Dynamics of emergent vegetation along natural gradients of water depth and salinity in a prairie marsh: delayed influences of competition

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Introduction

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 (Stewart and Kantrud 1971; Adams 1988). These systems experience natural fluctuations in water levels (i.e., alternating periods of flooding and drawdowns) that result in vegetation changes, which contribute 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 and perpetuation of the zonation patterns in prairie marshes (van der Valk and Davis 1978; Pederson 1981; Pederson and Smith 1988; van der Valk and Welling 1988; Welling *et al.* 1988a,b). Under a natural disturbance scenario, vegetation present in a marsh is primarily a function of water depth, while plant composition is a function of the soil seed bank (van der Valk and Davis 1976a).

An idealized vegetation cycle of prairie marshes recognizes four distinct stages: dry, regenerating, degenerating, and lake marsh phases (van der Valk and Davis 1978). This cycle gives a good general representation of vegetation changes in a prairie marsh subject to natural flood-drought disturbances. From observations of prairie marsh systems, it is clear that water depth is the primary determinant of plant species 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.* 1989)

Natural flood-drought cycles are widely recognized as essential to maintaining habitat diversity and productivity of 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). Northern prairie marshes are best described as resilient, disturbance-driven ecosystems (Kenkel 1997).

Disruption of these natural disturbance-regeneration cycles (i.e., flood-drawdowns) in wetlands affects 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, biodiversity, and productivity (Kantrud *et al.* 1989a). With no disturbance to rejuvenate the marsh system, the community enters into a state of degeneration or stagnation.

Although water depth appears to be the major determinant of marsh zonation, many secondary environmental factors further affect the position of plant species along this gradient, including wave action disturbance (Wilson and Keddy 1986a,b), soil organic matter content (Wilson and Keddy 1985) and salinity in salt marshes (Barbour 1978; Snow and Vince 1984). Salinity may also affect the distribution and growth of many prairie marsh plants (Stewart and Kantrud 1971, 1972; Leiffers and Shay 1982; Neill 1993). 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 dissolved salts (Neill 1993). Conversely, under a stable water level regime salts accumulate and persist. 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), it is conceivable that salinity could influence plant distribution over long-term stable water level periods.

Competition in plants can be described as interactions among two species which can potentially occupy the same habitat unit. Additionally, competitive displacement (or exclusion) from an area results from the negative effects one plant species has upon another by consuming (or controlling access to) a limited resource (Grubb 1985; Keddy 1989). Fundamental physiological response curves are described as resource-use patterns which occur in the absence of interspecific competition (Keddy 1989). Conversely, realized

response curves are patterns which 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).

Numerous experimental studies have found evidence to support the importance of interspecific competition in shaping wetland zonation patterns (Grace and Wetzel 1981; Snow and Vince 1984b; Wilson and Keddy 1985, 1986; Shipley *et al.* 1991). This suggests that competitive displacement may influence the position of species along a water depth gradient. In a natural disturbance regime, interspecific competition will remain low (Keddy 1989). This results in high species diversity and low levels of monodominance (van der Valk and Davis 1980). Conversely, stable water levels in a marsh system prevents further regeneration of vegetation while simultaneously increasing interspecific competition. Highly competitive emergent macrophytes are no longer held "in check" by flood-drawdown events. As a result, very distinct vegetation patterns develop as more competitive species eliminate the poorer competitors (Grace and Wetzel 1981; Czaran 1991).

The main objective of this study is to examine vegetation dynamics of a prairie marsh following a long-term stable water level state (i.e., absence of disturbance from water level fluctuations). Emphasis is placed on species' responses to natural gradients of water depth and salinity, as well as the hypothesized role of interspecific competition in further shaping these plant zonation patterns. It is hypothesized that disruption of the natural disturbance regime in prairie marshes (i.e., flood-drawdown cycle) will increase competition among emergent macrophyte species. This heightened competition can result in the elimination of competitively subdominant species, while consolidating the abundance of competitive dominants. Persistence of stable water levels is also expected to lead to increasingly distinctive vegetation zones over time, as dominant macrophytes competitively sort themselves along a water depth gradient.

