Reestablishment of perennial emergent macrophytes during a drawdown in a lacustrine marsh

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ABSTRACT

Temporal and spatial patterns in the recruitment of plant species during drawdowns of 1 and 2 years' duration in the Delta Marsh, Manitoba, are described. In a two-year drawdown, more emergents but fewer annuals were recruited during the first year than during the second. Within a growing season, most recruitment occurred in June except in certain species in June of 1983 when soil temperatures were low and soil moisture was very high. The densities of seedlings for all species combined were low at low elevations in open water or Scirpus lacustris ssp. glaucus sites, highest at intermediate elevations in the shoreline zone, and low again at high elevations where upland plants begin to dominate the vegetation. Soil moisture, soil conductivity, and litter cover also varied along the elevation gradient. With the exception of Scolochloa, the patterns of recruitment of dominant emergents in relation to elevation were not unique which leaves largely unanswered the question of how does zonation of dominant emergents along a water depth gradient develop?

INTRODUCTION

In wetlands, the distribution of plant species along a water depth gradient, usually in well-defined zones or bands, is a widespread phenomenon (see Spence 1982 for a review). However, it is often not clear what environmental and/or biological mechanisms produce such a pattern. The establishment patterns of different species in an area and their role in producing zonation in wetlands have received little attention, in spite of the fact that this is a crucial step and possibly is sufficient to explain such patterns (Grubb 1977; Keddy and Ellis 1985).

Naturally occurring periods of low water, often referred to as drawdowns, are important in the vegetation dynamics of prairie marshes because seeds of most perennial emergents, mud flat annuals, and wet meadow perennials can germinate only in the absence of standing water (see van der Valk and Davis 1978 for a description of the idealized cycle of vegetation change in these wetlands). This insight has led to the use of artificial drawdowns to manipulate the vegetation in these mid-continent wetlands, primarily to reestablish emergents (Kadlec 1962; Harris and Marshall 1963; Weller and Fredrickson 1974; Fredrickson and Taylor 1982). Walker (1959, 1965) described the development of vegetation during a natural drawdown in the Delta Marsh in Manitoba, Canada. Weller and Fredrickson (1974) studied vegetation development during an artificial drawdown at Rush Lake in northwestern Iowa. These studies were fairly general and did not emphasize the quantitative analysis of seedling abundance in relation to environmental factors.

Other studies which are relevant to understanding seedling recruitment patterns in mid-continent wetlands have examined the species composition and size of their seed banks (van der Valk and Davis 1978; Pederson 1981, 1983; Smith and Kadlec 1983), the effects of disturbance on seed banks (Smith and Kadlec 1985), and the germination requirements of seeds found in seed banks (Galinato 1985; Galinato and van der Valk 1986). A recent experimental study has also examined the effects of litter and annual plant species on the recruitment of emergents during a drawdown (van der Valk 1986).

This study focuses on temporal and spatial patterns in species establishment, i.e., the recruitment of seedlings, during drawdowns in a lacustrine wetland, the Delta Marsh, Manitoba. Specifically, my objectives were to:

1) Compare qualitatively and quantitatively the recruitment of species during the first and second years of a two-year drawdown,

2) compare qualitatively and quantitatively the recruitment of species during the first year a drawdown in two different years,

3) describe temporal patterns in species recruitment within a growing season, and

4) examine the spatial patterns in species recruitment along an elevation gradient, with special emphasis on dominant emergents, in relation to soil conductivity, soil moisture, soil temperature, and previous emergent vegetation type.

METHODS

Study Site and the Marsh Ecology Research Program

This study was conducted in the Delta Marsh, a large lacustrine wetland of about 15000 ha located on the south shore of Lake Manitoba at 50°11'N, 98°19'W. The marsh is separated from the lake by a narrow, forested sand ridge and is composed of interconnected bays which vary in size, the largest covering several hundred ha. The conductivity of the water ranges from 1.8 to 3.3 mmhos (Bossenmaier 1968).

At the higher elevations adjacent to the ridge, the vegetation is dominated by broad-leaved herbaceous perennials, including *Sonchus arvensis*, *Cirsium arvense*, *Urtica dioica*, and *Solidago* spp. Monodominant stands of *Phragmites australis*, *Scolochloa festucacea*, *Typha* spp., and *Scirpus lacustris* ssp. *glaucus* constitute the dominant emergent vegetation of the Delta Marsh. In areas of open and relatively deep water, submergent vegetation is found; common species include *Potamogeton* spp., *Utricularia vulgaris* L., *Myriophyllum spicatum* L., and *Ceratophyllum demersum* L. The original vegetation of the Marsh Ecology Research Program (MERP) experimental complex, within which this study was carried out, was similar to that found in the rest of the Delta Marsh (Love and Love 1954; Walker 1959, 1965; Anderson and Jones 1976).

In order to explain the context within which this study was conducted, it is necessary to describe the basic goal of MERP, which is to study experimentally the long term ecological effects of water level manipulations in a freshwater marsh (Batt et al. 1983). The MERP experimental complex consists of 10 separate, diked marshes of 2-5 ha in which water depth can be maintained within 2-5 cm of a specified level. The chronological sequence of water level manipulations relevant to this study began in 1981 when the 8 cells to be drawndown for 2 years were flooded to 1 m above the normal level, i.e., to 248.4 vs. a normal level of 247.4 m ASL. During this year, water levels in the 2 marshes to be drawndown for 1 year were held at the normal level. In 1982, water levels in all 10 marshes were maintained at a depth 1 m above normal. This period of high water levels in the MERP complex simulated periods of high water that occurred periodically in the Delta Marsh prior to stabilization of water levels in Lake Manitoba in 1961 by means of a water control stucture (Manitoba Department of Mines, Resources, and Environmental Management 1974).

The two years of abnormally high water levels killed most of the established emergent vegetation in the MERP experimental complex and thus created conditions favorable for the reestablishment of the vegetation from seed during drawdown. The soil of the MERP complex was known to contain populations of germinable seeds of many plant species (Pederson 1981, 1983).

The 8 marshes to be drawndown for 2 years were drained in the spring of 1983 while the 2 remaining marshes were still deep-flooded. In 1984, all 10 marshes were drawndown. The uneven replication of the 2 drawdown treatments resulted from considerations regarding treatments to be applied after the drawdown phase of the experiment when the marshes were reflooded.

