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Abundance, distribution, and diversity of buried seed populations in the Delta Marsh, Manitoba, Canada

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ABUNDANCE, DISTRIBUTION, AND DIVERSITY OF BURIED SEED POPULATIONS IN THE DELTA MARSH, MANITOBA, CANADA

Iowa State University PH.D. 1983

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Abundance, distribution, and diversity of buried seed populations in the Delta Marsh, Manitoba, Canada

by

Roger Lynn Pederson

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Botany
Major: Botany (Plant Ecology)

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In Charge of Major Work

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For the Graduate College

Iowa State University
Ames, Iowa

1983

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GENERAL INTRODUCTION

Prairie wetlands in western Canada and north central United States provide excellent examples of vegetation dynamics and community change because these habitats have characteristically fluctuating environments (Steward and Kantrud 1972). As conditions change, plant species are eliminated, introduced, or redistributed along new environmental gradients (Dodd and Coupland 1966, Dix and Smeins 1967, Walker and Coupland 1968, Millar 1973, van der Valk and Davis 1976). Seedling recruitment from the seed bank allows many wetland species to rapidly adjust to the changing environment (van der Valk and Davis 1978).

Despite the potentially important role of seed budgets in community development, population dynamics, and plant distribution (Harper 1977, Thompson 1978, Watkinson 1978, Thompson and Grime 1979, Cook 1980), populations of viable seeds in wetland plant communities have received little attention in the literature (Roberts 1981).

This dissertation describes experimental studies designed to quantify seed production, seed dispersal, and the distribution and temporal variation of buried seed populations in the Delta Marsh, Manitoba. The general objective of this research is to assess the significance of seed banks to vegetation dynamics of this lacustrine prairie marsh (Cowardin et al. 1979).

Explanation of Thesis Format

This dissertation is divided into two sections, each of which is written in a format suitable for publication in a technical journal. References cited in the general introduction may be found at the end of the dissertation. References cited within a section may be found at the end of that section. The first section of this dissertation discusses the nature of buried seed communities in a series of ten, 4-6 hectare experimental marshes. The second section discusses an intensive study of buried seed communities in four contrasting vegetation types (each type < .05 hectare).

PART I. THE DISTRIBUTION OF BURIED SEED POPULATIONS IN THE DELTA MARSH, MANITOBA, CANADA

ABSTRACT

Germinable seed densities from surface (0 to 5 cm) soil samples, soil cores (0 to 8 cm), and annual seed rain (seed traps) were measured in relation to elevation, soil salinity, and vegetation type (open water sites, *Scirpus acutus*, *Typha glauca*, *Scolochloa festucacea*, *Carex atherodes*, *Phragmites communis*, upland sites) in ten experimental marshes in the Delta Marsh, Manitoba. Numbers of germinable seeds were determined by observing seedling emergence in seed bank and seed trap soil samples placed under two simulated environmental conditions (drawdown and shallow-flooded) in outdoor greenhouses.

The drawdown treatment yielded four times as many seedlings and twice as many species (34) as the shallow-flooded treatment. The most abundant species in the drawdown treatment were *Scirpus validus*, *Typha* spp., *Chenopodium rubrum*, and *Ranunculus sceleratus*. The most abundant species in the shallow-flooded treatment were *Scirpus validus*, *Zannichellia palustris*, *Typha* spp., and *Scirpus maritimus*. The shallow-flooded treatment suppressed germination of all species except submersed aquatics (i.e., *Potamogeton pectinatus*, *Utricularia vulgaris*, *Zannichellia palustris*). Germinable seed densities in the soil varied widely among vegetation types, however, seed-bank seed densities of *Carex atherodes*, *Cirsium arvense*, *Scirpus*

validus, *Typha* spp., and *Zannichellia palustris* were significantly greater in certain plant communities. Open water sites contained the fewest seeds in the seed bank, while highest densities were located in the shoreline zone. Except for *Aster brachyactis*, *Atriplex patula*, and *Scolochloa festucacea*, buried seed densities were negatively correlated with soil salinity levels.

The presence of high seed densities of *Zannichellia palustris*, *Scirpus validus*, *Typha* spp., and mudflat annuals (*Aster brachyactis*, *Chenopodium rubrum*, *Ranunculus sceleratus*, *Rumex maritimus*) in lower depths of soil cores indicated a high water event (followed by a drying period) in recent history. Reduction in the size and diversity of the seed bank in the surface soil layers represents a recent temporal change in vegetation composition (fewer "disturbance" species) that is related to stabilization of water levels in the marsh since 1961. Under the present environmental regime in the Delta Marsh, reproduction by seed is less important than reproduction by vegetative means.

INTRODUCTION

Prairie wetlands in western Canada and north central United States range in size from small seasonally or semipermanently flooded marshes in shallow depressions (palustrine wetlands) to large marshes (covering several hundred hectares) associated with lakes (lacustrine wetlands) (Cowardin et al. 1979). Water regimes and water quality (particularly salinity) in prairie wetlands fluctuate from year to year in response to variations in runoff from snowmelt, summer precipitation, evaporation, and groundwater hydrology (Meyboom 1962, Eisenlohr 1966, Eisenlohr and Sloan 1968). These fluctuations are most extreme in palustrine wetlands. As a consequence, vegetation of prairie wetlands is constantly responding (both floristically and structurally) to water level and salinity changes (Dodd and Coupland 1966, Dix and Smeins 1967, Walker and Coupland 1968, Walker and Wehrhahn 1971, Dirschl and Coupland 1972, Steward and Kantrud 1972, Millar 1973).

Plant communities in prairie ponds and lakes are typically described as distinct zones of vegetation that follow shoreline contours (Steward and Kantrud 1972, Cowardin et al. 1979). However, Swindale and Curtis (1957), Mandossian and McIntosh (1960), Raup (1975), and van der Valk and Davis (1976a) demonstrated that different wetland species are distributed independently along environmental gradients. As environmental conditions change, plant species become redistributed along the new environmental gradient (van der Valk and Davis 1976a). This "resorting" of species along new portions of the gradient is often a result of seedling recruitment from the seed bank (buried viable seeds in the marsh substrate) (van der Valk and Davis 1976b, 1978).

Different marsh plants (mudflat annuals, emergent, submergent and free-floating species) survive periods of severe environmental change as dormant seeds in the seed bank (van der Valk and Davis 1978). Van der Valk and Davis (1979) used seed bank information (i.e., species present as viable seeds in different layers of the substrate) to explain vegetation cycles of a palustrine wetland in Iowa. Of particular interest were the presence or absence of seeds of annuals at different depths of the substrate, which indicated time periods when the marsh was dry (van der Valk and Davis 1979).

No information exists as to the nature of seed banks in lacustrine marshes or to the significance of seed banks to vegetation dynamics of large marsh systems. Presumably, the overriding effects of more stable water levels and wave action in large prairie marshes (Swindale and Curtis 1957, Spence 1967, Christiansen and Low 1970, Hutchinson 1975, Anderson 1978, Keddy 1983) will directly influence seed banks through the control of plant distribution, the transport of propagules, and the amount of (and environmental conditions on) exposed substrate during periods of low water.

In this study, my objectives were to: (1) quantify the distribution of buried seed communities of a lacustrine prairie marsh in relation to vegetation type and environmental gradients of elevation and soil salinity, (2) detect past changes in vegetation by examining seed profiles of soil cores, and (3) quantify the relationship between seed dispersal (seed rain) and seed banks. The general objective of this research is to elucidate the relationship of seed banks to vegetation dynamics of a lacustrine prairie marsh.

METHODS

Study Area

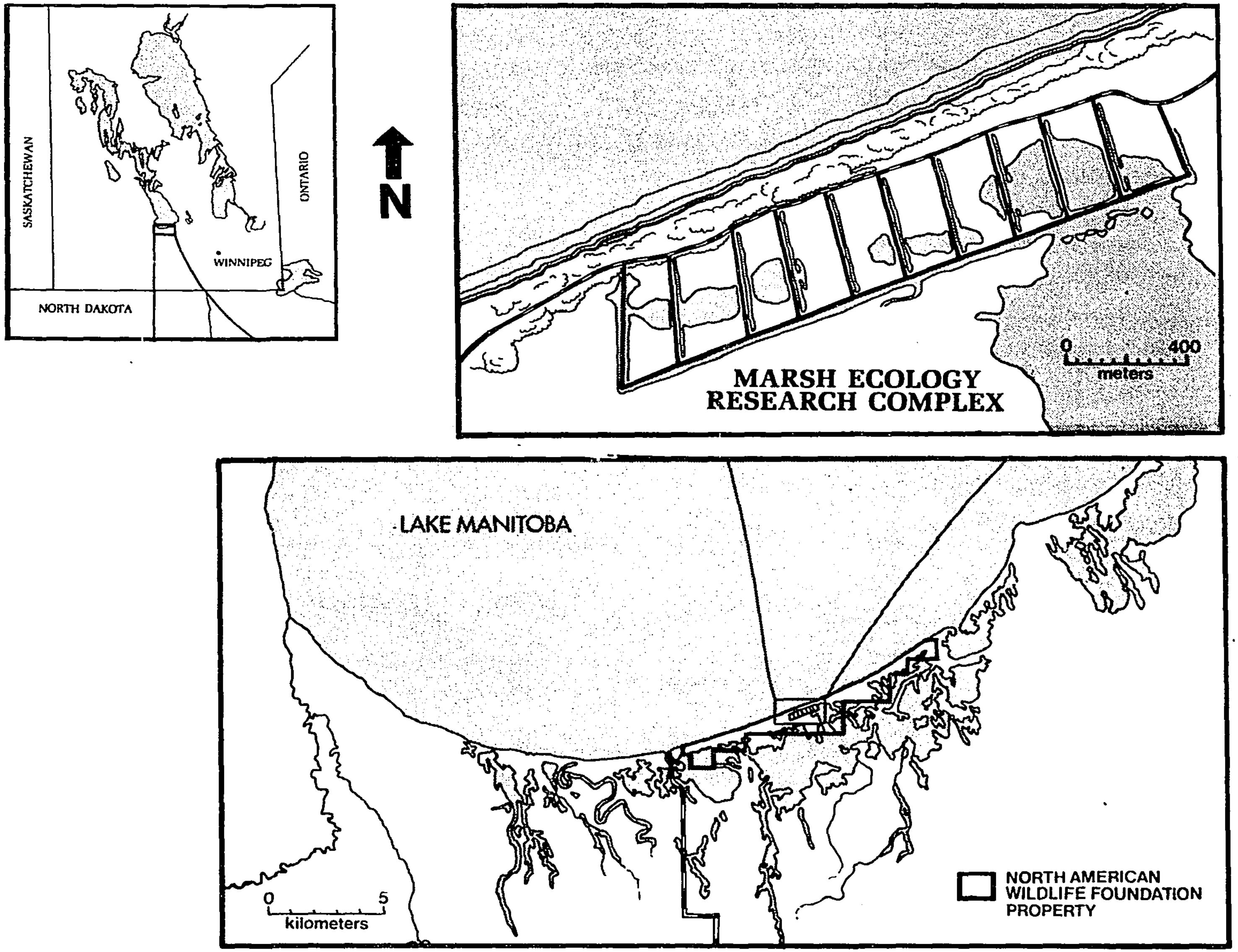
The study was conducted in the Delta Marsh, a large (ca. 15,000 ha) prairie marsh located along the south shore of Lake Manitoba (50° 11' N, 98° 19' W) in south central Manitoba. The marsh is an interconnected system of large and small bays, separated from the lake by a narrow forested sand ridge. The bays (some covering several hundred hectares) are never more than three meters deep, and usually less than one meter. The water in the marsh is saline, 1800-3300 umhos (Bossenmaier 1968), placing it in the moderately brackish category of Steward and Kantrud (1972). The specific research site was the experimental marsh complex (Figure I-1) of the Marsh Ecology Research Program (Batt et al. in press) developed by the Delta Waterfowl Research Station and Ducks Unlimited (Canada). The marsh complex consists of ten, contiguous, 4-6 hectare, diked marshes whose water levels are regulated by water control structures and electric pumps. The vegetation within these marshes is the same as described for the Delta Marsh by Love and Love (1954), Walker (1959, 1965), and Anderson and Jones (1976). Drier upland areas are dominated by Sonchus spp., Solidago spp., Calamagrostis canadensis (Michx.) Beauv., and Cirsium arvense (L.) Scop. The seasonally submersed uplands are dominated by *Phragmites communis* Trin., *Scolochloa festucacea* (Willd.) Link., and *Carex atherodes* Spreng. In areas regularly flooded, the main emergent species are *Typha* spp. and *Scirpus acutus* Muhl. Dominant submergent species include *Potamogeton* spp., *Utricularia vulgaris* L., *Myriophyllum spicatum* L., and *Ceratophyllum demersum* L.

Seed Bank Survey

In 1979, 25 sample sites were selected (in a stratified random design) and marked for each of the 10 marshes. The dominant species (within a radius of 1 m) and elevation (surveyed by transit) were recorded for each sample site. For this study, cover types were classified according to the dominant emergent species, i.e., open water (standing water with no emergent plants), *Scirpus* (monodominant *Scirpus acutus*), *Typha* (monodominant *Typha glauca*), *Scolochloa* (monodominant *Scolochloa festucacea*), *Carex* (monodominant *Carex atherodes*, or *Carex atherodes* with scattered individuals of one other dominant plant species), *Phragmites* (monodominant *Phragmites communis*), upland (combinations of *Calamagrostis canadensis*, *Cirsium arvensis*, *Solidago* spp. and *Sonchus* spp.), and mixed (combinations of two or more cover types).

In June 1980, a soil sample was collected at each of

FIGURE I-1. Location of study area


SASKATCHEWAN
ONTARIO
WINNIPEG
NORTH DAKOTA
N
MARSH ECOLOGY RESEARCH COMPLEX
0
400
meters
LAKE MANITOBA
0
5
kilometers
NORTH AMERICAN WILDLIFE FOUNDATION PROPERTY

the two hundred and fifty sample sites. Each soil sample consisted of a 30 cm x 30 cm x 5 cm block of substrate. Each sample was placed in a marked plastic bag, and stored in a styrofoam cooler while in the field. The samples were sorted and screened (1 cm^2 mesh) to remove rhizomes, tubers, and pieces of undecomposed litter, and subdivided into two major subsamples (a small portion of each soil sample was retained for analysis of salinity).

Each subsample was placed into a 20 cm x 20 cm x 3.5 cm plastic tray. These trays were arranged in a randomized design in an outdoor shelter. One set of subsamples was watered sufficiently to keep the soil surface moist (drawdown treatment). The other subsample set was continuously flooded to a depth 2 or 3 cm above the soil surface (shallow-flooded treatment). Algae were removed as necessary from the submersed samples. Both sets of subsamples were kept under their respective treatment conditions throughout the growing season (June-September). Air temperatures in the shelter ranged from a high of 38°C in July to a low of -2°C in early September.

Any seedling that became established was counted and removed as soon as it could be identified. Seedling identification of monocots was often on the basis of vegetative characters. Macaulay (1973) was used as a guide for <u>Scirpus</u> <u>acutus</u> and <u>Scirpus</u> <u>validus</u>. Best et al. (1971)

was used to identify seedlings of Scolochloa festucacea. Identification of monocots was hampered by stunted growth of plants in shallow plastic flats and the use of a field shelter (most monocots did not flower during the one growing season). Where possible, seedlings were grown from known seed sources to serve as identification guides. Voucher specimens were collected for all species and are deposited in the Herbarium of the Delta Waterfowl Research Station. Nomenclature follows Gleason and Cronquist (1963).

Soil Cores

In June 1980, within each of four monodominant vegetation types (Scirpus acutus, Typha glauca, Scolochloa festucacea, Phragmites communis), two sample sites were randomly selected. At each site, four soil cores (15 cm diameter) were extracted to a depth of approximately 20 cm. The upper 8 cm of the four soil cores was removed and carefully separated into 2 cm sections (0-2 cm, 2-4 cm, 4-6 cm, 6-8 cm), and similar sections (e.g., the four 0-2 cm sections) at each sample location were combined. Soil samples from all four depths at all eight sites were then tested for their germinable seed content (under drawdown and shallow-flooded conditions) in the manner previously described.

Seed Dispersal

In June 1979, at 65 randomly chosen seed bank sites, two seed traps (20 cm x 20 cm x 3.5 cm plastic trays filled with sterilized potting soil) were placed adjacent to the sample site. Seed traps remained in the field for one year to allow collected seed to stratify in the field. The pair of seed traps were retrieved in June of 1980, and placed in an outdoor shelter, with one trap under drawdown conditions and the other under shallow-flooded conditions. The species present within a one meter radius of the sample point were recorded in both 1979 and 1980.

Adjacent to nine randomly selected open water seed trap sites, sediment traps (trap design 9 of Hargrave and Burns 1979) were placed in the field during July and August 1981. Each sediment trap was attached by brackets to a wooden stake such that the trap was held in a vertical position approximately 30 cm away from the stake. The wooden stakes were pushed into the bottom sediments until the top of the trap was approximately 15 cm above the bottom sediments.

Outdoor Shelter

A field shelter was used for the seedling assay of germinable seeds in the seed bank and seed trap samples. The shelter design consisted of a wooden framework with a roof of chicken-wire overlaid by 6 mil plastic sheeting.

The plastic sheeting was held in place by lath. Large, shallow boxes (1.2 m x 2.5 m x 15 cm) were constructed from sheets of 2 cm marine plywood. The boxes were placed on low benches under the outdoor shelter. Each plywood box was lined with 6 mil plastic sheeting and held 55 plastic plant trays. Contamination by wind-dispersed seeds was monitored by placing control plastic flats (filled with sterilized soil) among the other seed bank and seed trap samples in the shelter. Tap water (non-saline) from a groundwater well was used as a water source.

Data Analysis

Log10(x+1) transformations were used where appropriate to stabilize variances of planned comparisons of seedling means (analysis of variance). When significant ($P < .05$) effects were determined, Tukey's Studentized HSD tests were used to rank means (Helwig and Council 1979). Pearson's product-moment correlation analysis ($P < .05$) was used to examine the relationship between seedling density and soil salinity level.

RESULTS

Seed Germination Analysis

Table I-1 summarizes the total number of seedlings which grew in soil samples under drawdown and shallow-flooded treatments. Seeds of 34 species (plus several unidentified grasses and mints) germinated and grew as seedlings in the treatments.

The most abundant species in the drawdown treatment were Scirpus validus (47% of the total number of seedlings), Typha spp. (17%), Chenopodium rubrum (14%), and Ranunculus sceleratus (5%). The most frequently occurring species in the drawdown treatment (species found in > 20% of the samples) were five annuals [Chenopodium rubrum (65%), Ranunculus sceleratus (53%), Aster brachyactis (25%), Rumex maritimus (25%), Atriplex patula (23%)], and seven perennials [Typha spp. (91%), Scirpus validus (74%), Phragmites communis (38%), Carex atherodes (28%), Scolochloa festucacea (28%), Scirpus maritimus (22%), Mentha arvensis (22%)]. These 12 species accounted for 95% of the total number of seedlings in the drawdown treatment.

The shallow-flooded treatment yielded less than one-half the number of seedlings as the drawdown treatment (free-floating plants and algae were not included in the count). The most numerous seedlings in the shallow-flooded

TABLE I-1. Total number of seedlings which grew in 250 substrate samples from the Delta Marsh, Manitoba (only species with a frequency of > 5% are included).

Species	Drawdown Treatment[1]		
	Number of Seedlings	Relative Abundance (%)	Frequency (%)
Scirpus validus	18161	47	74
Typha spp.	6697	17	91
Chenopodium rubrum	5403	14	65
Ranunculus sceleratus	1797	5	53
Carex atherodes	857	2	28
Scolochloa festucacea	851	2	28
Rumex maritimus	834	2	25
Mentha arvensis	488	1	22
Atriplex patula	486	1	23
Phragmites communis	419	1	38
Scirpus maritimus	410	1	22
Aster brachyactis	373	<1	25
Lycopus asper	290	<1	10
Cirsium arvensis	222	<1	14
Sonchus spp.	116	<1	17
Urtica dioica	101	<1	7
Salix spp.	75	<1	18
Scirpus acutus	71	<1	8
Populus deltoides	38	<1	11
Utricularia vulgaris	-----	--	--
Zannichellia palustris	-----	--	--
GRAMINAE (unidentified)	435	1	12
LABIATAE	147	<1	18

TOTAL	38883		

[1] Species found in drawdown treatment samples with a frequency < 5% include *Chenopodium glaucum*, *Cicuta maculata*, *Eleocharis* sp., *Epilobium glandulosum*, *Galium trifidum*, *Hordeum jubatum*, *Impatiens biflora*, *Puccinellia nuttalliana*, *Rorippa islandica*, *Senecio congestus*, *Solidago* sp., *Suaeda depressa*, and *Triglochin* sp.

[2] Species found in the shallow-flooded treatment samples with a frequency < 5% include *Cicuta maculata*, *Eleocharis* sp., *Potamogeton pectinatus*, and *Senecio congestus*.

TABLE I-1. (continued)

	Shallow-Flooded Treatment[2]		
Species	Number of Seedlings	Relative Abundance (%)	Frequency (%)
Scirpus validus	6713	67	70
Zannichellia palustris	1764	18	21
Typha spp.	1140	11	62
Scirpus maritimus	173	2	13
Ranunculus sceleratus	89	<1	10
Utricularia vulgaris	40	<1	6
Scolochloa festucacea	13	<1	1
Atriplex patula	11	<1	1
Rumex maritimus	10	<1	<1
Scirpus acutus	10	<1	2
Chenopodium rubrum	7	<1	<1
Phragmites communis	4	<1	1
Aster brachyactis	3	<1	1
Carex atherodes	---	--	--
Cirsium arvensis	---	--	--
Lycopus asper	---	--	--
Mentha arvensis	---	--	--
Populus deltoides	---	--	--
Salix spp.	---	--	--
Sonchus spp.	---	--	--
Urtica dioica	---	--	--
GRAMINAE (unidentified)	43	<1	<1
LABIATAE	1	<1	<1
TOTAL	10059		

treatment were Scirpus spp. (mainly validus) (67% of the total seedlings), Zannichellia palustris (18%), and Typha spp. (11%). These three species accounted for 96% of the total number of seedlings in the shallow-flooded treatment. In general, the shallow-flooded treatment suppressed germination of all species except submergents (e.g., Utricularia vulgaris, Zannichellia palustris). Seedlings of mudflat annuals (Aster brachyactis, Atriplex patula, Chenopodium rubrum, Ranunculus sceleratus) grew in the shallow-flooded treatment only when all or part of the soil sample floated to the surface.

Dominant emergent species in the marsh complex (Carex atherodes, Phragmites communis, Scirpus acutus, Scolochloa festucacea, Typha glauca) were well-represented in the seed bank, with the exception of Scirpus acutus (only 71 seedlings detected in 250 samples).

Seed Bank Distribution - Elevation

The distribution of buried germinable seeds (calculated from numbers of seedlings which grew in soil samples) is plotted against elevation in Figure I-2. The transition zone between aquatic and terrestrial habitats is located between elevations 247.4 m to 247.7 m (shoreline zone). Representative species were grouped according to life history attributes (Sculthorpe 1967) [G = seeds of emergent species (Carex, Scirpus, Scolochloa) with gravity-dispersed seeds (large achenes or grains), W = seeds of emergents with wind-dispersed seeds (Phragmites, Typha), A = seeds of annuals (Aster, Atriplex, Chenopodium, Ranunculus, Rumex), S = seeds of submergents (Potamogeton, Utricularia, Zannichellia), U = seeds of upland species (Cirsium, Lycopus, Mentha, Stachys, Sonchus, Solidago, Teucrium, Urtica)].

Seeds of submergents were only found in samples from sites located in standing water and were most abundant in samples from shallow water areas. Regardless of dispersal or life history type, highest seed concentrations of emergent species and annual species (with either gravity-dispersed or wind-dispersed seeds) were in soil samples from the shoreline zone. Conversely, seeds of upland species were most abundant in soil samples from higher elevations (>247.8 m). The two most distinctive features of the seed distribution pattern were the significantly greater number of seeds in soil samples from the shoreline zone and the very low number of seeds in samples from open water areas.

Seed Distribution - Vegetation Type

Table I-2 summarizes the average density of germinable seeds (m^{-2}) in different vegetation types for the most common seed bank species (Table I-1). Vegetation types are

FIGURE I-2. Distribution of buried seed populations (calculated from numbers of seedlings which grew in soil samples) along an elevational gradient in the Delta Marsh, Manitoba

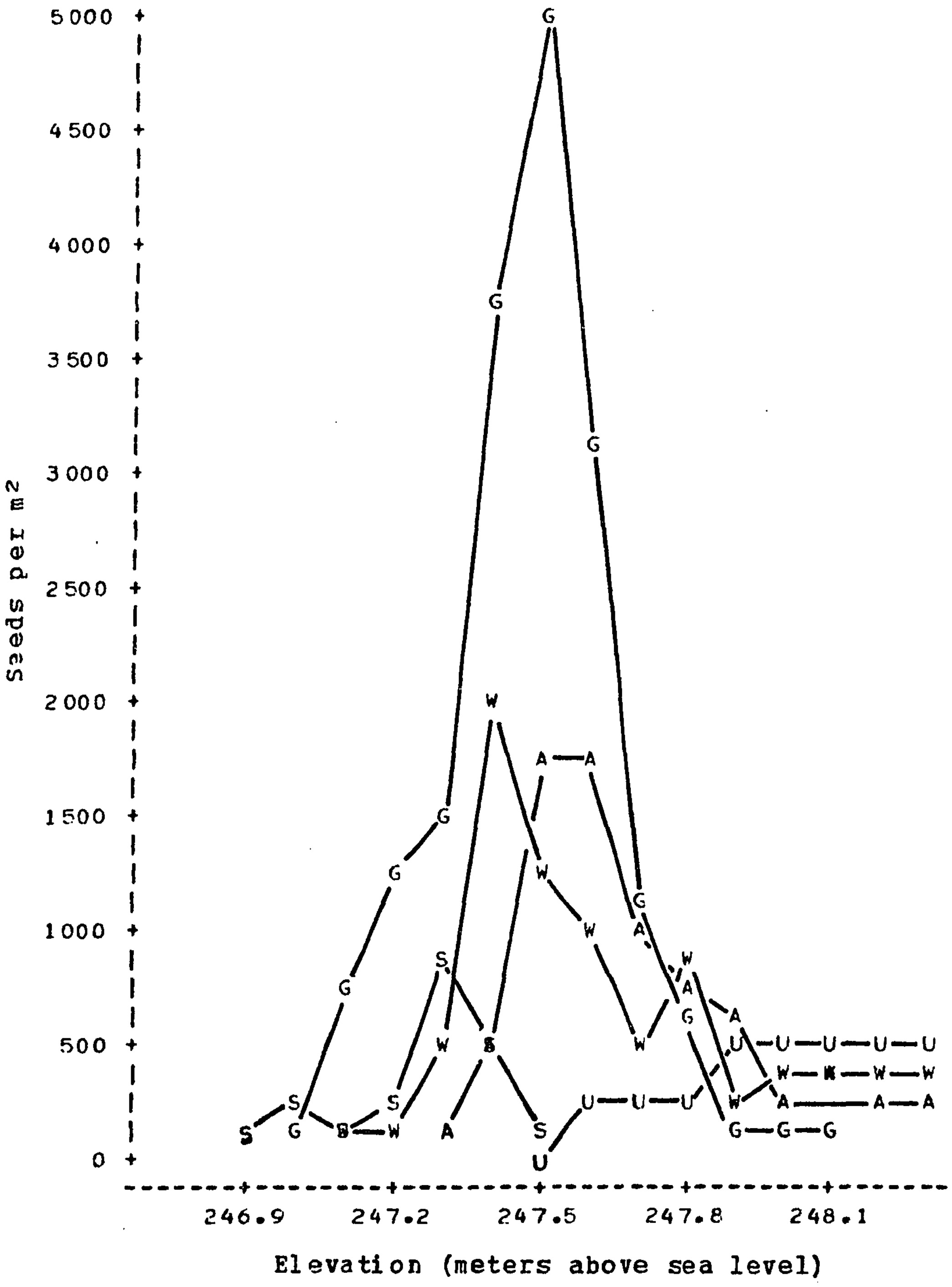
G = Seeds of emergent species (*Carex*, *Scirpus*, *Scolochloa*) with gravity-dispersed seeds (large achenes or grains)

W = Seeds of emergent species (*Typha*, *Phragmites*) with wind-dispersed seeds

A = Seeds of annuals (*Chenopodium*, *Atriplex*, *Aster*, *Rumex*, *Ranunculus*)

S = Seeds of submergent species (*Potamogeton*, *Utricularia*, *Zannichellia*)

U = Seeds of upland species (*Cirsium*, *Lycopus*, *Mentha*, *Solidago*, *Sonchus*)


Seeds per m2
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
246.9
247.2
247.5
247.8
248.1
Elevation (meters above sea level)
G
W
A
S
U

arranged in approximate elevational order [mean elevations for sites of open water (247.16 m), *Scirpus acutus* (247.33 m), *Typha glauca* (247.47 m), and upland (248.08 m) are significantly different from each other ($P < .05$), and from sites of *Carex atherodes* (247.64 m), *Scolochloa festucacea* (247.64 m), and *Phragmites communis* (247.71 m)]. The average number of germinable seeds (m^{-2}) ranged from 6,596 in samples from *Typha* sites to 1,039 in samples from open water sites. There was an average of 6.2 species per sample and the number of species per sample ranged from 0 to 14.

Among replicate soil samples within a vegetation type, there was a great deal of variation in the number of germinable seeds of a given species (standard deviations greater than the mean). Despite high spatial heterogeneity in the seed bank within a vegetation type, five species exhibited significantly different seed distributions between cover types (Table I-2). *Zannichellia palustris* seeds were most numerous in soil samples from *Scirpus* dominated areas. *Typha* and *Carex* seeds were most abundant in samples from sites where these species formed dominant stands. Seeds of upland perennials (*Cirsium arvense*, *Sonchus* spp.) were found in significantly higher densities in soil samples from upland vegetation. Although not separated statistically, seed densities of *Aster brachyactis*, *Atriplex patula*, *Ranunculus sceleratus*, *Rumex maritimus*, *Scolochloa*

TABLE I-2. Mean number (m^{-2}) of germinable seeds in substrate samples from monodominant vegetation types in the Delta Marsh, Manitoba (only selected species representing different life forms are shown)

	Vegetation Type			
Species	Open Water (n=31)	*Scirpus acutus* (n=18)	*Typha glauca* (n=21)	*Carex atherodes* (n=13)
Annuals				
Aster brachyactis	0	0	1	34
Atriplex patula	2	1	2	25
Chenopodium rubrum	2	26	533	561
Ranunculus sceleratus	2	7	334	157
Rumex maritimus	0	0	171	36
Submergent				
Zannichellia palustris	326	820[1]	382	0
Emergents				
Carex atherodes	0	0	61	773[1]
Phragmites communis	6	11	24	38
Scirpus maritimus	4	76	30	44
Scirpus validus	503	1873	1796	1292
Scolochloa festucacea	0	1	91	57
Typha spp.	172	226	3086[1]	934
Upland Species				
Cirsium arvensis	0	0	0	7
Lycopus asper	0	0	1	50
Mentha arvensis	0	0	12	83
Sonchus spp.	0	1	1	25
Urtica dioica	0	0	0	8
Totals ($\bar{X}$)	1039	3063	6596	4442
($\pm$1SD)	($\pm$1663)	($\pm$2802)	($\pm$10308)	($\pm$8047)

[1] Values were significantly different (Tukey's Studentized HSD test, $P < .05$) from those of other cover types. Analyses of variance were conducted on log10(x+1) transformed data. Vegetation types where a species did not occur were dropped from ANOVA tests.

TABLE I-2. (continued)

Species	Vegetation Type *Scolochloa festucacea* (n=26)	 *Phragmites communis* (n=26)	 Upland (n=15)	Totals (n=250) ($\bar{X}$) (±1SD)
Annuals				
Aster brachyactis	130	35	23	37(±136)
Atriplex patula	168	61	6	48(±175)
Chenopodium rubrum	711	811	58	540(±1506)
Ranunculus sceleratus	411	101	336	179(±704)
Rumex maritimus	193	61	0	84(±386)
Submergent				
Zannichellia palustris	0	0	0	176(±422)
Emergents				
Carex atherodes	108	39	65	85(±267)
Phragmites communis	27	54	90	41(±91)
Scirpus maritimus	24	0	21	41(±128)
Scirpus validus	756	2331	15	1816(±56400)
Scolochloa festucacea	307	25	26	85(±262)
Typha spp.	157	399	180	669(±1541)
Upland Species				
Cirsium arvensis	15	27	111[1]	22(±92)
Lycopus asper	83	54	43	29(±164)
Mentha arvensis	6	89	116	48(±183)
Sonchus spp.	8	8	55[1]	11(±36)
Urtica dioica	3	18	2	10(±65)
Totals ($\bar{X}$)	3145	4288	1491	
(±1SD)	(±4700)	(±12333)	(±2359)	

festucacea, and Lycopus asper were highest in seed bank samples from Scolochloa vegetation types. Seed numbers of Ranunculus sceleratus, Scirpus validus, and Urtica dioica were most abundant in seed bank samples from Phragmites vegetation types, while Phragmites communis and Mentha arvensis seeds were most numerous in soil samples from upland vegetation types.

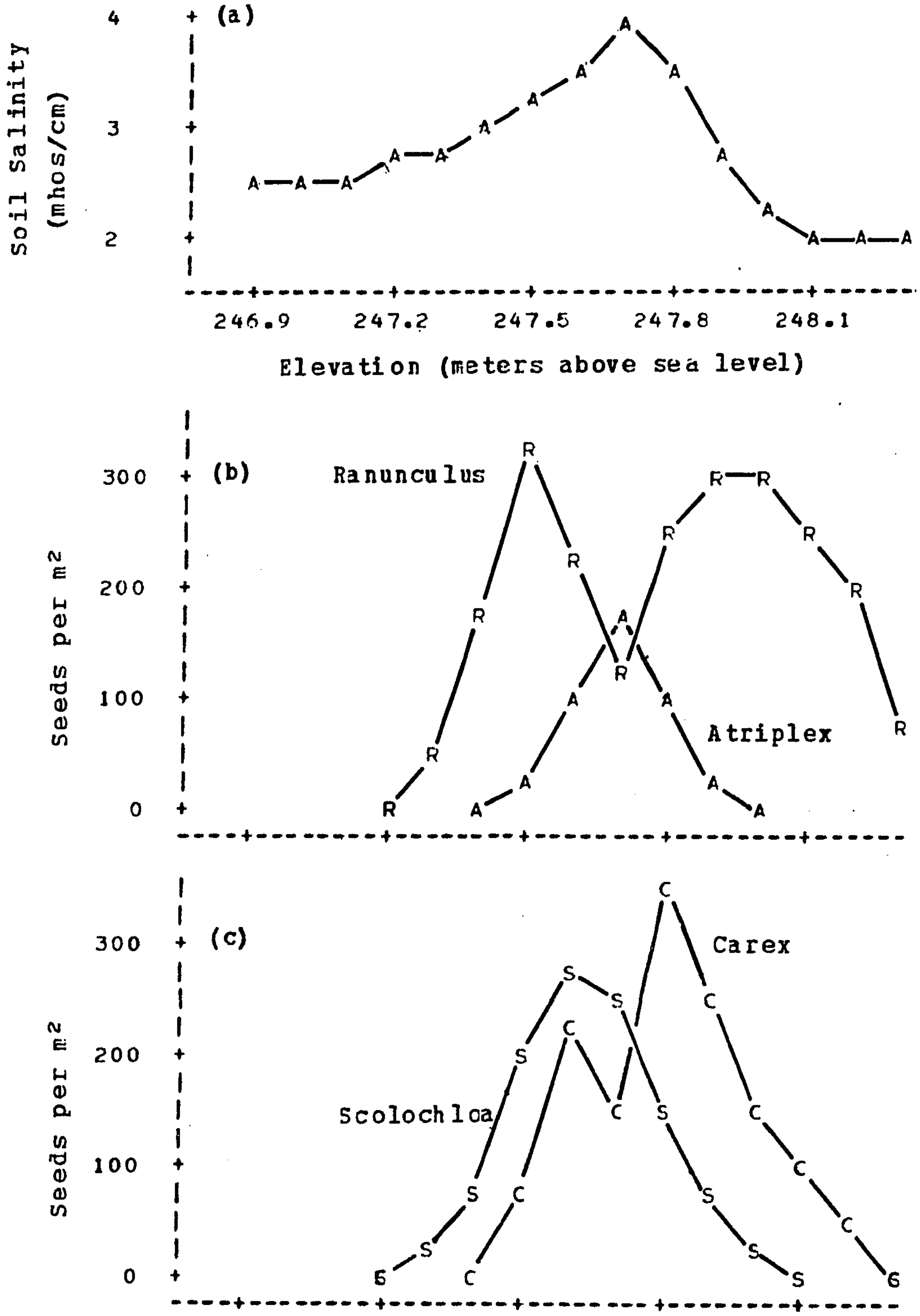
Seed Distribution - Soil Salinity

There were significant correlations between germinable seed densities and the salinity levels of the soil samples. Species with germinable seed densities positively correlated with soil salinity were Atriplex patula (r=.30), Scolochloa festucacea (r=.18), and Aster brachyactis (r=.17). Species with seed densities negatively correlated with soil salinity included Mentha arvensis (r=-.33), Phragmites communis (r=-.27), Cirsium arvense (r=-.24), Typha spp. (r=-.23), Salix spp. (r=-.22), Sonchus spp. (r=-.16), Carex atherodes (r=-.15), Urtica dioica (r=-.15), and Ranunculus sceleratus (r=-.11). Species with seed densities not significantly correlated to soil salinity levels included Chenopodium rubrum, Lycopus asper, Rumex maritimus, Scirpus acutus, Scirpus maritimus, Scirpus validus, and Zannichellia palustris. Figure I-3 illustrates the relationship between soil salinity and germination response (seed density) of two representative annuals (*Atriplex patula*, *Ranunculus sceleratus*) and two representative emergents (*Carex atherodes*, *Scolochloa festucacea*). A sharp rise in salinity occurred at elevation 247.7 m (Figure I-3a). This represents the evaporative zone of the shoreline where water levels were at or near the soil surface. This zone was associated with *Scolochloa festucacea* vegetation sites [*Scolochloa* soil samples were significantly more saline ($\bar{x}$ = 5.0 mmhos/cm) than soil samples from other vegetation types ($\bar{x}$'s range from .9 to 2.9 mmhos/cm)]. The bimodal curve in germinable seed numbers of *Ranunculus sceleratus* and *Carex atherodes* about elevation 247.7 m (Figure I-3b & c) suggests seed germination of both species was inhibited by high soil salinity, or that salinity controlled plant distribution to the extent that seed dispersal from these species did not occur at this elevation. Conversely, germinable seed numbers of *Atriplex patula* and *Scolochloa festucacea* increased through the zone where soil salinity was highest (Figure I-3b & c).

Seed Distribution - Seed Dispersal

Frequency of representative species in the existing Delta Marsh vegetation and densities of germinable seeds of those same species in soil samples (seed bank) and trapped seed populations (seed rain) are shown in Table I-3.

FIGURE I-3. Soil salinity levels and germination response (seed density) from soil samples collected along an elevation gradient in the Delta, Marsh, Manitoba


(a)
Soil Salinity (mhos/cm)
4
3
2
246.9
247.2
247.5
247.8
248.1
Elevation (meters above sea level)
(b)
Seeds per m²
300
200
100
0
Ranunculus
Atriplex
(c)
Seeds per m²
300
200
100
0
Carex
Scolochloa

Numbers of germinable seeds in the 1979 seed rain from annuals (*Aster brachyactis*, *Atriplex patula*, *Chenopodium rubrum*, *Ranunculus sceleratus*, *Rumex maritimus*, *Zannichellia palustris*) were significantly lower (at least 70% lower) than respective germinable seed densities in the seed bank (Table I-3). This difference is explained in that most annuals were not present in the vegetation at collection sites in 1979. Only *Chenopodium rubrum* and *Ranunculus sceleratus* were frequent in the 1979 flora (site frequencies of 11 and 18%, all other annuals were present at less than one percent of the sites).

Numbers of germinable seeds in the 1979 seed rain from four emergents (*Carex atherodes*, *Scirpus acutus*, *Scirpus maritimus*, *Scirpus validus*) were also lower (at least 80% lower) than germinable seed densities in the seed bank. *Carex atherodes* and *Scirpus acutus* individuals were present in the vegetation at 1979 collection sites (site frequencies of 15 and 26%) but despite obvious seed production and the presence of their seeds in seed traps, few seeds of these species germinated. The germination rate of *Scirpus acutus* seeds was also very low from the seed bank [germinable seed density (5 m^{-2})], whereas *Carex atherodes* seeds germinated in larger numbers from the seed bank (56 m^{-2}). *Scirpus maritimus* and *Scirpus validus* individuals were not present in the vegetation in 1979, yet germinable seeds of these

TABLE I-3. Relative frequency of representative species in the Delta Marsh vegetation, plus germinable seed densities of those same species from trapped seed populations (seed rain) and soil samples (seed bank)

Species	% Frequency in Existing Vegetation (1979)	Seed Density (m^{-2})		Difference (%) in Seed Density Between Seed Bank and Seed Rain
		1979 Seed Rain	1980 Seed Bank	
Annuals				
Aster brachyactis	0	2	27	-93*
Atriplex patula	1	7	27	-74*
Chenopodium rubrum	11	13	737	-98*
Ranunculus sceleratus	18	15	105	-86*
Rumex maritimus	1	3	63	-95*
Submergent				
Zannichellia palustris	--[1]	57	197	-71*
Emergents				
Carex atherodes	15	2	56	-96*
Phragmites communis	43	173	32	+440*
Scirpus acutus	26	1	5	-80*
Scirpus maritimus	0	7	41	-82*
Scirpus validus	0	143	1084	-87*
Scolochloa festucacea	24	45	48	-1
Typha spp.	34	457	433	+5
Upland Species				
Cirsium arvense	11	4	18	-77
Lycopus asper	6	76	6	+1166
Mentha arvensis	13	81	61	+32
Sonchus spp.	7	12	16	-25
Urtica dioica	7	20	5	+300

[1] No data available.

*Difference significant at $P < .05$; ANOVAs were conducted on log10(x+1) transformed data.

species were detected in the seed traps. Scirpus validus and Scirpus maritimus seeds were only found in seed traps from shallow open water sites where obvious sedimentation had occurred. Germinable seeds in trapped seed populations of Phragmites communis, Scolochloa festucacea, and Typha spp. were equal to or greater than densities in the seed bank. Numbers of germinable seeds of Phragmites communis were over 400% more abundant in seed traps than in seed bank samples. This increase probably reflects the sampling procedure as seed bank samples were mixed prior to treatment, whereas the seed trap samples were not. Seeds of Phragmites (on the soil surface of the seed bank sample) became buried during mixing of the sample which may have restricted germination. Seed densities of upland species (Cirsium arvense, Lycopus asper, Mentha arvensis, Sonchus spp., Urtica dioica) were highly variable (although not significantly) between seed traps and seed bank samples (% differences ranged from -77 to +1166).

Figure I-4 illustrates 1979 seed rain (calculated from numbers of germinable seeds in trapped seed populations) plotted against elevation. Seed values were combined for species with similar life histories. Seed rain from emergent species (Carex, Scirpus, Scolochloa) with large achenes or grains ("G") and from submergents ("S" = Zannichellia, Potamogeton, Utricularia) was highest in open water sites (elevation <247.5 m). In these areas, seeds were contained in sediment which washed into the traps (sediment traps placed adjacent to seed trap sites collected sediment at rates of 91 $ml/m^2/day$ to 411 $ml/m^2/day$). Many seeds in the sediment had been produced prior to 1979 (e.g., all of the Scirpus validus and Scirpus maritimus seeds must have been produced prior to 1979, as this species was not present in the vegetation in 1979). Low seed numbers in seed traps from deeper water areas and high seed numbers in traps from shallow water indicate a seed dispersal pattern where wave and water action concentrate seeds in the shoreline zone.

Although seed rain from emergents (Phragmites, Typha) with wind-dispersed seeds ("W"--Figure I-4) was widespread throughout the emergent plant communities (elevation >247.7 m), very few seeds dispersed to seed traps located in open water areas. Seed rain ("U"--Figure I-4) of upland species (Cirsium, Lycopus, Mentha, Solidago, Sonchus) only occurred at higher elevations (>248.00). Seed rain ("A"--Figure I-4) from annuals (Aster, Atriplex, Chenopodium, Ranunculus, Rumex) occurred at low densities in open water areas (most likely from seeds already present in the sediment), or along the shoreline zone (elevation 247.5 m).

FIGURE I-4. Distribution of 1979 seed rain (calculated from numbers of germinable seeds in trapped seed populations) along an elevation gradient in the Delta Marsh, Manitoba

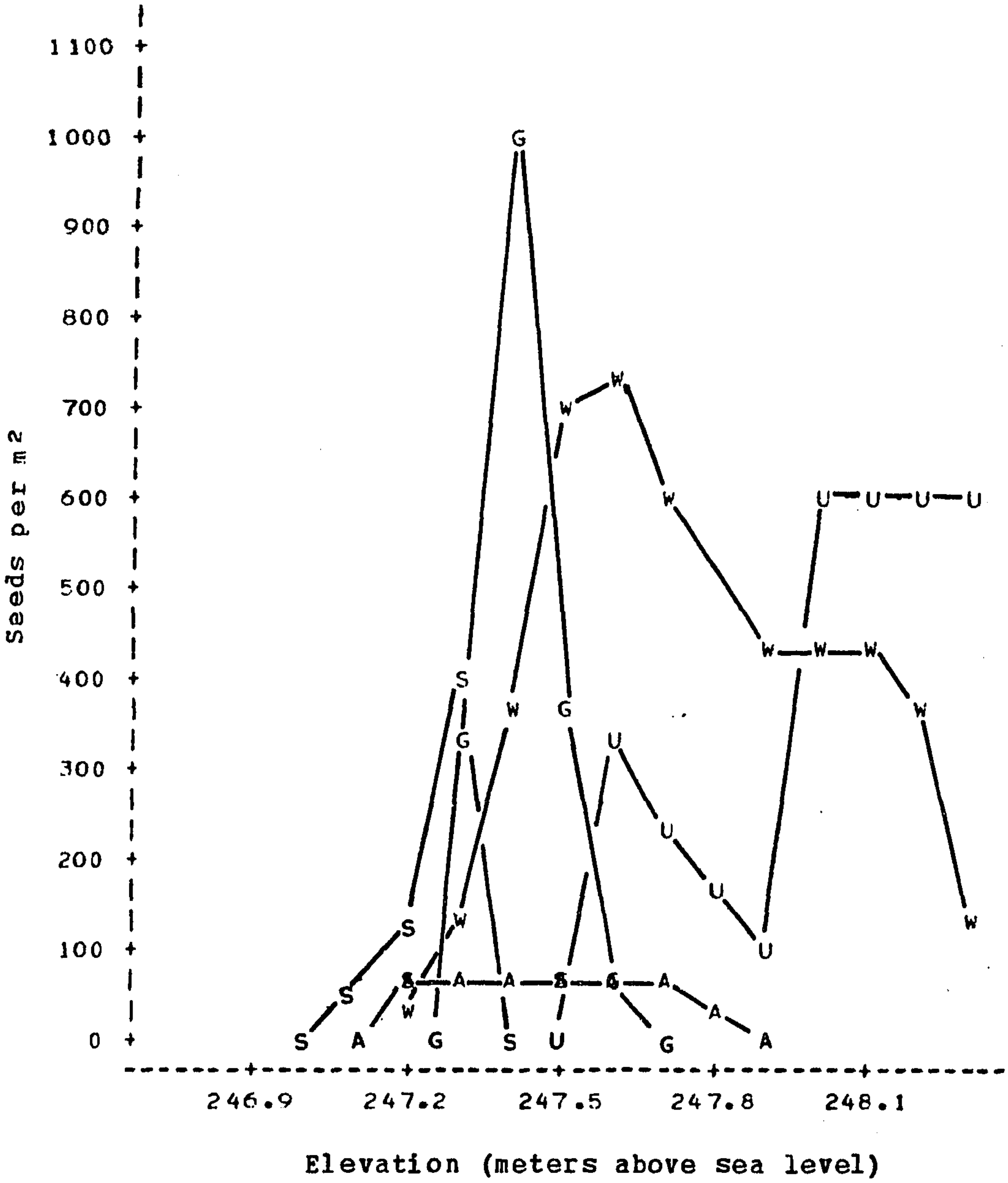
G = Seeds of emergent species (Carex, Scirpus, Scolochloa) with gravity-dispersed seeds (large achenes or grains)

W = Seeds of emergent species (Typha, Phragmites) with wind-dispersed seeds

A = Seeds of annuals (Chenopodium, Atriplex, Aster, Rumex, Ranunculus)

S = Seeds of submergent species (Potamogeton, Utricularia, Zannichellia)

U = Seeds of upland species (Cirsium, Lycopus, Mentha, Solidago, Sonchus)


Seeds per m²
1100
1000
900
800
700
600
500
400
300
200
100
0
246.9
247.2
247.5
247.8
248.1
Elevation (meters above sea level)
S
A
G
U
W

Seed Distribution - Soil Cores

Germinable seed profiles of soil cores taken from four vegetation types are given in Tables I-4 through I-7. Total seed density (seeds m^{-2}) in Scirpus acutus samples (Table I-4) was highest (2,637 seeds m^{-2}) in the 0-2 cm surface soil layer. Zannichellia palustris (an aquatic annual) seeds were the most abundant at all soil depths. Seeds of emergent and mudflat species were absent or present in very low densities throughout the core profile. The lowest total number of seeds were found at the 4-6 cm level (205 seeds m^{-2}), which may reflect a high water period (reduced seed deposition) as larger numbers of seeds (837 seeds m^{-2}) were present in the next lower soil layer (6-8 cm). Scirpus acutus seeds germinated only in the lower soil core layers (2-8 cm).

The seed profile of soil cores from Typha glauca communities (Table I-5) indicates these sites were once much drier (large numbers of mudflat annual seeds and the absence of seeds of submergent species at the 6-8 cm soil depth). The site then became wetter (presence of Zannichellia palustris seeds in the 4-6 cm layer) and was dominated by Scirpus validus and Scirpus maritimus (29,835 seeds m^{-2} at the 4-6 cm depth). Recent vegetation history (seed profiles of the upper 4 cm soil layer) suggests stable water levels (diminished seed input of mudflat annuals), in which Typha

TABLE I-4. Mean number (m^{-2}) of seeds (calculated from seedling emergence) found in 2 cm layers of soil (4 depths) from soil cores of *Scirpus acutus* communities in the Delta Marsh, Manitoba

	Soil Core Section (depth from surface)			
Species[1]	0-2 cm	2-4 cm	4-6 cm	6-8 cm
Chenopodium rubrum	50	25	0	0
Scirpus acutus	0	25	37[2]	37[2]
Scirpus validus	425	138	50	50
Typha spp.	162	25	0	25[2]
Zannichellia palustris	1988	887	118[2]	725
Total Number of Seeds	2637	1112	205	837
Number of Species	5	7	3	4

[1] Additional species present in samples: *Phragmites communis*, *Scirpus maritimus*. Seeds of these species are included in the totals.

[2] Species was absent from one of two replicate samples.

glauca has recently replaced *Scirpus* spp. (increasing number of *Typha* seed and decreasing numbers of *Scirpus* spp. seeds in the upper soil profile). The largest number of seeds m^{-2} (33,710) for any seed bank sample was recorded at the 4-6 cm soil depth in the *Typha* communities.

Soil-core seed profiles of *Scolochloa festucacea* communities (Table I-6) reveal the largest numbers of seeds (8,449 seeds m^{-2}) were present in the upper 2 cm of the soil. Seeds of some annuals (*Chenopodium rubrum*, *Ranunculus*

TABLE I-5. Mean number (m^{-2}) of seeds (calculated from seedling emergence) found in 2 cm layers of soil (4 depths) from soil cores of Typha glauca communities in the Delta Marsh, Manitoba

	Soil Core Section (depth from surface)			
Species[1]	0-2 cm	2-4 cm	4-6 cm	6-8 cm
Chenopodium rubrum	25[2]	0	475	775
Ranunculus sceleratus	0	250	1650	300
Rumex maritimus	0	0	950	25[2]
Scirpus maritiums	12[2]	122	585	95
Scirpus validus	606	6125	29250	4762
Typha spp.	625	125	63[2]	0
Zannichellia palustris	1775	812	737	0
Total Number of Seeds	3068	7446	33710	5957
Number of Species	7	6	7	5

[1] Additional species present in samples: Atriplex patula, Carex atherodes, Mentha arvensis. Seeds of these species are included in the totals.

[2] Species was absent from one of two replicate samples.

sceleratus, Atriplex patula) are most numerous in the surface sediment (which indicated the recent environment within these stands favored establishment of these species). Other annuals (Aster brachyactis, Rumex maritimus) had large seed concentrations in subsurface portions of the soil profile (2-4 cm). At these sites, vegetation shifts went from a wetter community dominated by Scirpus spp. (large numbers of Scirpus seeds and low seed numbers of annuals at the 6-8 cm depth) to a community dominated by *Scolochloa festucacea* (large increase in seed numbers of *Scolochloa* and annuals in the 2-4 cm soil layer). *Carex atherodes* and *Typha* spp. seeds were present throughout the soil profile which suggested continual seed input (via water and wind dispersal) from nearby communities.

Soil-core seed profiles from *Phragmites communis* communities (Table I-7) indicated these sites were once inundated (large numbers of *Typha* and *Scirpus* seeds, and presence of *Zannichellia palustris* seeds in the lower 4 cm of the soil core). During the flooded period, *Typha* evidently was a dominant component of the vegetation (large numbers of *Typha* seeds in the 6-8 cm depth). As the site became progressively drier, *Typha* and *Scirpus* decreased in importance. *Phragmites communis* and *Mentha arvensis* were most numerous in the surface soil layer.

Species diversity in seed profiles can be summarized from totals of all eight core sample sites. The 0-2 cm level of the soil cores contained seeds of 7.0 species, the 2-4 cm level averaged 8.5 species, the 4-6 cm level averaged 5.8 species, and the 6-8 cm level averaged 4.8 species. Certain species (*Aster brachyactis*, *Rumex maritimus*, *Scirpus maritimus*, *Scirpus validus*) all had their highest seed densities in lower sections of the soil profile. Both size and diversity of the seed bank was greater in lower sections

TABLE I-6. Mean number (m^{-2}) of seeds (calculated from seedling emergence) found in 2 cm layers of soil (4 depths) from soil cores of *Scolochloa festucacea* communities in the Delta Marsh, Manitoba

	Soil Core Section (depth from surface)			
Species[1]	0-2 cm	2-4 cm	4-6 cm	6-8 cm
Atriplex patula	50	12[2]	0	0
Aster brachyactis	50[2]	225	12[2]	0
Carex atherodes	787	288	175	88
Chenopodium rubrum	2875	512	125	0
Ranunculus sceleratus	3250	1825	725	25[2]
Rumex maritimus	438	3888	237[2]	38[2]
Scirpus validus	0	775	2975	3137
Scolochloa festuacea	350	50	12[2]	0
Typha spp.	637	138[2]	138	150
Total Number of Seeds	8449	7938	4399	3438
Number of Species	9	11	7	5

[1] Additional species present in samples: *Mentha arvensis*, *Phragmites communis*, *Sonchus arvensis*, and an unidentified Labiatae. Seeds of these species are included in the totals.

[2] Species was absent from one of two replicate samples.

of the soil cores than in surface layers.

In summary, the presence of large seed numbers of submergents, *Scirpus validus*, *Typha*, and mudflat annuals in the lower section of soil cores indicated the occurrence of a high water event (followed by a drying period) in recent history. Reduction in size and diversity of the seed bank

TABLE I-7. Mean number (m^{-2}) of seeds (calculated from seedling emergence) found in 2 cm layers of soil (4 depths) from soil cores of Phragmites communis communities in the Delta Marsh, Manitoba

Species[1]	Soil Core Section (depth from surface) 0-2 cm	2-4 cm	4-6 cm	6-8 cm
Carex atherodes	25[2]	39[2]	12[2]	0
Chenopodium rubrum	63[2]	50	0	0
Mentha arvensis	375	88	25[2]	12[2]
Phragmites communis	263	25[2]	0	12[2]
Ranunculus sceleratus	125[2]	125[2]	275	50[2]
Scirpus validus	0	75[2]	262[2]	387[2]
Typha spp.	225	313	462	575
Zannichellia palustris	0	0	205	0
Total Number of Seeds	1088	739	1241	1036
Number of Species	7	10	6	5

[1] Additional species present in samples: Atriplex patula, Cirsium arvense, Rumex maritimus. Seeds of these species are included in the totals.

[2] Species was absent from one of two replicate samples.

in the surface (0-2 cm) soil layer represented a temporal change in vegetation composition (fewer annuals and certain emergents) since the period of high water.

DISCUSSION

Delta Marsh Seed Banks

Although the dominant emergent vegetation in the marsh (Carex atherodes, Phragmites communis, Scirpus acutus, Typha glauca, Scolochloa festucacea) was represented in the seed bank, many of the important species in the Delta Marsh seed banks (e.g., Rumex maritimus, Scirpus maritimus, Scirpus validus) are not represented in the existing vegetation (Table I-3). Leck and Graveline (1979) and van der Valk and Davis (1978) found the species composition of the seed bank mirrored the vegetation composition of the marsh, while, as in this study, Thompson and Grime (1979) and Smith and Kadlec (1983) did not.

Seed numbers in the Delta Marsh were lowest in open water areas, and highest in shorelines (Figure I-2, Table I-2). This seed bank distribution resembles that of seed banks of lake shores (Keddy and Reznicek 1982), lake basins (Haag 1983), and saline wetlands (Smith and Kadlec 1983). Shoreline seed accumulations and the resultant spatial heterogeneity of the Delta Marsh seed banks (Table I-2) were undoubtedly caused by repeated seed dispersal along topographic drift lines (Figures I-2 and I-4). Seeds of nearly all emergent, mudflat, and submergent species float (Sculthorpe 1967), and rafts of seeds often float freely and are carried from one wetland community to another (McAtee 1925, Kelley and Burns 1975, Staniforth and Cavers 1976, van der Valk and Davis 1976b). Wave action and accompanying sedimentation are also processes by which water-logged seeds become concentrated in the shoreline zone (Figure I-4). Emergent plant communities (Scirpus acutus, Typha glauca) along the shoreline effectively trap both water and wind-dispersed seed, whereas in open water areas, there is little resistance to seed dispersal and subsequently little seed accumulation (Figure I-4, Hanson 1918, Smith and Kadlec 1983).

Other factors contributing to the depauperate seed bank in open water areas of the Delta Marsh are the presence of standing water over a period of years (which prevented establishment and subsequent seed drop from mudflat annuals and emergents--Table I-1), and possible salinity conditions of the mudflats when they were exposed. The negative impact of salinity on seed germination and seedling establishment has been reported by Christiansen and Low (1970), Lieffers and Shay (1982), and Smith and Kadlec (1983).

The distribution of seeds in the seed bank of the Delta Marsh is significantly different than seed banks of smaller marshes. Working in shallow, palustrine marshes in Iowa, van der Valk and Davis (1978) found just as many seeds in soil samples from open water areas as they did in soil samples from emergent vegetation. They also found seed densities of individual emergent species were not significantly different between vegetation types (because of dispersal and the frequency of plant community change in those smaller wetland systems). In the Delta Marsh, emergent communities seem to persist for longer periods of time, and as a result, greater seed densities of the dominant species (e.g., Carex atherodes, Typha spp.) were found in areas where those species are dominant (Table I-2). In addition, environmental factors (e.g., soil salinity, water levels--Table I-2) controlled buried seed distributions by excluding certain species from the site and permitting large, local seed input from species present at a particular location (Pederson 1983).

Seed Banks and Vegetation Dynamics

It has long been apparent that species diversity in wetland plant communities is related to environmental fluctuations, particularly with respect to water levels (Pearsall 1926, Rickett 1921, 1924, Love and Love 1954). Keddy and Reznicek (1982) specifically showed fluctuations of water levels in lakes were necessary to maintain the species diversity of shoreline habitats, which is consistent with views of Goodman (1975) and Huston (1979) who propose that environmental fluctuations enhance species richness by preventing a few species from competitively excluding others.

Historically, water levels in Lake Manitoba and the Delta Marsh fluctuated naturally with climatic cycles, and levels would dramatically rise or fall for prolonged periods of time (Bossenmaier 1968). However, since 1961, water levels in Lake Manitoba (and the Delta Marsh) have been stabilized (at approximately 247.5 m) by water control structures (Manitoba Dept. of Mines, Resources, and Environmental Management 1974).

The last "natural" fluctuation in water levels in the Delta Marsh occurred during the decade of 1954-1964. In 1955, water levels rose to 248.55 m and subsequently fell to a low of 247.05 m in 1964 (Bossenmaier 1968). During the 1954-1957 period of high water, most emergent vegetation in the marsh was destroyed (Bossenmaier 1968). Walker (1959) described the colonization of denuded areas as water levels fell. Important species pioneering on *Phragmites* stubble included *Scolochloa festucacea*, *Ranunculus sceleratus*, *Epilobium glandulosum*, and *Chenopodium rubrum*. Important species colonizing newly exposed mudflats were *Chenopodium rubrum*, *Aster brachyactis*, *Typha latifolia*, *Scirpus validus*, *Ranunculus sceleratus*, *Rumex maritimus*, and *Senecio congestus*. No seedlings of *Scirpus acutus* or *Phragmites communis* were observed on the mudflats, although surviving clumps of *Phragmites communis* quickly spread by runners. Since the stabilization of the marsh water levels in 1961, emergent perennials have increased in importance (particularly *Phragmites communis*, which now covers 75 percent of the marsh area occupied by emergent vegetation--Bossenmaier 1968).

The stabilization of water levels in 1961 and the subsequent spread of emergent perennial species have resulted in decrease in diversity and numbers of seeds in the present seed bank (Tables I-4 through I-7). The importance in the contemporary vegetation of "disturbance" species (*Aster brachyactis*, *Atriplex patula*, *Epilobium glandulosum*, *Rumex maritimus*, *Senecio congestus*, *Scirpus validus*, *Scirpus maritimus*) has greatly diminished in the recent history (i.e., low occurrence or absence in the present vegetation, high occurrence or presence only in the seed bank--Tables I-1 and I-3). Seeds of these species are unable to germinate from seed banks of existing vegetation because of shading (seeds of many wetland species require unfiltered light for germination--Thompson et al. 1977, Cresswell and Grime 1981), or temperature conditions (litter or water cover prevents seeds from exposure to germination requirements of fluctuating temperatures--Thompson et al. 1977), or competition (established seedlings are likely to be eliminated by shading by the dominant vegetation--Buttery and Lambert 1965).

If water levels in the marsh were lowered for a sufficient period of time to allow seedling recruitment from shoreline seed banks and dispersed seed populations, the species diversity of the marsh would greatly increase (Tables I-1 through I-3). However, under stabilized water level regimes, practically no seed germination of mudflat or emergent species can be expected to occur in areas covered by water (Harris and Marshall 1963, Linde 1969, Weller 1975, van der Valk and Davis 1978, Beule 1979, Smith and Kadlec 1983).

Vegetation change in the Delta Marsh is dependent on three factors: buried disseminule and seed reserves ("seed bank"), vegetative reproduction from existing plants ("bud bank"), and disseminule dispersal into the community ("seed rain"). The relative importance of the seed bank, bud bank, and seed rain to vegetation dynamics will vary according to the environmental factors which act on the individual seeds, ramets, and plants. The relatively stable environment created in the marsh by the control of water levels has produced conditions where perennial species are favored and reproduction is primarily accomplished by vegetative means.

Seed Banks and Marsh Management

Seed bank studies are good predictors of vegetation community change in marshes where most of the emergent vegetation is eliminated or where vegetation composition is primarily annuals (van der Valk and Davis 1978, Leck and Graveline 1979). In marshes where existing vegetation (i.e., bud bank) has not been destroyed or where environmental conditions (e.g., salinity, stable water levels) restrict germination, seed bank data are of more limited use in explaining vegetation change (Haag 1983, Lieffers and Shay 1982, Smith and Kadlec 1983). However, this study has shown that seed banks provide information on the potential flora, the distribution of buried seeds, the recent vegetation history, and the nature of seed dispersal. This information can be used by marsh managers to devise suitable management regimes (e.g., water level changes, burning, tilling) to exploit areas with large seed reserves, and to understand the direction and magnitude of vegetation change caused by various management practices.

Lowering the water level to expose the substrate of a marsh (drawdown) is a common management practice for increasing the productivity of a marsh (Fredrickson and Taylor 1982). This relationship is also well-recognized for the Delta Marsh (Bossenmaier 1968, Ducks Unlimited 1981). However, to date, efforts to instigate a management plan whereby water levels in the marsh can be controlled independently of the lake have been fruitless. This situation is especially unfortunate, considering the tremendous importance of the marsh for wildlife (Bossenmaier 1968) and the potential of management for creating diverse habitats for a variety of wildlife species (Fredrickson and Taylor 1982).

LITERATURE CITED

Anderson, M. G. 1978. Distribution and production of sago pondweed (Potamogeton pectinatus L.) on a northern prairie marsh. Ecology 59:154-160.

Anderson, M. G., and R. E. Jones. 1976. Submerged aquatic vascular plants of East Delta Marsh. Manitoba Dept. Renewable Resources and Transportation Services Wildl. Report. 120 pp.

Batt, B. D. J., P. J. Caldwell, C. B. Davis, J. A. Kadlec, R. M. Kaminski, H. R. Murkin, and A. G. van der Valk. In press. The Delta Waterfowl Research Station--Ducks Unlimited Canada Marsh Ecol. Research Program. Proceedings of the Symposium on Breeding Waterfowl, International Waterfowl Research Bureau, Edmonton, Alberta, Canada.

Best, K. F., J. Looman, and J. B. Campbell. 1971. Prairie grasses, identified and described by vegetative characters. Can. Dept. Agric., Pub. 1413. 239 pp.

Beule, J. D. 1979. Control and management of cattails in southeastern Wisconsin wetlands. Wisc. Dept. Nat. Res. Tech. Bull. No. 112. 39 pp.

Bossenmaier, E. F. (ed.). 1968. The Delta Marsh, its values, problems, and potentialities. Technical Committee Report, Manitoba Dept. of Mines and Natural Resources. 75 pp.

Buttery, B. R., and J. M. Lambert. 1965. Competition between Glyceria maxima and Phragmites communis in the region of Surlingham Broad. I. the competition mechanism. J. Ecol. 53:163-181.

Christiansen, J. E., and J. B. Low. 1970. Water requirements of waterfowl marshlands in northern Utah. Utah Div. of Fish and Game Pub. No. 69-12. 108 pp.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deep water habitats of the United States. FWS/OBS-79/31, Office of Biological Services, Fish and Wildlife Service, U.S.D.I., Washington, D.C. 103 pp.

Cresswell, E. G., and J. P. Grime. 1981. Induction of a light requirement during seed development and its ecological consequences. Nature (London) 291:583-585.

Dirschl, H. J., and R. T. Coupland. 1972. Vegetation patterns and site relationships in the Saskatchewan River delta. Can. J. Bot. 50:647-675.

Dix, R. L., and F. E. Smeins. 1967. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. Can. J. Bot. 45:21-58.

Dodd, J. D., and R. T. Coupland. 1966. Vegetation of saline areas in Saskatchewan. Ecology 47:958-968.

Ducks Unlimited-Canada. 1981. Delta Marsh development proposal. Ducks Unlimited-Canada, Winnipeg, Manitoba, Canada. 86 pp. (mimeo.)

Eisenlohr, W. S., Jr. 1966. Water loss from a natural pond through transpiration by hydrophytes. Am. Geophysical Union. Water Resources Research 2:443-453.

Eisenlohr, W. S. Jr., and C. E. Sloan. 1968. Generalized hydrology of prairie potholes on the Coteau du Missouri, North Dakota. U.S. Geological Survey Cir. 558. 12 pp.

Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Dept. of Interior Resource Publication 148. 29 pp.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. Van Nostrand Reinhold Co., New York. 810 pp.

Goodman, D. 1975. The theory of diversity-stability relationships in ecology. Q. Rev. Biol. 50:237-266.

Haag, R. W. 1983. Emergence of seedlings of aquatic macrophytes from lake sediments. Can. J. Bot. 61:148-156.

Hanson, H. C. 1918. The invasion of a Missouri river alluvial floodplain. Am. Mid. Nat. 5:196-201.

Hargrave, B. T., and N. M. Burns. 1979. Assessment of sediment trap collection efficiency. Limnol. and Oceangr. 24(6):1124-1135.

Harris, S. W., and W. H. Marshall. 1963. Ecology of water level manipulations on a northern marsh. Ecology 44:331-343.

Helwig, J. T., and K. A. Council (ed). 1979. SAS user's guide. SAS Institute Inc., Cary, North Carolina. 494 pp.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101.

Hutchinson, G. E. 1975. A treatise on limnology. Vol. III. Limnological botany. John Wiley and Sons, New York. 660 pp.

Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64:331-344.

Keddy, P. A., and A. A. Reznicek. 1982. The role of seed banks in the persistence of Ontario's Coastal Plain flora. Am. J. Bot. 69:13-22.

Kelley, A. D., and V. F. Burns. 1975. Dissemination of weed seeds by irrigation water. Weed Sci. 23:486-493.

Leck, M. A., and K. J. Graveline. 1979. The seed bank of a freshwater tidal marsh. Am. J. Bot. 66:1006-1015.

Lieffers, V. J., and J. M. Shay. 1982. Distribution and variation in growth of *Scirpus maritimus* var. *paludosus* on the Canadian prairies. Can. J. Bot. 60:1938-1949.

Linde, A. F. 1969. Techniques of wetland management. Res. Research Rept. No. 45. 156 pp.

Love, A., and D. Love. 1954. Vegetation of a prairie marsh. Bull. Torr. Bot. Club 81:16-34.

Macaulay, A. J. 1973. Taxonomic and ecological relationships of *Scirpus acutus* Muhl. and *S. validus* Vahl. (Cyperaceae) in southern Manitoba. Ph.D. Dissertation. University of Manitoba, Winnipeg, Manitoba. 212 pp.

Mandossian, A., and R. P. McIntosh. 1960. Vegetation zonation on the shore of a small lake. Am. Mid. Nat. 64:301-308.

Manitoba Department of Mines, Resources, and Environmental Management. 1974. Flood control. Water Resources Division, Dept. of Mines, Resources, and Environmental Management Publication.

McAtee, W. L. 1925. Notes on drift, vegetation balls, and aquatic insects as a food product of inland waters. Ecology 6:288-302.

Meyboom, P. 1962. Patterns of groundwater flow in the prairie profile. Proc. Hydrology Symp. No. 3:5-33.

Millar, J. B. 1973. Vegetation changes in shallow marsh wetlands under improving moisture regime. Can. J. Bot. 51:1443-1457.

Pearsall, W. H. 1926. Dynamic factors affecting aquatic vegetation. Pages 667-672 in Proceedings of 4th International Congress of Botany, Ithaca, N.Y.

Pederson, R. L. 1983. Spatial and temporal variation in seed banks of four emergent plant communities in the Delta Marsh, Manitoba. Part II. Ph.D. Dissertation. Iowa State University, Ames, Iowa. 97 pp.

Raup, H. M. 1975. Species versatility in shore habitats. J. Arnold Arbor. 56:126-163.

Rickett, H. W. 1921. A quantitative study of the larger aquatic plants of Lake Mendota. Trans. Wisc. Acad. Sci. Arts and Letters 34:149-166.

Rickett, H. W. 1924. A quantitative study of the larger aquatic plants of Green Lake, Wisconsin. Trans. Wisc. Acad. Sci. Arts and Letters 21:381-414.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold, London. 843 pp.

Smith, L. M., and J. A. Kadlec. 1983. Seed banks and their role during a drawdown of a North American marsh. J. Applied Ecol. 20:673-684.

Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J. Ecol. 55:147-170.

Staniforth, R. J., and P. B. Cavers. 1976. An experimental study of water dispersal in Polygonum spp. Can. J. Bot. 54:2587-2596.

Steward, R. E., and H. A. Kantrud. 1972. Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Geology Surv. Prof. Pap. 585-D. 36 pp.

Swindale, D. N., and J. T. Curtis. 1957. Phytosociology of the larger submerged plants in Wisconsin lakes. Ecology 38:397-407.

Thompson, K., and J. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67:893-921.

Thompson, K., J. P. Grime, and G. Mason. 1977. Seed germination in response to diurnal fluctuations of temperature. Nature (London) 267:147-149.

van der Valk, A. G., and C. B. Davis. 1976a. Changes in composition, structure, and production of plant communities along a perturbed wetland coenocline. Vegetatio 32:87-96.

van der Valk, A. G., and C. B. Davis. 1976b. The seed banks of prairie glacial marshes. Can. J. Bot. 54:1832-1838.

van der Valk, A. G., and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.

van der Valk, A. G., and C. B. Davis. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. Aquatic Bot. 6:29-51.

Walker, B. H., and R. T. Coupland. 1968. An analysis of vegetation environment relationships in Saskatchewan sloughs. Can. J. Bot. 46:509-522.

Walker, B. H., and C. F. Wehrhahn. 1971. Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. Ecology 52:85-95.

Walker, J. M. 1959. Vegetation studies on the Delta Marsh, Delta, Manitoba. M.S. Thesis. Univ. of Manitoba, Winnipeg. 203 pp.

Walker, J. M. 1965. Vegetation changes with falling water levels in the Delta Marsh, Manitoba. Ph.D. Thesis. Univ. of Manitoba, Winnipeg. 272 pp.

Weller, M. W. 1975. Studies of cattail in relation to management for marsh wildlife. Iowa State Journal of Research 49:383-412.

PART II. SPATIAL AND TEMPORAL VARIATION IN SEED BANKS OF FOUR EMERGENT PLANT COMMUNITIES IN THE DELTA MARSH, MANITOBA

ABSTRACT

Measurements were made over a two year period on the input, loss, and storage of germinable seeds in four vegetation communities (*Phragmites communis*, *Scolochloa festucacea*, *Typha glauca*, *Scirpus acutus*) in the Delta Marsh, Manitoba.

Spatial heterogeneity in germinable seed numbers in the seed bank was very high (coefficient of variation > 100% for 11 out of 18 species) in a relatively small area (thirty 400 cm^2 sediment samples from a 3 m X 3 m plot). Between 1980 and 1981, significant differences (210 to 1310%) in numbers of germinable seeds in soil occurred for 10 out of 18 species. Comparison of numbers of germinable seeds in soil samples collected at monthly intervals (June, July, August) revealed seeds of 14 species germinated more readily in the June sample. Only seeds of *Typha* consistently germinated in higher numbers in the July sample. Contrasting temporal seed germination patterns (for individual species) between vegetation types seemed to be due to local seed production, dispersal events (wave action), and ecotypic variation in germination requirements.

The dynamic nature of gains and losses of seeds to wetland communities indicates that sampling schedules for surveying seed banks should be considered in relation to dispersal events and annual seed rain.

INTRODUCTION

Gains, losses, and storage of viable seeds in wetland plant communities have received little attention in the literature (Roberts 1981), despite the importance of seed budgets in community development, population dynamics, and plant distribution (Harper 1977, Thompson 1978, Watkinson 1978, Thompson and Grime 1979, Cook 1980, van der Valk 1981). There is considerable evidence which indicates temporal differences in seed germination on mudflats of wetlands that are drained (Harris and Marshall 1963, Burgess 1969, Meeks 1969). Similarly, there exists a great deal of information on production of seeds by individual species (Kadlec and Wentz 1974). However, there are no studies of wetlands where there is a clear understanding of seed budgets (inputs, outputs, temporal and spatial distributions). Only van der Valk and Davis (1979) and Whigham (1979) have attempted a more comprehensive approach to examining seed budgets.

Temporal changes in kinds and numbers of germinable seeds in wetland seed banks may be due to (1) environmental factors which control plant distribution and seed production (Haslam 1973, Macaulay 1973, Smith 1973, Lieffers and Shay 1982), (2) allelopathy (McNaughton 1968), (3) seed predation (Thompson and Grime 1979), (4) gains and losses of seeds through dispersal events (McAtee 1925, Kelley and Burns

1975, Staniforth and Cavers 1976, van der Valk and Davis 1976, Pederson 1983, Smith 1983), (5) species-specific, phenotypic and ecotypic variation in requirements to break seed dormancy (Muenscher 1936, Sifton 1959, Smith 1967, Haslam 1973, Hutchinson 1975, Harper 1977), and (6) seed germination and mortality *in situ* (Bedish 1967, Smith 1973).

A standard technique for detecting buried seed densities is a germinable seed assay of soil samples collected from the field (Leck and Graveline 1979, van der Valk and Davis 1978). One problem with this approach is the small surface area the samples represent, and consequently, results really are estimates of species presence rather than seed density (Whipple 1978). Nevertheless, provided the limitations are recognized, useful and valid estimates of error can be assigned to mean values when the data are recorded in replicated groups or recorded separately for individual sampling units (Major and Pyott 1966, Moore and Wein 1977, Archibold 1979, Roberts 1981).

This paper presents results of a series of field studies on seed production, seed rain, and spatial and temporal variation in germinable seeds in the soil of four, contrasting wetland plant communities in a large prairie marsh. Emphasis was placed on examining the heterogeneity of the marsh seed banks in relatively small areas, the change in germination patterns from the seed bank over time, and the relationship of seed production of the dominant emergent species to temporal changes in densities of germinable seeds in the seed bank.

METHODS

Study Area

This study was conducted in the Delta Marsh, a large (ca. 15,000 ha) prairie marsh located along the south shore of Lake Manitoba (50° 11' N, 98° 19' W). The marsh is an interconnected system of large and small bays, which are never more than three meters deep and usually less than one meter deep. The water in the marsh is saline (Bossenmaier 1968), placing it in the moderately brackish category of Steward and Kantrud (1972). Vegetation in the marsh has been described by Love and Love (1954), Walker (1959, 1965), and Anderson and Jones (1976). The dominant emergent species in the marsh is *Phragmites communis*. Other common emergents include *Scirpus acutus*, *Scolochloa festucacea*, and *Typha* spp. (mainly *glauca*). Throughout the marsh, most emergents are found in monodominant stands with *Scolochloa festucacea* in the saline, seasonally-flooded uplands, *Typha glauca* in the shoreline zone, *Scirpus acutus* in deeper, permanently-flooded areas, and *Phragmites communis* at all elevations except in permanently-flooded areas.

Description of Study Sites

The four sites selected were each dominated by one of the four most common emergents in the marsh (*Phragmites* *communis*, *Scirpus acutus*, *Scolochloa festucacea*, *Typha glauca*) and were representative of the habitats in the marsh. Following is a brief description of the four sites.

Phragmites communis site

This site was located on an upland area seldom flooded. Underneath the *Phragmites* canopy, there was considerable amounts of *Phragmites* litter with an understory composed of *Urtica dioica*, *Cirsium arvense*, and *Stachys palustris*. Scattered individuals of *Mentha arvensis*, *Sonchus* spp., and *Teucrium canadense* were also present. Soils were highly organic (>55%).

Scolochloa festucacea site

This site was located in a seasonally (April-June) flooded upland. Because the 1980 site was mowed during a commercial haying operation, a new site was located in 1981 as close to the 1980 site as possible (approximately 100 m). Both 1980 and 1981 were dry years and most *Scolochloa festucacea* culms were either killed or failed to flower in 1981. A large number of *Atriplex patula* seedlings grew within the stand in 1981. Soils were organic and saline (conductivity = 8 mmhos/cm).

Typha glauca site

This site was located along the edge of a large (50 ha) bay and exposed to considerable wave action. The bay-ward edge of the stand was in approximately 40 cm of water. The land-ward edge of the *Typha* stand extended above the waterline and was bordered by *Phragmites*. There was a thick layer of *Typha* litter on the land-ward edge. No other species were found growing within the stand. Soils were mineral on the bay-ward edge of the stand and organic on the land-ward edge.

Scirpus acutus site

This site was on the border of a small slough (ca. 3 ha) and was part of a peripheral shoreline band of *Scirpus acutus* around the pothole. June water depths in the sample site ranged from 5 cm to 30 cm. In the shallower areas of the stand, considerable *Scirpus* litter was present. There were no other plant species growing within this stand. Soils were an organic muck.

Seed Bank Survey - Spatial Variation

In June 1980, 30 substrate samples (each 30 cm x 30 cm x 5 cm) were collected in a stratified random fashion from a 3 m x 3 m square plot in each of the four sites. Each substrate sample was placed in an outdoor shelter and assayed for amount of viable seed which would germinate under drawdown conditions (Pederson 1983). In an effort to exhaust the seed bank, all 1980 samples were retained and retreated in 1981. Twelve seed traps (plastic trays filled with sterilized soil) were placed randomly in the outdoor shelter to monitor contamination by wind-dispersed seeds.

Seed Bank Survey - Temporal Variation

In June 1980, nine substrate samples were collected randomly from a 3 m x 3 m square plot from all four sites. Each 3 m x 3 m square plot was located adjacent to the 3 m x 3 m square plot used for estimating spatial variability. All 36 samples were treated as in the spatial variation sampling.

In 1981, nine substrate samples were collected at the beginning of June, July, and August from each of the four sites. Each monthly sample was assayed for germinable seeds as previously outlined.

Seed Production Per Unit Area

In 1980, numbers of flowering culms were recorded for the dominant species (Phragmites communis, Scirpus acutus, Scolochloa festucacea, Typha glauca) in nine undisturbed 1 m x 1 m plots located adjacent to the two 3 m x 3 m sample plots in each vegetation type. Individual inflorescences of 25 randomly selected plants were collected for each dominant species. An average number of seeds per inflorescence was then determined for each species. Seed counts of *Scolochloa festucacea* were total counts. Seed counts for *Scirpus acutus* followed methods of van der Valk and Davis (1976), seed counts for *Typha glauca* were calculated by examining seeds from 25 randomly selected .5 cm sections of inflorescences and counting the number of viable seeds on the basis of visual appearance using criteria of Beal (1977). Number of seeds per flowering shoot of *Phragmites communis* was calculated by counting the number of spikelets per inflorescence and then examining 25 randomly selected spikelets for numbers of viable seeds (on the basis of visual appearance).

Seed Rain

In 1980, for each vegetation type, two seed traps (20 cm x 20 cm x 5 cm plastic trays filled with sterilized soil) were placed in three randomly selected 1 m x 1 m plots (total of six traps per vegetation type). Each trap was affixed to a wooden stake such that the trap was approximately 20 cm above the soil or water surface. Seed traps were retrieved in June 1981 and placed in an outdoor shelter under drawdown conditions. No seed trap data are available for the 1980 *Scolochloa* site.

Data Analysis

Log10(x+1) transformations were used where appropriate to stabilize variances of year-to-year and month-to-month comparisons of seedling means in ANOVAs. All year-to-year comparisons of seedling means were adjusted for shelter contamination by wind-dispersed seeds.

The number (n) of 400 cm^2 samples (from a 3 m x 3 m area) needed to obtain individual species' seed density estimates to within 10% of their population means was estimated using:

$$n = \frac{S^2 N}{N(.05\bar{X})^2 + S^2}$$

n = number of 400 cm^2 samples needed to obtain seed density estimates to within 90% of the population mean.

S^2 = seed population variance of a species (in a 3 m x 3 m area) estimated from thirty 400 cm^2 samples

$\bar{X}$ = seed population mean of a species (in a 3 m x 3 m area) estimated from thirty 400 cm^2 samples.

N = total number (225) of 400 cm^2 samples that could be collected from a 3 m x 3 m area.

Nomenclature follows Gleason and Cronquist (1963).

RESULTS

Seed Bank Survey - Spatial Variation

Table II-1 displays totals of numbers of germinable seeds m^{-2} in soil samples (from four vegetation types) assayed for two consecutive years. Seeds of 18 species, plus several unidentified mints and grasses, germinated in the treatment. Germinable seeds of Sonchus spp., Phragmites communis, Urtica dioica, Cirsium arvense, Solidago canadensis, and Mentha arvensis were most abundant in soil samples from the Phragmites site. Soil samples from the Scolochloa site contained the largest seed numbers of Scolochloa festucacea, Ranunculus sceleratus, Atriplex patula, Chenopodium rubrum, Aster brachyactis, and Rumex maritimus. Soil from the Typha site contained the highest amount of germinable seeds of Typha spp. and Scirpus validus, while the seed bank of the Scirpus site contained highest seed densities of Scirpus maritimus, Scirpus acutus, and Lycopus asper.

Fourteen species (Salix spp., Scirpus validus, Scolochloa festucacea, Ranunculus sceleratus, Atriplex patula, Chenopodium rubrum, Aster brachyactis, Rumex maritimus, Sonchus spp., Phragmites communis, Urtica dioica, Cirsium arvense, Solidago canadensis, Mentha arvensis) had at least 90% of their two-year seedling total germinate in the first year. Three species (Scirpus acutus, Scirpus maritimus, Typha spp.) had sizable percentages (16-47%) of their two-year seedling total germinate in the second year.

Variability in estimates of germinable seed density was high for all species in the four vegetative types. Only seven species had coefficients of variation less than 100% [Typha spp. (33%), Scolochloa festucacea (47%), Sonchus spp. (48%), Phragmites communis (69%), Chenopodium rubrum (75%), Ranunculus sceleratus (93%), Atriplex patula (97%)] (Table II-1). Even if sampling intensity had been increased from 30 to 100 samples (each sample = 400 cm^2) in each 3 m x 3 m vegetation type, seed density estimates of only 4 (Chenopodium rubrum, Scolochloa festucacea, Sonchus spp., Typha spp.) out of 18 species would have been within 10% of their population means. To obtain germinable seed density estimates to within 10% of the mean for dominant species, 103 samples would have been needed for Phragmites communis, 65 for Scolochloa festucacea, 38 for Typha spp., and 199 for Scirpus acutus.

Seed Bank Survey (1980 versus 1981)

Table II-2 shows germinable seed densities from 1980 seed bank samples compared with seed densities from 1981 seed bank samples. Seed bank samples for both years came from the same location (3 m x 3 m plot) in each of three

TABLE II-1. Total number of germinable seeds (m^{-2}) in 30 soil samples (from one of four vegetation types[1]) that were assayed for germinable seeds for two consecutive years

Species	Vegetation Type[2]	Two Year Total (Seeds m^{-2})[3]	% of Total Which Germinated in the First Year	Coeff. of Variation
Typha spp.	T	25984	53	33
Scolochloa festucacea	S	1896	95	47
Ranunculus sceleratus	S	963	99	93
Atriplex patula	S	541	99	97
Chenopodium rubrum	S	380	99	75
Sonchus spp.	P	325	98	48
Aster brachyactis	S	259	99	138
Phragmites communis	P	240	94	69
Scirpus validus	T	220	91	142
Urtica dioica	P	154	93	148
Rumex maritimus	S	82	99	195
Scirpus maritimus	H	73	84	153
Cirsium arvense	P	39	100	166
Solidago spp.	P	18	100	142
Mentha arvensis	P	17	100	183
Scirpus acutus	H	15	58	208
Lycopus asper	H	6	75	242
Salix spp.	H	5	100	388
GRAMINAE	S	29	80	490
LABIATAE	P	33	100	120

[1] Totals are displayed only for the vegetation type where the species was most abundant.

[2] "H" = *Scirpus acutus*, "T" = *Typha glauca*, "S" = *Scolochloa festucacea*, "P" = *Phragmites communis*.

[3] Totals were adjusted for contamination by wind-dispersed seeds [*Salix* spp. (10 seeds/sample), *Phragmites communis* (2.1 seeds/sample), *Typha* spp. (1.5 seeds/sample), *Sonchus* spp. (1.1 seeds/sample)].

sites (*Scirpus acutus*, *Typha glauca*, *Phragmites communis*). Comparisons in the fourth site (*Scolochloa*) were prevented because the 1980 site was mowed. Seedling assay conditions in the greenhouse (ambient summer temperatures) were not significantly different between years.

Except for *Salix* spp., increases in germinable seeds in the soil of most species was specific to vegetation type. Germinable seed densities of *Aster brachyactis*, *Atriplex patula*, *Chenopodium rubrum*, *Ranunculus sceleratus*, *Rumex maritimus*, *Scirpus maritimus*, and *Scirpus validus* were significantly higher in the 1981 *Scirpus acutus* seed bank. In 1981 *Phragmites* soil samples, numbers of germinable seeds of *Cirsium arvense*, *Mentha arvensis*, and *Typha* spp. increased over the 1980 totals, whereas the number of *Sonchus* spp. seeds declined. In the *Typha glauca* seed bank, germinable seed densities of *Phragmites communis* increased in 1981. Germinable seed numbers of *Carex atherodes*, *Lycopus asper*, *Scirpus acutus*, *Scolochloa festucacea*, *Solidgo canadensis*, *Sonchus* spp., and *Urtica dioica* did not change significantly between years.

Seed Bank Survey - Monthly Differences in 1981

Table II-3 displays differences in numbers of germinable seeds from soil samples collected in 1981 at three different sampling dates (June, July, August).

TABLE II-2. Mean number (m^{-2}) of germinable seeds in soil samples collected in 1980 and 1981 from three vegetation communities of the Delta Marsh, Manitoba (each value is an average of nine samples)

Species	Vegetation Type	Year 1980	 1981[1]	ANOVA[2]
Aster brachyactis	Scirpus	12	47	S
	Typha	3	8	NS
	Phragmites	0	3	NS
Atriplex patula	Scirpus	8	18	S
	Typha	0	4	NS
	Phragmites	196	180	NS
Carex atherodes	Scirpus	0	0	NS
	Typha	0	2	NS
	Phragmites	0	0	NS
Chenopodium rubrum	Scirpus	11	72	S
	Typha	8	3	NS
	Phragmites	47	69	NS
Cirsium arvense	Scirpus	0	3	NS
	Typha	0	0	NS
	Phragmites	12	51	S
Lycopus asper	Scirpus	3	5	NS
	Typha	0	1	NS
	Phragmites	0	2	NS
Mentha arvensis	Scirpus	0	0	NS
	Typha	0	0	NS
	Phragmites	8	88	S
Phragmites communis	Scirpus	30	40	NS
	Typha	9	118	S
	Phragmites	74	125	NS

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[1] All data were adjusted for contamination by wind-dispersed seeds.

[2] All data were log10(x+1) transformed; S, significant year effect ($P < .05$); NS, no significant year effect.

TABLE II-2. (continued)

Species	Vegetation Type	Year 1980	Year 1981[1]	ANOVA[2]
Ranunculus sceleratus	Scirpus	5	32	S
	Typha	3	3	NS
	Phragmites	0	5	NS
Rumex maritimus	Scirpus	14	54	S
	Typha	4	8	NS
	Phragmites	0	1	NS
Salix spp.	Scirpus	0	14	S
	Typha	1	12	S
	Phragmites	0	14	S
Scirpus acutus	Scirpus	8	8	NS
	Typha	0	1	NS
	Phragmites	0	0	NS
Scirpus maritimus	Scirpus	21	43	S
	Typha	0	1	NS
	Phragmites	0	0	NS
Scirpus validus	Scirpus	74	161	S
	Typha	18	22	NS
	Phragmites	0	0	NS
Scolochloa festucacea	Scirpus	16	14	NS
	Typha	0	0	NS
	Phragmites	0	0	NS
Solidago spp.	Scirpus	0	0	NS
	Typha	0	0	NS
	Phragmites	8	2	NS
Sonchus spp.	Scirpus	1	1	NS
	Typha	0	0	NS
	Phragmites	112	17	S
Typha spp.	Scirpus	81	80	NS
	Typha	4839	4183	NS
	Phragmites	5	28	S
Urtica dioica	Scirpus	0	0	NS
	Typha	0	0	NS
	Phragmites	56	126	NS

TABLE II-2. (continued)

Species	Vegetation Type	Year 1980	Year 1981[1]	ANOVA[2]
GRAMINAE	Scirpus	0	2	NS
	Typha	0	0	NS
	Phragmites	1	0	NS
LABIATAE	Scirpus	0	0	NS
	Typha	0	0	NS
	Phragmites	19	73	S

Germinable seed densities of *Carex atherodes*, *Lycopus asper*, *Solidago canadensis*, and *Sonchus* spp. did not change over time. In soil samples from the *Scirpus acutus* site, the June sample had the most germinable seed of *Aster brachyactis*, *Atriplex patula*, *Chenopodium rubrum*, *Ranunculus sceleratus*, *Rumex maritimus*, *Salix* spp., *Scirpus acutus*, *Scirpus maritimus*, *Scirpus validus*, and *Scolochloa festucacea*. June soil samples from the *Typha glauca* site had the most germinable seeds of *Phragmites communis* and *Salix* spp., while the July sample yielded more seeds of *Chenopodium rubrum*, *Scirpus maritimus*, and *Typha* spp. In soil samples from the *Scolochloa festucacea* site, the June sample yielded the most germinable seeds of *Atriplex patula* and *Salix* spp., while the July sample had the most *Ranunculus sceleratus* seeds, and the August sample had the most *Phragmites communis* seeds. June soil samples from the *Phragmites communis* site yielded the most germinable seeds of *Atriplex patula*, *Cirsium arvense*, *Mentha arvensis*, *Phragmites communis*, *Salix* spp. and *Urtica dioica*. In short, the largest number of seeds of any given species usually germinated in June samples; only seeds of *Typha* spp. seem to germinate consistently in larger numbers in July.

TABLE II-3. Mean number (m^{-2}) of germinable seeds in soil samples collected at three different sampling dates in four vegetation communities of the Delta Marsh, Manitoba (each value is an average of nine samples)

Species	Vegetation Type	Month June	 July	 August	ANOVA[1]
Aster brachyactis	Scirpus	47	26	5	S
	Typha	8	1	1	NS
	Scolochloa	4	6	0	NS
	Phragmites	3	2	3	NS
Atriplex patula	Scirpus	18	12	2	NS
	Typha	4	0	0	NS
	Scolochloa	1859	1308	349	S
	Phragmites	180	129	32	S
Carex atherodes	Scirpus	0	0	0	NS
	Typha	2	1	0	NS
	Scolochloa	3	6	5	NS
	Phragmites	0	0	0	NS
Chenopodium rubrum	Scirpus	72	19	8	S
	Typha	3	96	5	S
	Scolochloa	47	463	230	NS
	Phragmites	69	36	27	NS
Cirsium arvense	Scirpus	3	0	0	NS
	Typha	0	0	0	NS
	Scolochloa	1	2	0	NS
	Phragmites	51	30	8	S
Lycopus asper	Scirpus	5	2	1	NS
	Typha	1	0	0	NS
	Scolochloa	2	1	0	NS
	Phragmites	2	0	0	NS
Mentha arvensis	Scirpus	0	0	0	NS
	Typha	0	0	0	NS
	Scolochloa	2	0	0	NS
	Phragmites	88	29	8	S

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[1] All data was log10(x+1) transformed; S, significant monthly effect; NS, no significant monthly effect.

TABLE II-3. (continued)

Species	Vegetation Type	Month			ANOVA[1]
		June	July	August	
<u>Phragmites</u> <u>communis</u>	Scirpus	40	23	12	NS
	Typha	118	24	20	S
	Scolochloa	6	3	11	S
	Phragmites	125	65	44	S
<u>Ranunculus</u> <u>sceleratus</u>	Scirpus	32	11	7	S
	Typha	3	24	3	NS
	Scolochloa	9	31	11	S
	Phragmites	5	7	2	NS
<u>Rumex</u> <u>maritimus</u>	Scirpus	54	21	7	S
	Typha	8	12	10	NS
	Scolochloa	4	3	2	NS
	Phragmites	1	0	0	NS
<u>Salix</u> spp.	Scirpus	14	3	0	S
	Typha	12	2	0	S
	Scolochloa	13	0	0	S
	Phragmites	14	18	0	S
<u>Scirpus</u> <u>acutus</u>	Scirpus	8	3	0	S
	Typha	1	0	0	NS
	Scolochloa	0	0	0	NS
	Phragmites	0	0	0	NS
<u>Scirpus</u> <u>maritimus</u>	Scirpus	43	3	2	S
	Typha	1	2	1	NS
	Scolochloa	0	0	0	NS
	Phragmites	0	0	0	NS
<u>Scirpus</u> <u>validus</u>	Scirpus	161	21	15	S
	Typha	33	42	6	NS
	Scolochloa	1	0	0	NS
	Phragmites	0	0	0	NS
<u>Scolochloa</u> <u>festucacea</u>	Scirpus	14	1	1	S
	Typha	0	0	0	NS
	Scolochloa	109	184	102	NS
	Phragmites	0	0	0	NS

TABLE II-3. (continued)

Species	Vegetation Type	Month			ANOVA[1]
		June	July	August	
Solidago spp.	Scirpus	0	0	0	NS
	Typha	0	0	0	NS
	Scolochloa	0	0	1	NS
	Phragmites	2	1	1	NS
Sonchus spp.	Scirpus	1	1	0	NS
	Typha	0	3	1	NS
	Scolochloa	2	8	4	NS
	Phragmites	17	22	11	NS
Typha spp.	Scirpus	80	135	126	NS
	Typha	4183	5261	2127	S
	Scolochloa	13	3	6	NS
	Phragmites	28	63	28	NS
Urtica dioica	Scirpus	0	0	0	NS
	Typha	0	0	0	NS
	Scolochoa	1	0	0	NS
	Phragmites	126	63	6	S
GRAMINAE	Scirpus	2	0	0	NS
	Typha	0	4	0	NS
	Scolochloa	0	0	0	NS
	Phragmites	0	0	0	NS
LABIATAE	Scirpus	0	0	0	NS
	Typha	0	0	0	NS
	Scolochloa	9	19	1	NS
	Phragmites	73	25	17	S

Seed Production and Seed Rain

The average number of seeds per flowering shoot, annual seed production m^{-2}, and number of germinable seeds from trapped seed populations are given in Table II-4. Of the four emergents, *Typha glauca* (6842 seeds/culm) produces the largest numbers of seed (3/6,310 seeds m^{-2}). Seed production in 1980 of the other emergents is at least an order of magnitude less than *Typha glauca*: *Phragmites communis* (796 seeds/cuhm, 28656 seeds m^{-2}), *Scirpus acutus* (243, 11124), and *Scolochloa festucacea* (188, 940). Numbers of germinable seeds in 1980 seed rain from *Phragmites communis* (475 seeds m^{-2}) and *Typha glauca* (1065 seeds m^{-2}) were several orders of magnitude lower than annual seed production (Table II-4). No seedlings of *Scirpus acutus* grew in 1980 seed traps.

TABLE II-4. Annual seed production in 1980 and numbers of germinable seeds from 1980 trapped seed populations of four emergent species in the Delta Marsh, Manitoba

Species[1]	Number of Seeds Per Flowering Shoot	Number of Flowering Shoots m^{-2}	Annual Seed Production m^{-2}	Germinable Seeds m^{-2} in 1980 Seed Traps
Phragmites communis	796	36	28656	475
Scirpus acutus	243	45	11124	0
Scolochloa festucacea	188	5	940	----[2]
Typha glauca	6842	55	376310	1065

[1] Other species whose seeds were collected in the traps include Cirsium arvense, Mentha arvense, Stachys palustris, and Urtica dioica.

[2] No data available.

DISCUSSION

Seed Bank Spatial Variation

Even in a relatively small area (3 m x 3 m), spatial heterogeneity in germinable seed densities in the seed bank is very high (Table II-1). Only significantly increasing the number of samples will result in a worthwhile gain in precision in estimating seed densities. Increasing the volume of the sample would be a better strategy for improving precision and accuracy.

Ideally, a preliminary seed bank study in wetlands should ascertain the minimum volume sample needed to detect most species in the seed bank. The volume of soil for each sample could then be obtained by collecting several small subsamples from a unit area. Because of known variations in the size and composition of seed banks along elevational gradients in wetlands, replicate seed bank samples would yield the most information if they were collected perpendicular to the elevational gradient.

Previous seed bank studies of wetland habitats (van der Valk and Davis 1978, Leck and Graveline 1979, Smith and Kadlec 1983) all used seedling assay methods similar to this study. In those studies, seedling emergence from soil samples was monitored for one year and data were expressed as density estimates. Results of the two-year seedling assay in this study (Table II-1) indicated a one-year treatment would provide accurate seed bank estimates (>90%) of germinable seed numbers for 14 out of 18 species. However, seed bank densities of four species would have been underestimated by 16-47% (Table II-1). These data imply that seed banks of certain species would not be depleted after a single germination event; however, treatment conditions were highly artificial and optimal for germination (i.e., removal of litter and mixing of the soil sample, continual sample exposure to high light intensities, daily watering of samples). Whether or not depletion of wetland seed banks after disturbance events is a significant factor in vegetation dynamics is unclear, for Leck and Graveline (1979) found three to five times more seeds in the seed bank than those which actually germinated in the field. Smith and Kadlec (1983) were of the opinion that after disturbance, depletion of seeds from marsh seed banks was insignificant.

Seed Bank Temporal Variation

There were significant yearly differences in numbers of germinable seeds present in the seed banks of the four sites (seeds of 10 out of 18 species were more numerous (210 to 1310%) in 1981 than 1980--Table II-2). These differences seem attributable to annual seed production within sites (e.g., increased seed numbers of Cirsium arvense and Mentha arvense in the 1981 Phragmites seed bank) and dispersal into the sites of seeds produced elsewhere (e.g., increased seed densities of several annuals in the 1981 Scirpus seed bank, Phragmites communis seeds in the 1981 Typha seed bank, and Typha spp., seeds in the 1981 Phragmites seed bank). Gains and losses of seeds (via wave action--Pederson 1983) in the sediment of the Scirpus and Typha sites would also explain monthly germination pattern differences among habitats for a variety of species (Table II-3). Dispersal of seeds from one wetland community to another has also been documented by McAtee (1925), Kelley and Burns (1975), Staniforth and Cavers (1976), van der Valk and Davis (1976), and Smith (1983).

Another possible explanation for contrasting temporal germination patterns between habitats is ecotypic variation in germination requirements. Seeds of Ranunculus sceleratus and Phragmites communis germinated in contrasting patterns in the Scolochloa and Phragmites soil samples (i.e., depending on the site, seeds of the same species germinated in significantly larger numbers in different months). This germination pattern may reflect two distinct populations of buried seeds, each with different germination requirements. A similar situation was found by van der Vegte (1978), who detected two distinct populations of Stellaria media growing side by side. In one population, all the seeds germinated in autumn and the seed bank was replaced annually; in the other, there was a persistent and phenotypically diverse seed reserve.

Regardless of dispersal events, seeds of most species in this study (Table II-3) germinated from the seed bank samples more readily in June (14 species) or in equal numbers throughout the sampling period (3 species).

Seed Banks and Annual Seed Production

Germinable seed densities from annual seed production and in the soil seem surprisingly high for Phragmites communis (Table II-4), as Walker (1959, 1965) did not detect a single seedling of this species during a massive natural drawdown of the marsh in the late 1950s. Also, Love and Love (1954) stated viable seed production by Phragmites was improbable in normal years in the Delta Marsh because the species flowered so late. The results in this study probably reflect the high variability in viable seed production for this species. Haslam (1973) has found the potential germination of Phragmites communis seeds varies between panicles, habitats, seasons, and biotypes.

The relatively few germinable seeds of Phragmites communis which persist in the soil (Pederson 1983) reveal this species has a transient seed bank which is largely a function of annual seed rain. Phragmites communis seeds germinated most readily in June (Table II-3), which infers adaptation for seedlings to begin growth as early in the growing season as possible. This germination trait may offset the long period of time (3 months to 3 years) Phragmites seedlings need to become established (Haslam 1973).

Annual seed production of Scirpus acutus was also high (11,124 seeds m^{-2}) but evidently the germination requirements of this species are very narrow (Isley 1944, Macaulay 1973): no seeds germinated from trapped seed populations and only 15 germinable seeds were detected in the seed bank. However, Smith and Kadlec (1983) reported large numbers of Scirpus acutus seedlings which grew in seed bank samples from a Utah marsh. The reasons for the conflicting results between this study and the Utah study are unclear. Perhaps greenhouse conditions in this study failed to meet the germination requirements for this species. This technique problem has also been documented by van der Valk and Davis (1978, 1979) and Smith and Kadlec (1983).

Annual seed production of Scolochloa festucacea (940 seeds m^{-2}) was not representative for this species (Smith 1973) as the stand examined in this study was under stress from drought conditions of 1980 and 1981. However, results from another study (Pederson 1983) indicate this species can produce large numbers of germinable seeds from annual seed rain (although the seeds are not persistent in the seed bank). Scolochloa festucacea seeds do not require stratification in order to germinate (Smith 1973), and they readily germinate from the soil throughout the growing season (Table II-3). Since an individual Scolochloa seedling needs 60 days in order to develop an overwintering rhizome (Smith 1973), seedling populations of this species (which establish late in the growing season) must suffer heavy mortality.

Annual seed rain of Typha glauca (376,310 seeds m^{-2}--Table II-4) is considerably less than the maximum seed production reported for Typha (9,546,750 seeds m^{-2}--Yeo 1964), but this number is consistent with other reported values (<95,000 seeds m^{-2}--van der Valk and Davis 1979). Large numbers of seeds are capable of germinating from trapped seed populations, from the seed bank (Table II-4), and are persistent in the soil (Table II-1, Pederson 1983, van der Valk and Davis 1979). Results from this study do not support McNaughton's (1968) hypothesis that Typha inhibits germination of its own seeds. The largest germinable seed densities of Typha were found in soil samples from the Typha site (Table II-1).

Most seeds of Typha spp. germinated in July (Table

II-3). This germination pattern suggests high temperatures are needed for optimal germination. Sifton (1959) found the optimum temperature for _Typha_ seed germination was 30°C. Linde (1969) noted during a 1962 drawdown of the Horicon Marsh that, although the marsh was dry in May and other species were prevalent on the mudflats, cattail seedlings were not numerous until late June. The late germination pattern of _Typha_ seeds might place this species at a disadvantage if disturbance events (e.g., fire, drainage) occurred early in the season.

In summary, extreme heterogeneity in numbers of germinable seeds in marsh seed banks occurs spatially and temporally and is a result of dispersal events and species-specific seed germination patterns. The dynamic nature of gains and losses of seeds to the seed banks indicates that sampling should be considered in relation to the annual cycle, for if samples are taken on a single occasion only, the results may be influenced by recent major inputs of seeds.

Each of the dominant emergent species in the Delta Marsh is capable of annually producing seeds in quantities (Table II-4) of at least an order of magnitude larger than germinable seed densities in the soil (Table II-1). Mortality of seeds in the soil occurs exponentially, with most mortality due to a breakdown of dormancy mechanisms and subsequent germination while buried in the soil (Schafer and Chilcote 1970). In addition, large numbers of seeds are capable of germinating late in the growing season (Table II-3), even though most seedlings of emergent species would perish with the onset of winter. From an evolutionary point of view, natural selection should lead to specific dormancy-breaking requirements where seeds would only germinate when seedlings have a high probability of completing their life cycle. That they do not, implies that life history strategies for reproduction by seeds contain many non-adaptive traits.

LITERATURE CITED

Anderson, M. G., and R. E. Jones. 1976. Submerged aquatic vascular plants of East Delta Marsh. Manitoba Dept. Renewable Resources and Transportation Services Wildl. Report. 120 pp.

Archibold, O. W. 1979. Buried viable propagules as a factor in post-fire regeneration in northern Saskatchewan. Can. J. Bot. 57:54-58.

Beal, E. O. 1977. A manual of marsh and aquatic vascular plants of North Carolina, with habitat data. N. C. Agric. Exp. Stn., Tech. Bull. No. 247. 298 pp.

Bedish, J. W. 1967. Cattail moisture requirements and their significance to marsh management. Am. Mid. Nat. 78:288-300.

Bossenmaier, E. F. (ed.). 1968. The Delta Marsh, its values, problems, and potentialities. Technical Committee Report, Manitoba Dept. of Mines and Natural Resources. 75 pp.

Burgess, H. 1969. Habitat management on a mid-continent waterfowl refuge. J. Wildl. Mgt. 33:843-847.

Cook, R. 1980. The biology of seeds in the soil. Pages 107-129 in O. Solbrig, ed. Demography and evolution in plant populations. