247.34	3118.0	7.58	43.6	9.8	13.0	0.0	0.0	22.4	21.2	21.9	0.3	46.8	0.0	0.1	0.0	0.0
247.39	3342.0	7.63	35.4	7.8	7.2	0.0	0.0	20.0	25.8	24.0	0.1	49.2	0.0	1.2	0.0	0.0
247.43	3201.9	7.53	28.3	3.5	5.0	0.2	0.0	26.1	13.7	10.9	3.4	52.6	0.5	2.1	0.0	0.1
247.48	3309.9	7.45	25.1	3.0	0.3	0.0	0.0	12.6	20.1	13.5	4.9	51.4	2.9	5.8	1.1	0.4
247.53	3058.7	7.18	12.2	3.9	0.1	0.0	0.0	9.9	5.5	3.6	1.9	61.1	7.0	12.0	0.8	0.4
247.59	3234.4	7.16	2.0	2.0	0.0	0.0	0.0	2.6	10.3	7.5	0.4	63.5	13.9	13.5	2.8	0.4
247.63	4005.0	7.25	3.6	5.1	0.0	0.0	0.0	4.5	7.3	3.9	3.1	40.2	47.2	8.5	3.6	1.0
247.69	4624.8	7.51	0.7	3.4	0.0	0.0	0.0	0.0	6.8	5.3	0.5	36.3	36.6	20.0	5.2	0.5
247.73	4393.2	7.86	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	2.1	37.6	53.2	21.6	2.4	1.0
247.79	4660.0	7.45	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.4	27.1	46.3	32.0	7.5	0.0
247.87	3573.0	7.78	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	4.0	34.0	50.7	0.0	0.2
248.09	2982.8	7.85	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	12.9	51.3	4.7	0.0

Appendix V. cont'd. Mean percent cover of all species within mean elevation ranges (masl) of the MERP experimental marshes.

Elev. (masl)	Sol	Cia	Sow	D Bul	D Sm	D Cat	D Car	DWhtop	D Phrag	Moss	Stach	Teucr	Menth	Skull	Urtica	Lact
246.99	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.05	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.08	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.13	0.0	0.0	0.0	0.1	0.0	13.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.18	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.23	0.0	0.0	0.0	0.0	0.0	38.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.29	0.0	0.0	0.0	0.0	0.0	39.3	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.34	0.0	0.0	0.0	0.0	0.0	43.6	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.39	0.0	0.0	0.0	0.0	0.0	50.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.43	0.0	0.0	0.0	3.1	0.0	56.4	0.0	0.3	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.48	0.0	0.0	0.0	1.8	0.0	54.6	0.0	2.4	9.7	0.0	0.0	0.1	0.0	0.0	0.0	0.0
247.53	0.0	0.0	0.0	0.8	0.0	65.8	0.0	7.4	15.2	2.0	0.0	0.0	0.0	0.0	0.0	0.0
247.59	0.6	0.5	0.2	0.0	0.1	69.9	0.0	13.4	9.1	0.9	0.5	0.0	0.4	0.0	0.0	0.0
247.63	0.0	0.0	1.1	1.1	0.2	38.9	0.4	52.4	4.6	1.7	0.0	0.6	0.1	0.0	0.0	0.0
247.69	0.0	0.4	1.8	0.9	0.0	41.8	0.0	34.0	20.0	4.3	0.0	2.9	2.4	0.6	1.6	0.0
247.73	0.0	5.2	5.5	0.1	0.2	33.7	0.0	62.7	15.3	0.7	0.0	4.3	4.9	0.1	0.5	0.0
247.79	1.3	5.3	7.3	0.0	0.0	32.1	3.3	47.7	20.3	1.1	0.0	7.0	2.2	2.1	1.3	0.0
247.87	1.6	8.9	5.2	0.2	0.0	1.6	0.0	28.6	64.9	0.0	0.1	6.5	5.0	0.3	14.2	0.0
248.09	20.9	28.3	28.1	0.0	0.0	0.6	0.0	12.7	48.7	0.0	0.2	3.8	11.4	0.0	12.3	0.1

Appendix V. cont'd. Mean percent cover of all species within mean elevation ranges (masl) of the MERP experimental marshes.