In this paper, the treatment in which 8 cells were drawndown for both 1983 and 1984 will be referred to as the 'two-year drawdown'. The treatment in which 2 marshes were drawndown only in 1984 will be referred to as the 'one-year drawdown'. Additional information on the marshes of the MERP complex and the overall design of the project has been presented by Batt *et al*. (1983) and Murkin *et al*. (1985).

Permanent Quadrats

Ten 2 m X 2 m square permanent quadrats were established in each of the 10 marshes of the MERP complex. The following method of locating the quadrats was used to obtain a representative distribution of quadrats with respect to environmental variation within a marsh. A map of a given marsh was divided into 5 equal segments from N to S; each segment was then subdivided into an E and W half to delineate 10 strata of equal area within a marsh. A permanent quadrat was then located within each stratum using a grid overlay and randomly chosen coordinates. In the field, the site on the map was located in the marsh and the permanent quadrat established by driving steel fence posts at each corner and the center of the quadrat. The quadrat was then divided into 4 triangles, each with an area of 1 m^2, by stringing wire along the diagonals between opposite corners of the quadrat as well as around the outside perimeter of the quadrat.

Quadrats were visited once during the first half of June, July, and August in both 1983 and 1984 and also during September, 1984.

Vegetation Sampling

Shoot density was used to estimate the abundance of seedlings of different species in the permanent quadrats. In some quadrats at higher elevations, Typha and/or Phragmites shoots produced by rhizomes which survived the deep flooding were found. These shoots were clearly distinguishable from seedling shoots and were recorded as vegetative shoots. All seedling shoots recorded in June were considered 'new'. In subsequent months, seedlings less than 5 cm tall were classified as 'new' while taller shoots were classified as 'old'.

'Cumulative new shoot density' is a minimum estimate of the total number of 'new' shoots to emerge during a season. This value was determined for each quadrat by summing the estimated June shoot density plus the minimum number of 'new' seedling shoots for each of the following months within a season. The latter value was determined by subtracting the combined estimates of the densities of 'new' and 'old' shoots for a given month from the estimated density of old shoots for the following month. If this difference was greater than zero, then it was added to the estimated density of 'new' shoots for the following month. In this way, shoots emerging after a quadrat was visited during one month and growing large enough to be classified as 'old' shoots during the following month were included in the estimate of cumulative new shoot density for a season.

Plant shoot densities for the different taxa present were estimated in 2 of the 4 triangular subquadrats contained within each permanent quadrat. Populations of a single species with a density greater than approximately 100 shoots per m^2 were subsampled 3 times within the outside half of each of the 2 subquadrats with a wire frame delineating an area of 100 cm^2. The mean of the 6 subsamples from each quadrat was used to estimate the population density. Seedling populations with a density less than 100 shoots per m^2 were sampled by counting the shoots in each 1 m^2 subquadrat.

Scirpus lacustris ssp. glaucus, Typha, Scolochloa, and Phragmites will be referred to as 'dominant emergents' because stands of these 4 plants form most of the vegetation in the Delta Marsh. Scirpus lacustris includes 2 subspecies, S. lacustris ssp. validus (Vahl.) Koyama and S. lacustris ssp. glaucus (Sm.) Hartm.; the latter is synonymous with S. acutus Muhl. In the field, these 2 subspecies were separated on the basis of stem color and hardness, primarily the former. In 1983, the 2 subspecies were not distinguished from one another in the permanent quadrats. In 1984, many but not all shoots were assigned to 1 of the 2 subspecies. When it was unclear to which subspecies a given shoot belonged, it was simply recorded as S. lacustris.

Environmental Variables

The mean elevation of each permanent quadrat was calculated from the elevations of the 4 corners and the center of the quadrat which were obtained using standard procedures with a level transit. The mean elevations of permanent quadrats were used to calculate correlation coefficients when examining relationships between elevation and other variables. Quadrats were classified by elevation intervals of 10 cm, e.g., a quadrat in the 247.4 m elevation interval has an elevation greater than 247.34 and less than 247.45 m. In the text, elevation intervals are referred to simply as elevations.

The soil moisture and conductivity of each permanent quadrat were estimated each month by collecting approximately 300 gm of soil from the upper 5 to 8 cm of the substrate within 2 m of the quadrat.

Soil extracts were made using distilled water and their conductivities in mmhos were measured with a conductivity meter (Yellow Springs Co. Model 33). In June and July, 1983, these extracts were prepared by mixing 25-30 g of fresh sample with an amount of distilled water equal to 3 times the weight of the fresh soil. In August, 1983, fresh soil was used but the ratio of distilled water to sample was 5:1 by weight. In 1984, extracts were prepared by mixing 50 g of oven dried soil with 250 ml of distilled water following the method described by Nelson (1954) to produce a 5:1 distilled water to dry soil extract. In order to compare 1983 soil conductivities with 1984 measurements, conductivities were determined by the different methods for each 1 of a series of samples collected in 1984.

The multiple regression equation relating the conductivities of 3:1 extracts and the moisture content of fresh soil extracts to the conductivity of the 5:1 distilled water to dry soil extracts for 17 samples was:

$$[1] \quad Y = 2.35\, X_1 + 6.92\, X_2 - 1380 \quad (R^2 = 0.82)$$

where Y is the conductivity of the 5:1 distilled water to dry soil extract, X_1 is the conductivity of the 3:1 extract, and X_2 is the fresh moisture content of the 3:1 extract.

On the basis of 25 samples, the multiple regression equation relating the conductivity of the 5:1 distilled water to fresh soil extract and the moisture content of the fresh sample to the conductivity of the 5:1 distilled water to dry soil extract was:

$$[2] \quad Y = 2.24\, X_1 + 5.80\, X_2 + 467 \quad (R^2 = 0.67)$$

where Y is the conductivity of the 5:1 distilled water to dry soil extract, X_1 is the conductivity of the 5:1 distilled water to fresh soil extract, and X_2 is the moisture content of the fresh soil. These equations were used to generate the estimates of 1983 soil conductivities presented in this paper.

Soil moisture was determined by weighing fresh samples and then oven drying them at 100°C to constant weight. The weight of water in a sample is expressed as a percentage of the weight of dry soil in the sample.

Soil temperatures were measured with bimetal thermometers at 12 randomly chosen points in each permanent quadrat. Six points were located in litter-covered ground and 6 were located in bare ground.

The percentage of surface area in a quadrat covered by standing or fallen litter was visually estimated. In addition, the litter in each quadrat was examined to determine which species of emergent vegetation dominated the site prior to above-normal flooding and thereby classify each permanent quadrat by vegetation type. Quadrats were classified as *Scirpus lacustris* ssp. *glaucus* mixed if litter of *Scirpus lacustris* ssp. *glaucus* and at least one other emergent, either *Typha* or *Phragmites* or both, was found. *Carex* rarely forms monodominant stands in the Delta Marsh but does occasionally occur as a subdominant in *Scolochloa* stands. Any areas that formerly had *Carex* were classified as belonging to the *Scolochloa* vegetation type.

Nomenclature

The nomenclature in this study follows Scoggan (1978-79).

RESULTS

Temporal Patterns

One- and two-year drawdowns

There was no difference in the species richness of the vegetation between the first and second years of the two-year drawdown with respect to commonly occurring species, i.e., those found in at least 5 % of the permanent quadrats in at least 1 of the 2 years (Table 1). Species found in less than 5% of the permanent quadrats included *Eleocharis palustris* (L.) R. and S., *Suaeda maritima* (L.) Dumort., *Salicornia europaea* L., *Senecio congestus* (R. Br.) DC., *Polygonum* L. spp., *Cicuta maculata* L., *Epilobium glandulosum* Lehm., *Scutellaria epilobiifolia* Hamilton, *Populus deltoides* Marsh., and *Acer negundo* L.

During the first year of drawdown, mean cumulative new shoot densities of emergents were in the range of thousands to tens of thousands per 100 m^2 with the exceptions of *Phragmites* and *Puccinellia* (Table 1), both of which were less abundant. In addition to *Phragmites*, seedlings of the other 3 dominant emergents, *Scirpus lacustris* ssp. *glaucus*, *Typha*, and *Scolochloa* were also found during the drawdown. Most recruitment of emergents occurred immediately after drawdown; there was little subsequent recruitment. The shoot densities of most emergents were higher, often by 1-2

TABLE 1. Mean cumulative new shoot densities per 100 m^2 of the species frequently found in the seed bank[1] and during the two-year drawdown in the MERP complex, the Delta Marsh, Manitoba

Species	Seed Bank n=250	Year of Drawdown: Year 1 n=80	Year of Drawdown: Year 2 n=80
EMERGENT PERENNIALS			
Scirpus lacustris L.	-	40000	2500
S. lacustris ssp. validus (Vahl.) Koyama	61000	-	200
S. lacustris ssp. glaucus (Sm.) Hartm.	240	-	200
Typha L. spp.[2]	22000	3000	200
Scolochloa fetucacea (Willdl.) Link	3000	10000	300
Phragmites australis (Cav.) Trin. ex Steud.	1400	100	100
Carex atherodes Spreng.	3000	3000	100
Puccinellia nuttalliana (Schultes.) Hitchc.	-	10	1000
Scirpus maritimus L.	1400	2000	20
Hordeum jubatum L.	50	2000	1000
MUD FLAT ANNUALS			
Atriplex patula L.	1600	70000	80000
Aster laurentianus Fern.	1200	2000	180000
Chenopodium rubrum L.	18000	5000	90000
Ranunculus sceleratus L.	6000	600	300
Rumex maritimus L.	2800	200	400
WET MEADOW PERENNIALS			
Stachys palustris L.	290	400	400
Mentha arvensis L.	1600	100	500
Teucrium occidentale Gray	230	5	800
Lycopus asper Greene	1000	20	200
Sonchus arvensis L.	390	300	700
Cirsium arvense (L.) Scop.	740	100	200
Urtica dioica L.	340	600	300

[1]Mean seedling densities per 100 m^2 from Pederson (1981, 1983).

[2]Predominantly T. glauca Godr.

orders of magnitude, during the first year of the two-year drawdown than during the second year of this treatment. Again, *Phragmites* and *Puccinellia* were the exceptions to this pattern; the former occurred at similar but low densities in both years while the latter was more abundant in the second year than in the first. With the exception of *Phragmites*, the greater recruitment of dominant emergents during 1984 in the one-year drawdown treatment than in the second year of the two-year drawdown suggests that the reduced recruitment of emergents during the second year of drawdown is due to the length of the drawdown rather than to differences in environmental conditions between 1983 and 1984 (Table 2).

Seedlings of *Scirpus lacustris* ssp. *validus* were found at the same density as those of *S. lacustris* ssp. *glaucus* in the second year of the two-year drawdown (Table 1). During 1984 in the one-year drawdown, the mean cumulative new shoot density for *S. lacustris* was 60000 per 100 m^2 (n=20). Of these, 8000 were considered *S. lacustris* ssp. *glaucus*, 20000 were considered *S. lacustris* ssp. *validus*, and the remainder were not assigned to a subspecies.

Atriplex, *Aster*, and *Chenopodium* were the most abundant annuals, occurring in densities ranging from 1200 to over 100000 shoots per 100 m^2 during both years of the drawdown (Tables 1 and 3). These 3 species will be referred to as

TABLE 2. New shoot densities per 100 m^2 of dominant emergents in different months in the first and second years of the one-year and two-year drawdowns in the MERP complex, the Delta Marsh, Manitoba

		Scirpus lacustris		*Typha glauca*		*Scolochloa festucacea*		*Phragmites australis*	
		Length of Drawdown		Length of Drawdown		Length of Drawdown		Length of Drawdown	
Yr	Mon	2-Yr n=80	1-Yr n=20	2-Yr n=80	1-Yr n=20	2-Yr n=80	1-Yr n=20	2-Yr n=80	1-Yr n=20
	Jun	30000	-	0	-	6000	-	1	-
83	Jul	10000	-	3000	-	6000	-	80	-
	Aug	200	-	20	-	10	-	20	-
	Jun	2000	20000	100	30000	170	3000	100	2000
84	Jul	500	5000	40	9000	20	100	0	0
	Aug	0	0	0	300	0	0	0	0

the dominant mud-flat annuals. Two other annuals, Ranunculus and Rumex, along with all the wet meadow perennials occurred in relatively low densities not exceeding 800 shoots per 100 m^2.

Shoot densities of Atriplex, Ranunculus, and Rumex were similar during the first and second years of the two-year drawdown (Table 1). Chenopodium and especially Aster were more abundant during the second year of the two-year drawdown than during the first.

Shoot densities of common wet meadow perennials were either similar during the first and second years of the two-year drawdown or somewhat greater during the second year than the first (Table 1).

Seasonal patterns

In this paper, seasonal patterns of recruitment are examined only in dominant emergents and dominant mud-flat annuals. Most seedlings were recruited during June when soil conductivities were low, moisture levels were high, and temperatures were moderate (Tables 2, 3, and 4). After June, recruitment of seedlings declined during the remainder of the season (Tables 2 and 3). In 1983 during the first year of the two-year drawdown, however, recruitment in Typha, Phragmites, Aster, and Chenopodium was greater in July than June (Tables 2 and 3). Although the MERP complex was generally free of standing water during June, 1983, soil

TABLE 3. New shoot densities per 100 m^2 of dominant mud-flat annuals in different months in the first and second years of the one-year and two-year drawdowns in the MERP complex, the Delta Marsh, Manitoba

		Atriplex patula		*Aster laurentianus*		*Chenopodium rubrum*	
		Length of Drawdown		Length of Drawdown		Length of Drawdown	
Yr	Mon	2-Yr n=80	1-Yr n=20	2-Yr n=80	1-Yr n=20	2-Yr n=80	1-Yr n=20
	Jun	50000	-	30	-	300	-
83	Jul	3000	-	2000	-	4000	-
	Aug	100	-	50	-	200	-
	Jun	80000	30000	160000	9000	60000	500
84	Jul	2000	0	13000	2000	20000	200
	Aug	100	0	1000	0	3000	0
	Sep	20	0	200	100	200	200

moisture levels were the highest observed while soil temperatures were the lowest recorded in this study (Table 4).

In 1984, no new seedlings of dominant emergents were encountered after August while new seedlings of all 3 dominant mud-flat annuals were found in September (Table 3).

Soil conductivities were consistently lower in June and July than in August and September (Table 4). In the 8 marshes drawndown for two years, conductivities were similar in both years. Conductivities in the two marshes drawndown for one year only were higher than those in the other 8 marshes.

Soil moisture levels were higher in June and July than in August and September (Table 4). During June in the first year of the two-year drawdown, average soil moisture was higher than the soil moisture levels in June of the following year in either the two-year or one-year drawdown treatments. Soil moisture was lower in July during the second year of the two-year drawdown than during July of the first year of drawdown in either treatment. In August and September of both years, moisture levels were similar in all cases.

Seasonal trends and differences between years in temperatures were similar in bare and litter-covered ground, consequently, only bare ground temperatures are presented

TABLE 4. Temporal patterns in soil conductivities (mmhos), moisture (%), and temperature (°C) during drawdown in the MERP complex, Delta Marsh, Manitoba

			Conductivity		Moisture		Bare Ground Temperature	
			Length of Drawdown		Length of Drawdown		Length of Drawdown	
Yr	Mon		2-Yr (n=80)	1-Yr (n=20)	2-Yr (n=80)	1-Yr (n=20)	2-yr (n=45-61)	1-yr (n=18-19)
	Jun	Mean	6.5	-	550	-	14	-
		S.E. /Range	(0.3)	-	(30)	-	(10-24)	-
83	Jul	Mean	5.8	-	420	-	23	-
		S.E. /Range	(0.3)	-	(20)	-	(14-34)	-
	Aug	Mean	8.5	-	200	-	24	-
		S.E. /Range	(0.4)	-	(10)	-	(19-31)	-
	Jun	Mean	6.3	8.6	350	410	20	21
		S.E. /Range	(0.5)	(0.8)	(10)	(30)	(14-31)	(15-32)
84	Jul	Mean	6.5	9.8	340	390	23	26
		S.E. /Range	(0.4)	(0.7)	(10)	(20)	(16-36)	15-37)
	Aug	Mean	7.6	11.1	230	240	22	25
		S.E. /Range	(0.4)	(0.6)	(10)	(10)	(16-30)	(20-33)
	Sep	Mean	8.7	10.1	200	240	16	16
		S.E. /Range	(0.5)	(1.1)	(10)	(10)	(9-25)	(11-22)

here (Table 4). Temperatures in soil covered by litter were 2°C lower on average than bare ground temperatures. Bare soil temperatures increased from an overall average of 18°C in June to 24°C on average in July and August and then declined in September (Table 4). Thompson and Grime (1983) documented the importance of fluctuating temperatures to the germination of wetland plants so consideration of ranges of temperature rather than means is probably more meaningful. In June, 1983, temperatures ranged from 10 to 24°C while in June of the following year, temperatures ranged from 14 to 32°C in both treatments combined (Table 4).

Recruitment and Elevation

The distribution of seedlings of each species during this drawdown can not be explained as a response to any one environmental factor, such as salinity, but to a number of interacting and probably interrelated factors. The cumulative new shoot density during the first year of drawdown for individual species or combinations thereof are examined in relation to elevation and environmental conditions at different elevations. The relationships between pre-flooding vegetation type and patterns of species recruitment are also examined.

Cumulative new shoot densities for all species combined were lowest at the low end of the environmental gradient, high from 247.4 to 247.8 m, and low at 247.9 m and above (Table 5).

Emergents

Seedlings of Scirpus lacustris were most abundant at an elevation of 247.4 m where their density was 130000 shoots per 100 m^2, over 4 times greater than the next highest density for this species (Table 5). Excluding this peak, S. lacustris shoot densities were intermediate from 247.2 to 247.5 m. This species occurred at low density from 247.6 to 247.8 m and was absent at the 2 highest elevations. S. lacustris also was found at low density at 247.1 m.

Maximum densities of 10-20000 Typha shoots per 100 m^2 were found from 247.3 to 247.5 m (Table 5). Typha was moderately abundant at 247.2 m and an order of magnitude less numerous at 247.6 and 247.7 m. This species was absent from the the lowest as well as the 3 highest elevations along the gradient.

Scolochloa reached its highest densities of 20-30000 shoots per 100 m^2 at elevations from 247.5 to 247.8 m (Table 5). The abundance of this species decreased rapidly as elevation decreased; it was absent at the 3 lowest elevations. Scolochloa was moderately abundant at 247.8 m and was encountered at low densities at the two highest elevations.

TABLE 5. Mean cumulative new shoot densities per 100 m^2 for all species combined and dominant emergents by elevation intervals during the first year of drawdown in the MERP complex, the Delta Marsh, Manitoba

Elevation	n	All Species Combined	*Scirpus lacustris*	*Typha glauca*	*Scolochloa fetucacea*	*Phragmites australis*
247.1	3	3100	700	0	0	0
247.2	4	34000	25000	2400	0	0
247.3	13	43000	30000	10000	0	90
247.4	22	180000	130000	20000	4000	2000
247.5	18	82000	20000	20000	20000	1000
247.6	14	170000	6000	800	20000	60
247.7	13	210000	10000	500	30000	40
247.8	4	740000	8000	0	14000	80
247.9	6	84000	0	0	130	0
248.0	3	20000	0	0	700	0

Phragmites was most abundant at elevations of 247.4 and 247.5 m where it attained a density of 1-2000 shoots per 100 m^2 (Table 5). The density of this emergent declined rapidly above and below elevations from 247.4 to 247.5 m and this species was absent from the 2 lowest and 2 highest elevations along the gradient.

Scirpus maritimus had a bimodal distribution with respect to elevation with 1 peak at 247.1 m and another, larger value of 9000 shoots per 100 m^2 at 247.6 m (Table 6). Discounting the lesser peak at the lowest elevation, S. maritimus seedlings were present in low densities at low elevations. Shoot density was low at 247.7 m and S. maritimus was absent from elevations higher than this.

Carex atherodes reached a peak density of 30000 shoots per 100 m^2 at 247.6 m and was also abundant at 247.7 m (Table 6). Densities of this species were 3 orders of magnitude less at 247.3 to 247.5 m and Carex was absent from the high and low ends of the elevation gradient.

Puccinellia was most abundant at 247.6 and 247.7 m where the average shoot density was 6000 shoots per 100 m^2 (Table 6). This species was present at low densities at the next two lower elevations and absent from the remainder of the elevation gradient.

Hordeum was most abundant at 248.0 m where the density was 10000 shoots per 100 m^2 (Table 6). The density of this

TABLE 6. Mean cumulative shoot densities per 100 m^2 for subdominant emergents by elevation intervals during the first year of drawdown in the one-year and two-year drawdowns in the MERP complex, the Delta Marsh, Manitoba

Elevation	n	*Scirpus maritimus*	*Carex atherodes*	*Puccinellia nuttalliana*	*Hordeum jubatum*
247.1	3	1600	0	0	0
247.2	4	400	0	0	0
247.3	13	30	30	0	8
247.4	22	300	60	200	0
247.5	18	4000	50	300	0
247.6	14	9000	30000	5000	6000
247.7	13	200	10000	7000	0
247.8	4	0	30	0	0
247.9	6	0	0	0	3000
248.0	3	0	0	0	10000

species was somewhat lower at 247.9 m and then the species was essentially absent from the remainder of the elevation gradient except at 247.6 m where it occurred in moderate density. This apparent anomaly is due to the fact that Hordeum was abundant in only 4 permanent quadrats, all of which were located in an area which was a Hordeum meadow prior to creation of the MERP complex. The discontinuity in the distribution of Hordeum is primarily a consequence of the distribution by elevation of the very few permanent quadrats in which this species occurred.

Annuals

The Atriplex density of 700000 shoots 100 m^{-2} at 247.8 m is the highest recorded for any species during this study (Table 7). This species occurred at intermediate densities above this peak at 247.9 and 248.0 m and below the peak at 247.6 and 247.7 m. Immediately below 247.7 m, Atriplex shoot densities were low and the species was absent at the 2 lowest elevations.

Aster densities were high, 8000 shoots per 100 m^2 on average, from 247.7 to 247.4 m (Table 7). Its overall density was lower than that of the other 2 abundant annuals, Atriplex and Chenopodium.

Chenopodium attained a peak density of 20000 shoots per 100 m^2 at 247.6 m (Table 7). Densities of this species were intermediate below this elevation at 247.5 and 247.4 m, and

TABLE 7. Mean cumulative shoot densities per 100 m^2 for annuals and wet meadow perennials by elevation intervals during the first year of drawdown in both treatments in the MERP complex, the Delta Marsh, Manitoba

Elevation	n	*Atriplex patula*	*Aster laurentianus*	*Chenopodium rubrum*	*Ranunculus & Rumex*	Wet Meadow Perennials
247.1	3	0	0	800	0	0
247.2	4	0	3000	2100	0	0
247.3	13	50	210	2200	300	30
247.4	22	900	8000	6000	4000	600
247.5	18	700	4000	8000	6000	2000
247.6	14	60000	10000	20000	2000	6000
247.7	13	130000	10000	3000	2000	10000
247.8	4	700000	400	1100	100	7000
247.9	6	70000	500	1400	0	9000
248.0	3	30000	70	3000	30	5700

were low along the rest of the elevation gradient.

Ranunculus and Rumex densities were combined because their distributions in relation to elevation were similar. The highest densities for these 2 species, 4000 shoots per 100 m^2, occurred at 247.4 m (Table 7). Densities of Ranunculus and Rumex from 247.5 to 247.7 m were intermediate, low at 247.8 and 247.3 m. These species were nearly absent elsewhere along the elevation gradient.

Wet meadow perennials

The shoot densities of the wet meadow perennial plant species listed in Table 1 were combined because they all had similar distributions and occurred at low densities by comparison with most emergents and dominant mud-flat annuals (Table 7). Collectively, the wet meadow perennials were most abundant from 247.7 to 247.9 m where their shoot density averaged approximately 9000 shoots per 100 m^2. Wet meadow perennial shoot densities decreased steadily from 247.6 down to 247.3 m and these species were absent at the 2 lowest elevations.

Environmental factors

Conductivity was negatively correlated with elevation ($r=-0.47$, $p<0.05$, $n=100$). Maximum conductivities of approximately 10 mmhos were recorded at the two lowest elevations along the gradient (Table 8). Intermediate conductivities averaging approximately 8 mmhos were encountered from 247.3 to 247.6 m. Above 247.6 m, conductivities declined as elevation increased to a minimum of 3.4 mmhos at 248.0 m.

Moisture was not linearly related to elevation which resulted in the lack of a significant correlation between these 2 variables ($r=-0.17$, $p>0.05$, $n=100$). Peak soil moistures of 440-450% occurred at 247.4 and 247.5 m; both above and below these elevations moisture declined steadily as distance from this peak increased (Table 8). Minimum soil moistures of 190-200 % were encountered at the extreme high and low ends of the elevation gradient.

Percent litter cover had a bimodal distribution in relation to elevation (Table 8) which likely accounts for the low, nonsignificant correlation between the 2 factors ($r=0.14$, $p>0.05$, $n=100$). Litter cover attained levels of 60% at 247.5m and 70% at 248.0 m (Table 8).

In addition to the relationships between elevation and the other environmental factors described above, as percent litter cover increased, soil conductivity tended to decrease ($r=-0.30$, $p<0.05$, $n=100$) while soil moisture increased ($r=0.38$, $p<0.05$, $n=100$).

TABLE 8. Mean values for environmental variables by elevations during the first year of drawdown in the one-year and two-year drawdowns in the MERP complex, the Delta Marsh, Manitoba

Elevation Interval	n	Soil Conductivity (mmhos)[1]	Soil Moisture (%)	Litter (%)
247.1	3	9.6 (1.6)	200 (30)	30 (30)
247.2	4	10.0 (0.6)	300 (40)	20 (20)
247.3	13	7.5 (0.6)	380 (30)	20 (10)
247.4	22	8.6 (0.5)	440 (30)	40 (10)
247.5	18	7.3 (0.5)	450 (30)	60 (10)
247.6	14	8.4 (0.7)	330 (40)	30 (10)
247.7	13	6.1 (0.5)	340 (30)	40 (10)
247.8	4	6.7 (1.5)	330 (80)	20 (10)
247.9	6	4.2 (0.8)	300 (50)	60 (20)
248.0	3	3.4 (1.6)	190 (30)	70 (30)

[1]Standard error in parentheses.

Pre-flooding vegetation type and dominant emergents

The preceding analyses have shown the over-riding importance of elevation in the distribution of seedlings in the MERP complex and that there are changes in environmental conditions along the elevational gradient. Other factors that may be responsible for observed recruitment patterns include the type of vegetation which occurred at an elevation prior to the high water years. Consequently, the distribution of permanent quadrats as classified by pre-flooding vegetation type has been examined in relation to elevation (Table 9) and related to the distribution and abundance of seedlings of dominant emergents.

As expected, open water sites occupied the lowest elevations. *Scirpus lacustris* ssp. *glaucus* sites and *S. lacustris* ssp. *glaucus* mixed sites were found from 247.2 to 247.5 m and overlapped with the lower half of the elevation range of *Typha* sites. The most frequently encountered preflooding vegetation type was *Typha* which accounted for 33 of the 100 permanent quadrats. This vegetation type was most numerous at 247.5 m, the middle of its broad elevation range. The upper half of the *Typha* elevation range overlapped with all the remaining pre-flooding vegetation types. The *Phragmites-Typha* and *Scolochloa-Phragmites* pre-flooding vegetation types were found primarily at intermediate elevations from 247.4 to 247.7 m while

TABLE 9. Distribution of permanent quadrats by pre-flooding vegetation type expressed as a proportion of the number of quadrats at each elevation in the MERP complex, the Delta Marsh, Manitoba

Elevation (m)	Pre-flooding Vegetation Type[1,2] OPWA	SCAC	SCAC MIX	TYPH	PHRA TYPH	SCOL PHRA	SCOL	PHRA	HORD	TOTAL
247.1	0.7				0.3					3
247.2	0.5	0.3		0.3						4
247.3	0.1	0.3	0.2	0.5						13
247.4		0.2	0.3	0.4	0.1	0.1		0.1		22
247.5			0.1	0.6	0.1	0.1		0.1		18
247.6				0.2	0.1	0.1	0.4	0.1	0.1	14
247.7				0.2	0.1		0.4	0.2	0.1	13
247.8				0.3		0.3	0.3			3
247.9					0.2		0.2	0.5	0.2	6
248.0								0.7	0.3	3
TOTAL	5	9	9	33	7	6	12	13	5	99

[1] OPWA=open water, SCAC=*Scirpus lacustris* ssp. *glaucus*, TYPH=*Typha*, PHRA=*Phragmites*, SCOL=*Scolochloa*, and HORD=*Hordeum*.

[2] Only 1 permanent quadrat was classified as 'upland' and it is not included in this table.

Scolochloa sites occupied a slightly higher elevation range from 247.6 to 247.9 m. Phragmites was found over as broad an elevation range as was the Typha vegetation type but occupied the upper two thirds of the elevation gradient. Hordeum sites were few in number and confined to elevations above 247.5 m.

Overall, the peaks in the frequency of occurrence of the Scirpus lacustris ssp. glaucus, Typha, Scolochloa, and Phragmites pre-flooding vegetation types seem to be separated along the elevation gradient although there is much overlap in their overall distributions and sample sizes are small (Table 9).

The cumulative new shoot densities of Scirpus lacustris, Typha, and Phragmites were maximum over elevations from 247.3 to 247.5 m (Table 5). The locations along the elevational gradient of peak densities of S. lacustris and Typha seedlings correspond fairly closely to the maximum frequencies of occurrence of the S. lacustris ssp. glaucus and Typha pre-flooding vegetation types, respectively. Most permanent quadrats of the Phragmites pre-flooding vegetation type were found at elevations above those where seedlings of this species were most dense (Tables 5 and 9). Over elevations from 247.3 to 247.5 m, no dominant emergent was most abundant in quadrats which it dominated prior to deep flooding and no particular differences in environmental conditions among different vegetation types were found (Table 10).

Scolochloa reached peak densities of cumulative new seedling shoots from 247.5 to 247.7m along the elevational gradient (Table 5) which coincides closely with the location of the *Scolochloa* pre-flooding vegetation type (Table 9). The mean cumulative new shoot density of *Scolochloa* was highest in the *Scolochloa* pre-flooding vegetation type over elevations from 247.6 to 247.8 m (Table 11). Soil conductivity was higher while both soil moisture and litter were lower in the *Scolochloa* vegetation type than in either of the other 2 types considered (Table 11).

It should also be noted that all dominant emergents were present in all pre-flooding vegetation types over both elevation ranges examined (Tables 10 and 11).

TABLE 10. Environmental conditions and shoot densities of dominant emergents in pre-flooding vegetation types at elevations from 247.3 to 247.5 m during drawdown in the MERP complex, the Delta Marsh, Manitoba

		Pre-flooding Vegetation Types		
		Scirpus lacustris ssp. *glaucus* (N=8)	*Typha* (N=25)	*Phragmites* (N=4)
Soil Conductivity (mmhos)	Mean	8.8	7.4	7.2
	(S.E.)	(0.9)	(0.4)	(0.5)
Soil Moisture (%)	Mean	410	400	530
	(S.E.)	(60)	(20)	(80)
Litter (%)	Mean	30	50	60
	(S.E.)	(10)	(10)	(20)
Scirpus lacustris		40000	20000	75000
Typha glauca		40000	20000	40000
Scolochloa fetucacea		100	2000	17000
Phragmites australis		500	2000	180

TABLE 11. Environmental conditions and shoot densities of dominant emergents in pre-flooding vegetation types at elevations from 247.6 to 247.8 m during drawdown in the MERP complex, the Delta Marsh, Manitoba

		Pre-flooding Vegetation Types		
		Typha (N=7)	*Scolochloa* (N=11)	*Phragmites* (N=4)
Soil Conductivity (mmhos)	Mean	5.4	9.0	6.1
	(S.E.)	(0.8)	(0.7)	(0.9)
Soil Moisture (%)	Mean	380	270	510
	(S.E.)	(40)	(10)	(110)
Litter (%)	Mean	60	8	90
	(S.E.)	(10)	(3)	(10)
Scirpus lacustris		6000	5000	900
Typha glauca		700	900	500
Scolochloa fetucacea		6000	40000	500
Phragmites australis		30	20	100

DISCUSSION

Walker (1959, 1965) studied the vegetation which developed in the Delta Marsh in the late 1950s during a period of low water, i.e., a 'natural' drawdown, that followed a period of unusually high water levels. The species composition of the 1950s drawdown was very similar to that of the 1980s drawdown with the exception of some rare species found by Walker but absent from the MERP complex. Walker's studies covered an area of the Delta Marsh which was much larger than the MERP experimental complex but she found seedlings of neither Scirpus lacustris ssp. glaucus nor Phragmites, both of which were present in the MERP complex during drawdowns in 1983 and 1984. Comparisons of plant densities between Walker's studies and this one can not be made due to differences in methodology.

The species composition of the seed bank in the MERP complex in 1980 was essentially the same as that of the drawdown vegetation in 1983 (Table 1). The Spearman rank correlation coefficient for cumulative new shoot densities in the first year of drawdown in the two-year drawdown and the density of germinable seeds found in the marsh soil (Table 1) was 0.55 ($p=0.01$). With the exception of Scolochloa, dominant emergents were less abundant in the field than in the seed bank samples, while dominant mud-flat annuals were much more abundant in the field than in the seed bank samples. For example, the mean density of *Atriplex* seedlings in the seed bank samples was 1600 per 100 m^2 and the mean cumulative new seedling shoot density was 70000 per 100 m^2 for this species in the field (Table 1).

The difference in the density of a given species between the seed bank and the drawdown has two possible explanations. Either the actual numbers of viable seeds were different in the 2 situations or seed germination and seedling emergence were different because of differences in environmental conditions. It is not possible to determine which explanation is correct with the data available.

The similarity of the species composition and numbers of germinable seeds in wetland seed banks to the species composition and plant density in the field varies from relatively high (Thompson and Grime 1979; van der Valk and Davis 1978) to relatively low (Leck and Graveline 1979; Smith and Kadlec 1983).

Temporal Patterns

One- and two-year drawdowns

In the Delta Marsh, there was no difference in the species composition of the vegetation with respect to commonly occurring species between the first and second years of the two-year drawdown treatment. In the two-year drawdown, recruitment of emergents occurred predominantly during the first year while that of dominant mud-flat annuals was higher during the second year (Table 1).

The study conducted in northwestern Minnesota by Harris and Marshall (1963) seems to have produced the only published report on recruitment during a multi-year drawdown. Harris and Marshall (1963) did not describe seedling densities in sufficient detail to allow direct quantitative comparisons to be made with this study. Nonetheless, there are some qualitative similarities between the results of the two studies. Harris and Marshall (1963) found that during the second year of drawdown, emergents generally were less numerous while upland and shoreline weeds were more abundant than during the first year.

Differences in the seed bank between years may have been responsible for differences in recruitment between the first and second years of drawdown. In a marsh in Utah, Smith and Kadlec (1985) found no overall dramatic impact of a drawdown on the size of the seed bank. They noted that seeds of *Chenopodium rubrum* were more abundant after drawdown than before, likely due to seed production during the drawdown. The increased densities of *Aster* and *Chenopodium* in the second year of drawdown in this study may be due at least in part to production of seeds by these species during the first year of the drawdown. In Utah, germinable seeds of two emergents, *Scirpus maritimus* and

Distichlis spicata, were less abundant after the drawdown than before, suggesting that germination combined with a lack of seed production during the drawdown may have depleted the seed bank of these species (Smith and Kadlec 1985). Similarly, the reduced new shoot densities during the second year of drawdown observed in all dominant emergents other than Phragmites may be due to depletion of the seed bank (Table 1).

From the standpoint of seedling recruitment alone, there appears to be little advantage to a second year of drawdown as far as marsh management is concerned since most seedlings of emergent species were recruited during the first year of the two-year drawdown. In addition, no new species were recruited during the second year of drawdown. I concur with Harris and Marshall (1963) who concluded that "...in most cases, properly handled 1-year drawdowns were more successful in establishing stands of desired emergents than 2-year drawdowns."

The higher density of dominant mud-flat annuals during the second year of drawdown as compared to the first might be expected to have a negative impact on the recruitment of emergents. van der Valk (1986) found that removal of annuals significantly increased the density of grass shoots but did not affect the number of species recruited in the MERP complex. He concluded that, as far as establishment of perennials is concerned, there is no reason to try to control annuals during a drawdown.

Seasonal patterns

The occurrence of peak recruitment of dominant emergents and mud-flat annuals during June and July, followed by reduced recruitment during the remainder of the season, seems to be related to changes in environmental conditions. During drawdown in the MERP complex, soil conductivity increased while soil moisture decreased over a growing season, as was observed in Utah (Smith and Kadlec 1983). High levels of salinity may inhibit seed germination during a drawdown (Christiansen and Low 1970; Howard-Williams 1975; Lieffers and Shay 1982) or in the lab (Galinato 1985; Galinato and van der Valk 1986). Low levels of soil moisture may also inhibit germination at least of emergents (Harris and Marshall 1963). The presence of vegetation later in the growing season reduces the amount of light reaching the soil surface and also alters the spectral composition of that light (Harper 1977). Many wetland plants are known to require exposure to light in order to germinate (Thompson and Grime 1983; Galinato and van der Valk 1986) and the spectral composition of that light may also affect germination (Bonnewell *et al*. 1983).

In addition, the seed bank may have been depleted by germination early in the season (see the discussion of

Kadlec and Smith (1985) above). The seed bank may not be replenished until late in the same season or even until the following spring.

It is difficult to evaluate the possibility that the very high soil moisture levels of 550% in June, 1983 as compared to 440% in the one-year drawdown might have been related to the observed reduction in recruitment during June 1983 (Tables 2, 3, and 4). Although standing water as little as 2 cm deep is known to inhibit the germination of many emergents and annuals (van der Valk and Davis 1978; Pederson 1981, 1983; Smith and Kadlec 1983, 1985), little is known about the effects of soil moisture on germination. There are a few studies of seed germination under anaerobic conditions (e.g., Bonnewell et al. 1983; Smith 1972) but it is difficult to relate these to soil moisture levels in the field.

In the lab, Typha (Bonnewell et al. 1983; Galinato 1985; Galinato and van der Valk 1986) and Phragmites (van der Toorn 1972; Haslam 1973; Galinato 1985; Galinato and van der Valk 1986) both showed reduced germination at low temperatures comparable to those recorded during June 1983 (Table 4) while Scolochloa, Atriplex, and Aster did not (Galinato 1985; Galinato and van der Valk 1986). Chenopodium germinated in the lab at least as well at low temperatures as it did at high temperatures (Galinato 1985;

Galinato and van der Valk 1986) but germination in this species during drawdown was low in June, 1983 when soil temperatures were low (Tables 3 and 4).

Recruitment and Elevation

Elevation *per se* is not directly responsible for the patterns of species recruitment observed (Tables 5, 6, and 7). Elevation is the best predictor of recruitment patterns because it reflects the composition of the seed bank (Pederson 1983; Pederson and van der Valk 1985) as well as soil conductivity, soil moisture, litter, and the distribution of pre-flooding vegetation types (Tables 8 and 9). Of these factors, the composition of the seed bank seems to be most strongly related to the recruitment patterns observed.

The pattern of cumulative new shoot densities for all species combined at different elevations (Table 5) is similar to the pattern of germinable seed densities at different elevations (Pederson 1983; Pederson and van der Valk 1985). The densities of both germinable seeds in the soil and seedlings during the drawdown were low at low elevations. Prior to deep flooding and drawdown, these sites at low elevations were either in open water areas or stands of *Scirpus lacustris* ssp. *glaucus* (Table 9). Smith and Kadlec (1983, 1985) also have reported low densities of germinable seeds in open water areas in a Utah marsh. This may be due to dispersing seeds being washed over these areas since they lack physical obstructions to trap the seeds (Pederson 1981, 1983; Smith and Kadlec 1983, 1985). High salinities at lower contours within a wetland may be a factor limiting germination at these lower elevations although average salinities in this study do not appear to be high enough, e.g., greater than 20 mmhos, to severely inhibit germination (Lieffers and Shay 1982).

The highest densities of both germinable seeds in the soil and seedlings during the drawdown were found at the middle elevations in the shoreline zone. At these elevations, emergent vegetation was dominant prior to deep flooding (Table 9) and seeds appeared to accumulate in this zone due to wave action (Pederson 1981). Densities of both germinable seeds in the soil and seedlings during the drawdown were low at the high end of the elevational gradient where upland plants begin to dominate the vegetation.

If patterns of recruitment in dominant emergents lead to the zonation patterns observed in adult plants, then it may be reasonable to expect that during drawdown the density of seedlings of a particular dominant emergent would be higher at sites dominated by that species rather than others prior to the flooding period. Nevertheless, with the exception of Scolochloa, the densities of seedlings of dominant emergents were not highest in pre-flooding vegetation types of the same species (Tables 5, 9, 10, and 11).

A few studies have examined recruitment patterns in wetland plants in an attempt to elucidate the mechanisms which produce zonation patterns in adult plants. Rabinowitz (1978) found little congruence between zonation patterns of adults and patterns of recruitment in 4 mangrove species. She hypothesized that zonation in these mangroves may be the result of differential distribution of propagules by tide according to their size and their varying abilities to become established in deep water. Keddy and Ellis (1985) found that recruitment patterns in 6 of 11 wetland species varied along a water level gradient and were consistent with the distribution of adult plants on lakeshores. Recruitment patterns in the 5 remaining species did not vary along the gradient.

The results of this study of seedling recruitment in the Delta Marsh during drawdown point to the importance of examining processes occurring before recruitment, i.e., seed production and dispersal, as well as processes occurring after recruitment such as seedling survival and growth in order to understand how these plants will be distributed after recruitment, i.e., how zonation develops in a wetland.

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