Methods

The study area

This study was conducted in the Marsh Ecology Research Complex (MERC; Fig. 1) located in the Delta Marsh, a 20,000 ha freshwater lakeshore marsh at the southern end of Lake Manitoba (50° 10'N, 98° 19'W). Water levels in this lake, and the adjoining marsh, have historically fluctuated. These recurrent high and low water periods caused vegetation to undergo cyclical succession, maintaining plant and habitat diversity within the marsh. Since 1961, lake levels have been regulated at a mean level of 247.5 m asl. Disruption of the natural wet-dry cycle has prevented marsh regeneration, resulting in dense monodominant plant zones of low species and habitat diversity. The MERC complex consists of ten continuous sand-diked marshes, or 'cells'
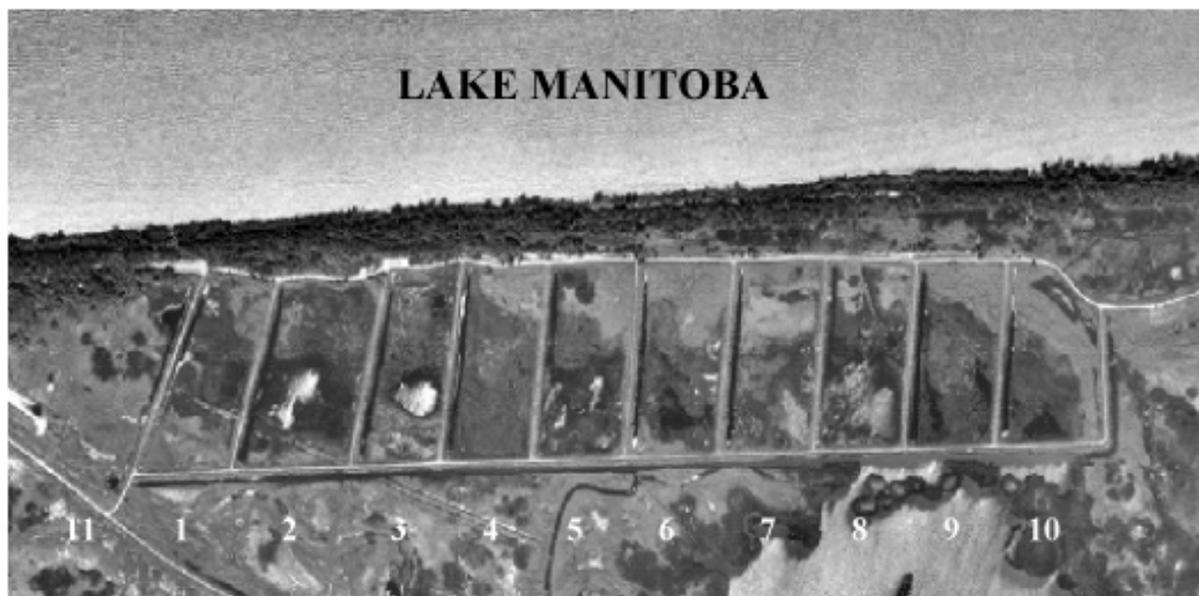

Figure 1. The Marsh Ecology Research Complex (MERC) located in Delta Marsh, Manitoba, 6 km east of the Delta Waterfowl and Wetlands Research Station.

Table 1. Stable water level periods of the treatment and control cells in the Delta Marsh Ecology Research Complex (MERC) and associated mean water levels.

Cell	Treatment Group (1985) -1989)	Water level (m asl) (1985) -1989)	Stable-state (time period)	Stable-state (years)
4	normal	247.5	1992-1997	5
5	medium	247.8	1992-1997	5
2	high	248.1	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	12
9	medium	247.8	1985-1997	12
11	n/a	247.5	1961-1997	36

(5-7 ha each), constructed along the natural beach ridge separating the lake and marsh (Fig. 1). There is also an undiked area of similar size within the marsh monitored as a control.

The MERC complex was constructed for the Marsh Ecology Research Program (a long-term manipulation study) to examine the effects of water level fluctuations on prairie marsh vegetation dynamics, composition and structure (Murkin *et al.* 1985). From 1985 - 1989, the 10 experimental marshes were subject to 3 different water level regimes (Table 1). Since 1989, water levels in these cells have been left to equilibrate with the adjacent marsh, which has limited water level fluctuations (i.e., no flood-drought cycle). Five of the cells (3,7,8 and 1,9) have been in a stable state for 12 years (normal and medium treatment groups respectively), two cells (6 and 10) for 8 years (high treatment group), and three cells (2, 4, 5, which were manipulated for waterfowl management purposes in the early 1990s) for 5 years (Table 1). Additionally, cell 11 (the control cell) has been in a stable state for 36 years. The stable water level regime of the Delta Marsh, and the long-term biological information available for the MERC complex, offers a unique opportunity to track the long-term vegetation dynamics of a prairie marsh following water level stabilization.

The dominant vegetation zones in the Delta Marsh consist of (1) wet-meadow vegetation at higher elevations (i.e. grasses, forbs and shrubs); (2) giant reed grass (*Phragmites australis*), sedge (*Carex spp.*) and whitetop (*Scolochloa festucacea*) at seasonally flooded elevations; (3) cattail (*Typha spp.*) and bulrush (*Scirpus spp.*) at lower permanently flooded elevations; and (4)

submersed aquatics (e.g., pondweed, *Potamogeton pectinatus)* in water too deep for emergents. More detailed descriptions of Delta Marsh vegetation are in Löve and Löve (1954) and Walker (1959, 1965). Soils in this region of the marsh have a high content of silt and sand.

Field sampling

Eleven permanent transects (established in 1980) divide each cell into 10 equal zones, with colour coded flags (8 m high) to aid in positioning during sampling. Distances between transects were measured, and each corner of cells 1-11 were surveyed. These points were defined on elevation contour maps to locate sample sites within vegetation zones, and to determine relative elevation (m asl) at each site. A systematic sampling design was used, as it results in a highly equitable distribution of sample points (excellent for use in pattern determination, gradient analysis and mapping). Eight sample sites were established along each of 10 of the 11 transects in each cell (transects 11 were not used). To prevent influences from dikes surrounding the cells (van der Valk 1994), vegetation within a 10 m area of a dike was excluded from analysis.