Elev. (masl)	Polyg	Cicuta	Echino	Aster	Atrip	Suae	Cheno	Stell	Agrop	Hord	Pucc	Poa	Grass	JoPWd	MGlory	SnowB	Rose
246.99	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.05	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.08	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.23	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.29	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.34	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.39	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.43	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.48	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.53	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.59	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.6	0.0	0.0	0.0	0.0
247.63	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0
247.69	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.73	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.5	0.0	0.0
247.79	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
247.87	0.2	1.7	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
248.09	0.3	0.2	0.0	0.0	0.4	1.5	0.0	1.5	1.3	6.5	4.7	4.4	2.7	0.1	0.0	0.9	0.2

Appendix VI. Abbreviations used throughout this study to identify species within the MERP experimental marshes.

Species abbrev.	NAME Scientific (Kartesz 1994)	Common
Aster	<i>Brachyactis ciliata</i> ssp. <i>Angusta</i>	rayless aster
Agrop	<i>Elytrigia repens</i>	quackgrass, couch-grass
Atrip	<i>Atriplex patula</i>	orache, spearscale
Bul, Scr	<i>Scirpus</i> spp.	bulrush
Bladw	<i>Utricularia macrorhiza</i>	common bladderwort
Poa	<i>Poa palustris</i>	fowl blue grass, fowl meadow-grass
Car	<i>Carex</i> spp.	sedge
Cat, T	<i>Typha</i> spp.	cattail
Cheno	<i>Chenopodium album</i>	lamb's quarters
Cia, Cirs	<i>Cirsium arvense</i>	Canada thistle
Cicuta	<i>Cicuta maculata</i>	water hemlock, spotted cowbane
CoonT	<i>Ceratophyllum demersum</i>	coontail
Echino	<i>Echinocystis lobata</i>	wild cucumber
Grass	<i>Poa pratensis</i>	Kentucky blue-grass
Hord, Hj	<i>Hordeum jubatum</i>	foxtail, wild barley, squirrel-tail grass
JoPWd	<i>Eupatorium maculatum</i>	Joe-Pye-Weed
L Min	<i>Lemna minor</i>	lesser duckweed
L Tri	<i>Lemna trisulca</i>	star duckweed
MGLory	<i>Calystegia sepium</i>	morning glory, hedge bindweed
Menth	<i>Mentha canadensis</i>	common mint
Meta	<i>Cladophora</i> spp.	metaphyton algae
Lact	<i>Lactuca tatarica</i>	blue lettuce
Mil	<i>Myriophyllum sibiricum</i>	water milfoil
Moss	unknown	moss
Phrag, P	<i>Phragmites australis</i>	Phragmites, cane reed
Polyg	<i>Polygonum amphibium</i> var. <i>emersum</i>	smartweed, swamp persicaria
Pucc	<i>Puccinellia nuttalliana</i>	salt meadow grass, alkali-grass
Pwd	<i>Potamogeton</i> sp.	pondweed
Rose	<i>Rosa arkansana</i>	low prairie rose
Sm	<i>Scirpus maritimus</i>	alkali bulrush
Skull	<i>Scutellaria galericulata</i>	marsh skullcap, common skullcap
SnowB	<i>Symphoricarpos occidentalis</i>	snowberry
Sol	<i>Solidago canadensis</i> var. <i>gilvocanescens</i>	Canada goldenrod
Sow	<i>Sonchus arvensis</i> ssp. <i>uliginosus</i>	sowthistle, field-sowthistle
Stach	<i>Stachys palustris</i> ssp. <i>Pilosa</i>	marsh hedge-nettle, woundwort
Stell	<i>Stellaria longifolia</i>	long-leaved chickweed
Suae	<i>Suaeda calceoliformis</i>	sea-blite
Teucr	<i>Teucrium canadense</i> var. <i>occidentale</i>	mint, germander
Urtica	<i>Urtica dioica</i> ssp. <i>gracilis</i>	stinging nettle
Whtop, Sf	<i>Scolochloa festucacea</i>	whiteweed, spangle-top