Vegetation was sampled in approximately 80 sites per cell (876 total) using 1½ m x 1½ m quadrats. Plant composition and relative percent cover were recorded to determine vegetation diversity, level of monodominance within zones and degrees of species dominance. Water depth (or depth to water) was measured to the nearest cm and used in conjunction with elevation contour maps (accuracy to 10 cm) to examine plant species distribution along the elevation/water depth gradient. Water and/or soil samples were collected at each site dependent on whether site was above or below water. Salinity (EC) and pH of water and/or soil was measured for each sample site. All sample sites were surveyed with relative distance to adjacent sites.

Environmental variable analysis

pH was measured in the lab using an Orion Research Ionalyzer, model 407A. Conductivity [μmhos (1 mho = 1 S)] readings were taken in the field when possible, or 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).

Oven dried 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 water ratio, 1:5 (20 g: 100 ml) or 1:6 (20 g: 120 ml) if high organic content. Slurries were stirred 4-5 times for 30 minutes, and let stand for 30 minutes.

Data Analysis

Emphasis was placed on seven main dominant plant species: including the three major dominant emergents, cattail (*Typha spp.*), whitetop (*Scolochloa festucacea*), and giant reed grass (*Phragmites australis*); the submergent species pondweed (*Potamogeton pectinatus)*; and the wet meadow species goldenrod *(Solidago canadensis)*, Canada thistle *(Cirsium arvense)*, and sow thistle *(Sonchus arvensis)*. Three environmental variables were considered: pH, salinity (electrical conductance) and water depth (elevation). Correspondence analysis (CA) and canonical correspondence analysis (CCA) were used to examine relationships between species, sample sites and environmental variables (Ter Braak 1987).

A realized physiological response curve (realized niche responses as opposed to fundamental niche responses of species) of each of the seven dominant macrophytes was produced for both the treatment and control cells, utilizing mean species percent cover along a water depth (elevation) gradient. Conductivity profiles over the elevation range were also produced and compared to species' distributions.

Results

Realized elevation response curves of species (mean percent cover) were produced for seven of the ten experimental marshes (cells 2,4 and 5 were not included due to the post-1989 manipulations), for the seven dominant species present within the MERC complex (Fig. 2; 6 emergent, 1 submergent species, Table 2). Although these seven cells were subject to 3 different treatments from 1985-1989 (Table 1), they produced very similar elevation responses from the dominant species. For the purposes of this paper, these treatments were considered together.

The elevation ranges of the three dominant emergent macrophytes (cattail, whitetop and giant reed) are very distinct (Fig. 2). Cattail is present from 247.0 to 248.0 m asl, decreasing dramatically at approx. 247.6 m asl. Whitetop increases dramatically at this elevation, and was present from 247.4 to 248.1 m asl. Additionally, at the elevation where whitetop cover decreases (247.85 m asl) giant reed abundance increases (present from 247.4 to 248.2 m asl). The wet meadow species goldenrod, Canada thistle and sow thistle increase around 247.9 m asl. The highest mean conductivity levels (3500 to 4800 mhos) correspond directly with the peak in whitetop abundance (247.6 to 247.85 m asl) and the decrease in cattail abundance. Furthermore, it is also not until after conductivity levels drop (3500 mhos) that giant reed abundance increases (Fig. 2).

CCA ordinations produced for each of the seven treatment marshes individually were very similar to the CCA ordination of all seven combined (Fig. 3). Based on the dominant plant species within the MERC complex, water depth is 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 (Fig. 3) and its low correlation to either axes (r = -0.172, r = 0.182 respectively) suggests it is not significant. The macrophyte species appear to be sorted along axis 1; cattail in deep water areas to wet meadow species (goldenrod, Canada thistle and sow thistle) on higher ground. This provides further evidence that their location in the marsh is highly dependent on water depth (i.e., relative elevation). There is also arrangement of the sample sites and plant species along axis 2, suggesting salinity influences the location of vegetation within the marsh as well. Whitetop is associated with higher salinities, while giant reed is normally associated with lower salinities.

A CCA ordination was also produced for cattail, whitetop and giant reed, the three major dominant macrophytes found in both the MERC complex and the surrounding Delta Marsh (Fig. 4). Salinity and water depth are again correlated with axes 1 and 2 respectively (r = 0.720, r = 0.434). Cattail, whitetop and giant reed are sorted along both axes, suggesting that salinity and water depth both influence the distributions of these three dominants. A triangular shaped CCA ordination was produced illustrating the transitional areas which exist between these species: cattail-whitetop, whitetop-giant reed, giant reed-cattail. The few sample sites having mixed communities of all three species occur in the interior of the triangle. In essence, this species triangle is comparable to a soil triangle for sand, silt and clay. By knowing the abundance of two, one can determine the relative abundance of the third.

Realized elevation response curves for cell 11 were produced utilizing water depth data to create average elevation ranges (Fig. 5). Cattail is restricted to deeper water depths (0-8), with no more than 50 percent average cover. Giant reed abundance occurs in two peaks: the cattail-whitetop transition range (5-9) and higher elevation ranges (10 +). Whitetop's highest abundance is restricted to a narrow water depth region (8-10) between these two peaks, with a corresponding drop in giant reed abundance. Additionally, the lower range giant reed peak (5-9) corresponds with a small peak found in the same range in the treatment cells (247.5 m asl, Fig 5). On average, the wet meadow species have increased in abundance compared to the treatment cells. The highest mean conductivity levels (5000 to 7500 mhos) again correspond directly with a peak in whitetop and a drop in giant reed abundance (range 8-9).

Table 2. Mean elevation ranges and associated mean soil conductivities, mean water depth and average percent cover of the dominant macrophytes in the MERC complex. Highest abundance range of each species is indicated by bold typeface.

| Elev (m asl)	Cond. (µmhos)	Depth (cm)	Potamogeton pectinatus	Typha spp.	Scolochloa festucacea	Phragmites australis	Solidago canadensis	Cirsium arvense	Sonchus arvensis
246.99	2,500	56	**75**	0	0	0	0	0	0
247.05	3,009	50	**29**	0	0	0	0	0	0
247.08	2,765	47	**41**	12	0	0	0	0	0
247.13	2,864	42	**30**	14	0	0	0	0	0
247.18	2,963	37	23	**26**	0	0	0	0	0
247.23	3,014	32	17	**33**	0	0	0	0	0
247.29	3,173	26	15	**41**	0	0	0	0	0
247.34	3,118	21	13	**47**	0	0	0	0	0
247.39	3,342	16	7	**49**	0	1	0	0	0
247.43	3,202	12	5	**53**	0	2	0	0	0
247.48	3,310	7	0	**51**	3	6	0	0	0
247.53	3,059	2	0	**61**	7	12	0	0	0
247.59	3,234	-4	0	**63**	14	14	1	0	0
247.63	4,005	-8	0	40	**47**	9	0	0	1
247.69	4,625	-14	0	36	**37**	20	0	0	2
247.73	4,393	-18	0	38	**53**	22	0	5	6
247.79	4,660	-24	0	27	**46**	32	1	5	7
247.87	3,573	-32	0	4	34	**51**	2	9	5
248.09	2,983	-54	0	1	13	**51**	**21**	**28**	**28**
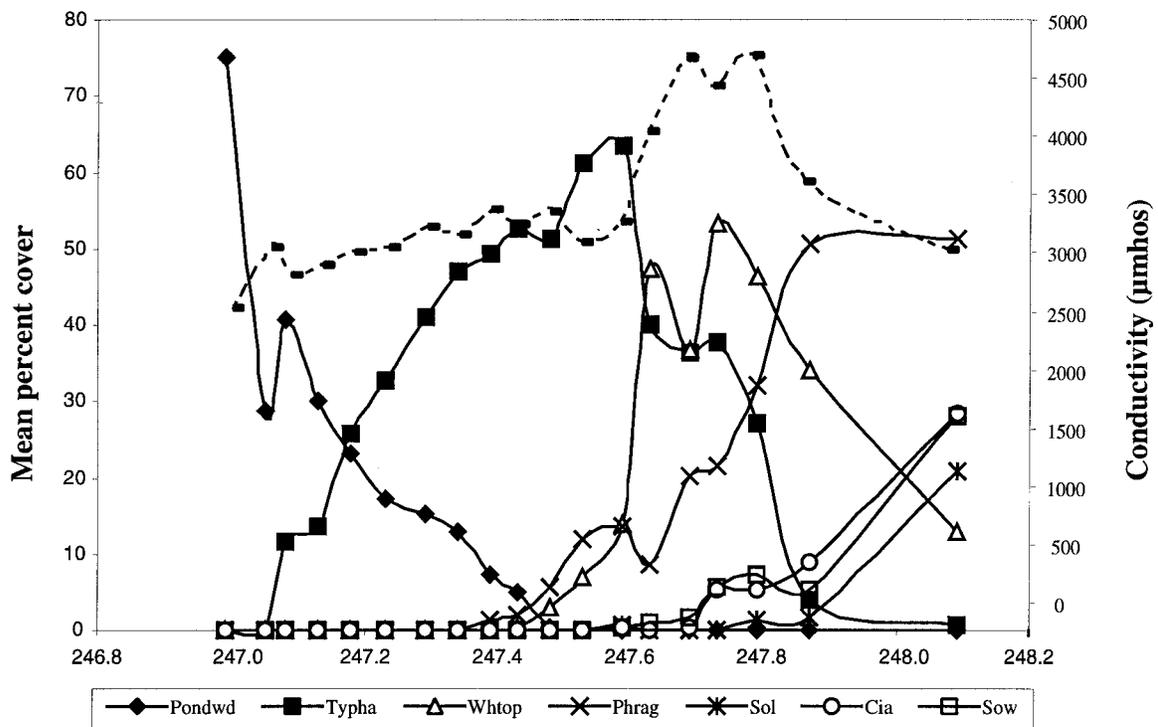
Figure 2. Realized elevation response curves of the dominant macrophytes in the MERC complex (excluding cells 2, 4 and 5). Dominant macrophytes include pondweed (Pondwd), cattail (Typha), whitetop (Whtop), giant reed (Phrag), goldenrod (Sol), Canada thistle (Cia) and sow thistle (Sow). Mean conductivity (µmhos) over the elevation range (m asl) is also given (dotted line).
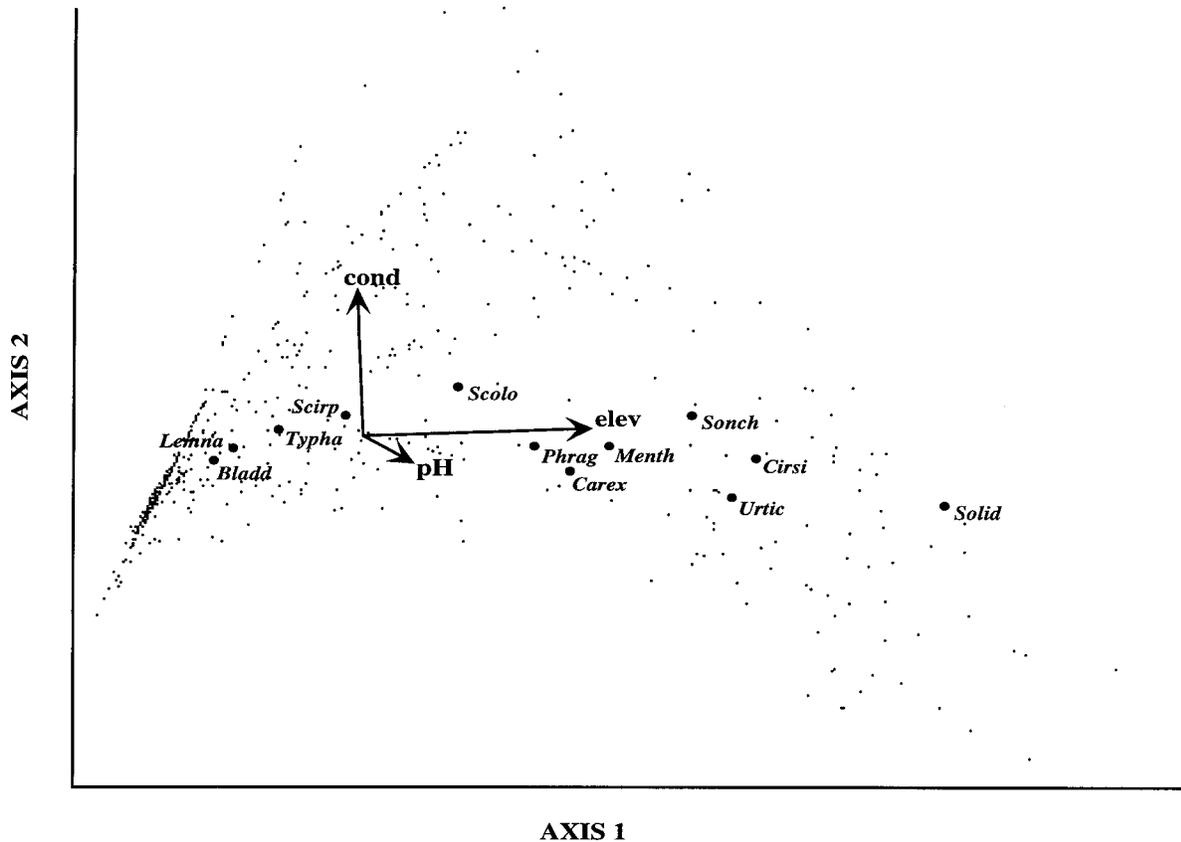
Figure 3. CCA ordination of the dominant macrophytes (large dots), environmental variables (vectors) and sample sites (small dots) in the MERC complex. Dominant macrophytes include cattail (Typha), whitetop (Scolo), giant reed (Phrag), goldenrod (Solid), Canada thistle (Cirsi) and sow thistle (Sonch). Minor plant species include bulrush (*Scirpus* sp.) (Scirp), duckweed (*Lemna* sp.) (Lemna), bladderwort (*Utricularia vulgaris*) (Bladd), sedge (*Carex atherodes*) (Carex), mint (*Menta arvensis*) (Menth) and stinging nettle (*Urtica dioica*) (Urtic). Environmental variables include conductivity (cond), pH and water depth (elev). Species-environmental correlations on axis 1 = 0.867, axis 2 = 0.575. Redundancy (ratio of canonical to constrained total inertia) = 18.44%.

The CA ordination produced for cell 11 (Fig. 6) is somewhat similar to the CCA ordination for the treatment cells (Fig. 4). Both ordinations produce a triangular shape for the three dominants, however, the cattail-whitetop transitional area is missing in cell 11. Note that the realized elevation response curves produced from the species in cell 11, also lack a transititonal area between cattail and whitetop (Fig. 5).

Discussion

Water depth appears to be the primary determinant of plant zonation patterns in prairie marshes, during both a natural disturbance regime and periods of water level stability. However, many secondary factors further affect the exact position of plant species along a water depth gradient (Wilson and Keddy 1985, 1986a,b; Barbour 1978; Snow and Vince 1984b). In experimental trials, Squires and van der Valk (1992) found that the water depth distribution ranges of the dominant macrophytes in Delta Marsh overlapped more when grown in monoculture than when found in the marsh. These fundamental water depth responses were also much wider than the realized water depth responses determined from this study (Figs. 3, 5). In addition, Smith (1972) found whitetop in water levels from -50 cm to 150 cm deep, while Grace and Wetzel (1981) found cattail from -15 to 100 cm. These studies provide evidence to support the influence of competition, suggesting the water depth ranges of these species are suppressed when grown in the presence of one another. We can only presume it is competition for space, light, or nutrient resources.

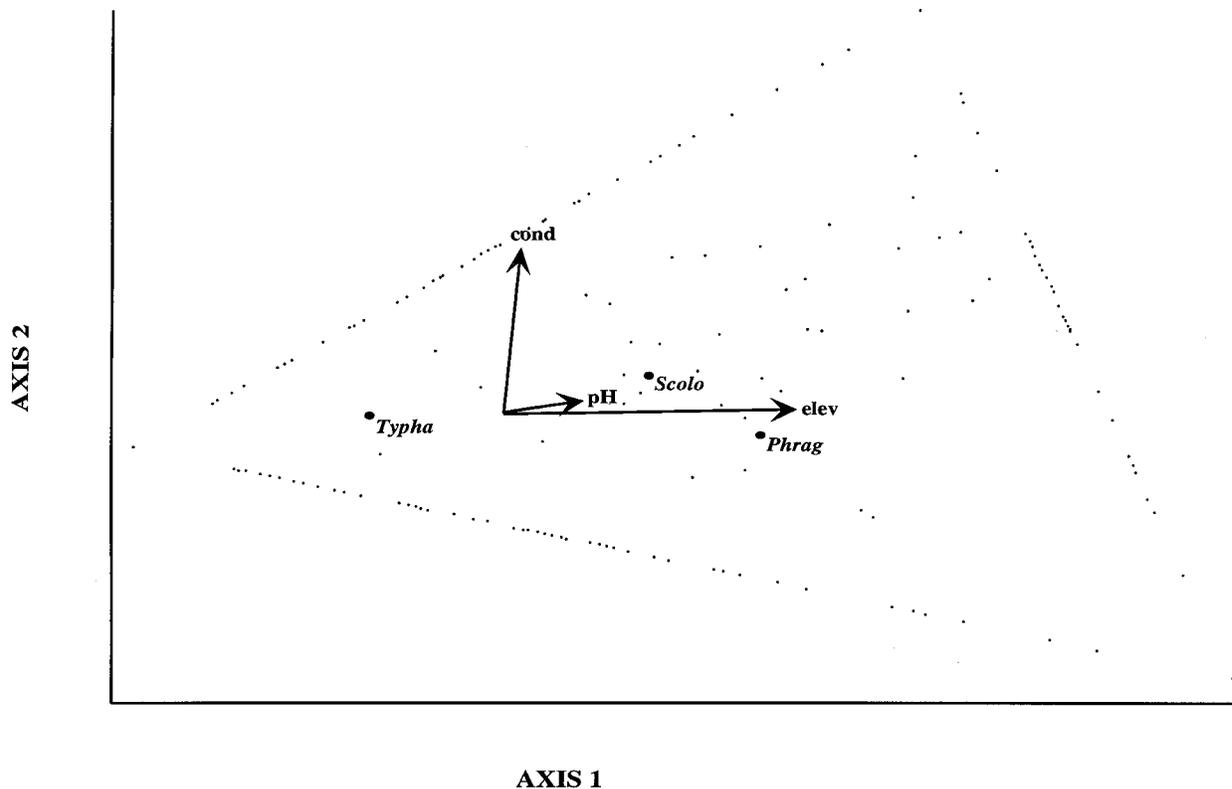Soil salinity was suggested as a possible secondary environmental effect influencing the distribution of

Figure 4. CCA ordination of the three dominant macrophytes (large dots): cattail (Typha), whitetop (Scolo), and giant reed (Phrag), environmental variables (vectors) and sample sites (small dots) in the MERC complex. Environmental variables include conductivity (cond), pH and water depth (elev). Species-environmental correlations on axis 1 = 0.726, axis 2 = 0.435. Redundancy (ratio of canonical to constrained total inertia) = 38.7%.

species along a water depth gradient (Squires and van der Valk 1992). Our results indicate that during a stable water level regime (i.e., in the absence of flood inundations) the salinity gradient indeed appears to greatly influence plant zonation patterns in prairie marshes. Soil salinity remains highest near the soil-water transition (-5 to -10 cm depth to water table range). This range is consequently where whitetop is high and cattail and giant reed are low in abundance. Whitetop grass is quite salt tolerant, inhabiting saline soils of 0.6 - 14.7 mmhos/cm, while most abundant in moderately saline soils of 2.5 - 7.5 mmhos/cm (Neckles *et al.* 1985). Conversely, although giant reed can tolerate high salt levels, it grows best in freshwater. Cattail also mainly inhabits freshwater, but can grow in saline waters of up to 8.5 mmhos (Glenn 1995).

Greater salt-tolerant species are often excluded from low saline areas due to competitive exclusion. These species will shift to the higher end of the salinity gradient as a result of being suppressed by more competitive species at the lower end of the salinity gradient (Kenkel *et al.* 1991; Snow and Vince 1984). Whitetop is dominant in these relatively high saline areas 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), but rather its salt tolerance, combined with its preference for this water depth range, makes it a better competitor during stable water level periods. Conversely, giant reed is much more competitive in lower rather than high saline areas due to its low salt tolerance. It is often suggested that there is a physiological tradeoff between salt tolerance and competitive ability (Kenkel *et al.* 1991).

Control cell 11, which has been in a stable water level state for 36 years, provides further evidence of the influence of competition (Table 1). In the absence of fluctuating water levels macrophyte species have experienced increasing competitive interactions that have further shaped vegetation patterns. The cattail-whitetop transition range present in the treatment cells (Figs 2, 4) has all but disappeared in cell 11 (Figs 5, 6). Giant reed has dramatically increased in abundance within this transitional range, competitively restricting whitetop to a very narrow region of water depth. Giant reed is less competitive during natural water level fluctuations where changes in water depth controls its vegetative spread. It is
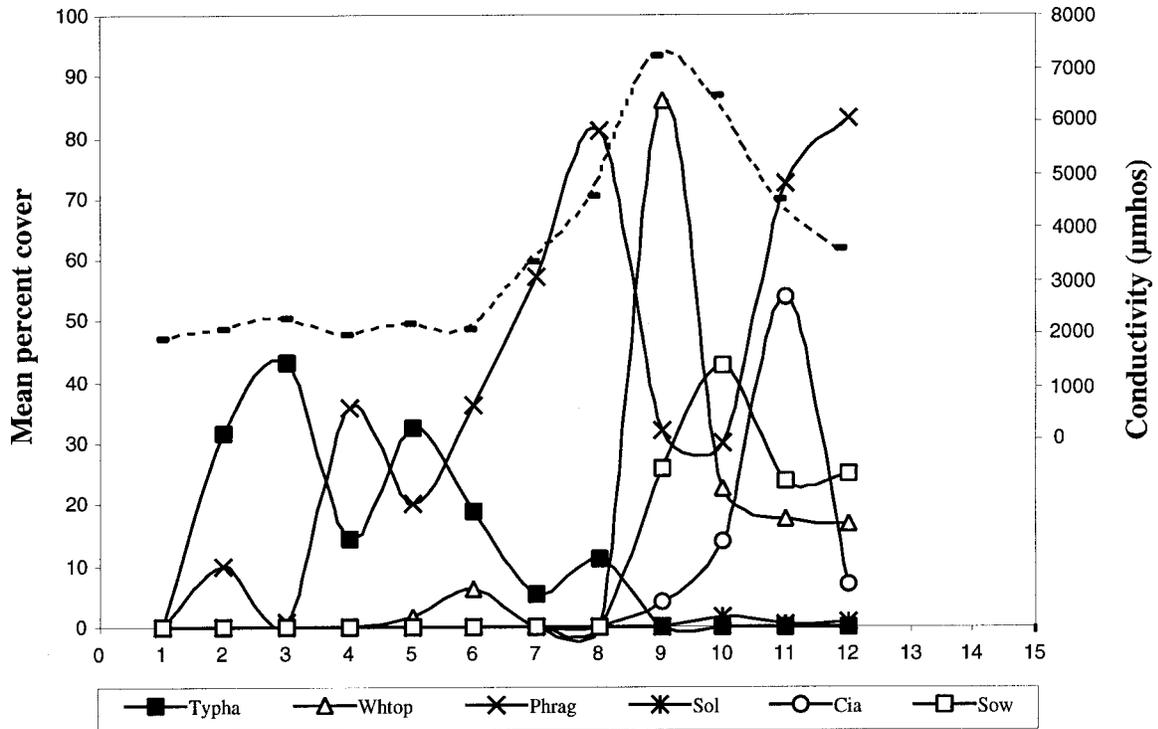
Figure 5. Realized elevation response curves of the dominant macrophytes in the MERC complex control cell 11. Dominant macrophytes include cattail (Typha), whitetop (Whtop), giant reed (Phrag), goldenrod (Sol), Canada thistle (Cia) and sow thistle (Sow). Mean conductivity (μmhos) over the elevation range (m asl) is also given (dotted line).
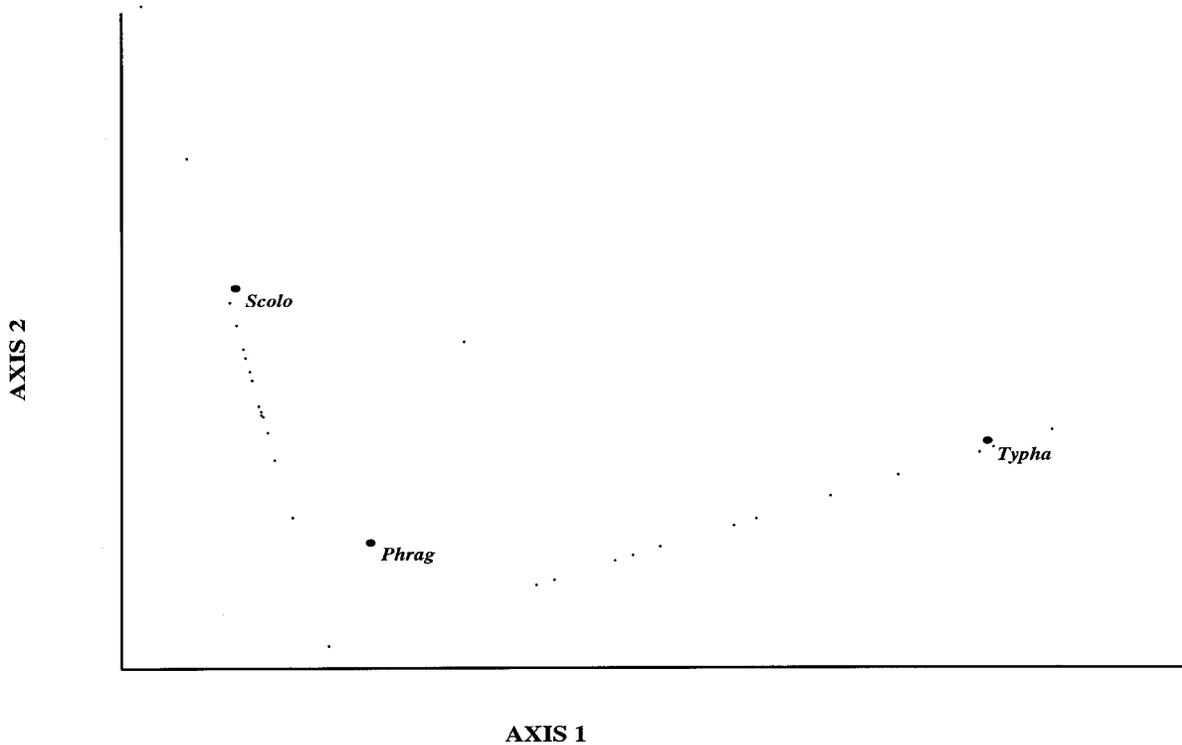

Figure 6. CA ordination of the three dominant macrophytes (large dots): cattail (Typha), whitetop (Scolo), giant reed (Phrag), and sample sites (small dots) in the MERC complex control cell 11.

an excellent competitor, however, in the absence of water level fluctuations and rapidly spreads by vegetative clonal growth (Cross and Fleming 1989). Without salinity suppressing it, the more competitive giant reed can invade this range of less saline soils (Figs 2, 5). It will ultimately exclude whitetop from these areas, while restricting it to high saline habitats. Giant reed cannot completely eliminate whitetop, however, since whitetop is much more tolerant of saline soils.

The large peak in giant reed abundance in cell 11 (Fig. 5) also corresponds to a small peak found in the treatment cells near the mean water level of the marsh (247.5 m asl, Fig. 2). This suggests that after an 8-12 year stable state environment in the treatment cells, giant reed has begun to invade this water depth range. After a 36 year stable state in the Delta Marsh, it has almost completely taken over. Sow thistle has also taken advantage of the stable water level environment, with increased abundance in cell 11. It competitively occupies an area in the upper whitetop-giant reed transition range. Water depth, combined with seed bank composition, appears to initially determine positioning of species throughout the marsh. Grace (1987) found that the initial seed density between competing species strongly influenced the early outcome of competition. In a stable-state environment (with continued lack of disturbance), however, vegetative spread and competitive displacement by giant reed can overcome these initial effects of spatial and temporal preemption (Grace 1987). Ultimately, over time in a stable water level regime, giant reed appears to exclude whitetop from certain water level ranges.

Since this was not an experimental study, we can only speculate on competitive influences. Being a taller plant, giant reed has better access to incoming light and will simultaneously reduce the growth of the shorter whitetop by a positive feed-back loop (Keddy 1990). It continually improves its access to light, while increasingly denying whitetop access to it. Additionally, giant reed produces copious amounts of deadfall. With no fluctuating water levels, this litter rapidly accumulates increasingly preventing whitetop growth (van der Valk 1986). Examination of the raw data confirms there is more standing deadfall in cell 11 than in the treatment cells.

Many experimental studies have described the combined causal influences of salt tolerance and interspecific competition on plant zonation in various ecosystems (Barbour 1978; Snow and Vince 1984; Badger and Unger 1990; Kenkel *et al.* 1991). These studies all showed that certain plant species grown in monoculture perform better at the lower end of the salinity gradient. These species are only restricted to higher saline areas due to competitive exclusion, suggesting they are facultative rather than obligate halophytes (Kenkel *et al.* 1991; Glenn 1995). Species having higher tolerance to extreme levels of salinity are usually less competitive at moderate levels. Although this study does not directly examine interspecific competition, effects from its influence are consistent with results from these studies.

The optimum water depth ranges of cattail, giant reed and whitetop may not necessarily coincide with their fundamental physiological water depth range optimas. Salinity and competitive interactions from neighbours exclude these species from certain water depths. It is often suggested there is a physiological tradeoff between tolerances and competitive ability. Giant reed is extremely competitive in a stable state environment with low levels of salinity, rapidly spreading by vegetative clonal growth (Cross and Fleming 1989). It sacrifices, however, its tolerances to deep water and high salinity. Cattail, on the other hand is better able to survive in deep water habitats because of its tall thin leaves and great rhizome storage capacity (Grace and Wetzel 1981). These characteristics, which enable it to grow in deeper water, reduce its competitive ability in drier habitats. Finally, whitetop is a comparatively poor competitor in flooded and upland areas, but is highly tolerant of soil salinity. This study indicates that in a stable water level environment (i.e. lack of disturbance), the gradient that these marsh macrophyte species are sorted along becomes a multivariate gradient, combining influences from water depth, salinity and competitive interactions. Additionally, the influences of these gradients increase with prolonged periods of water level stability.

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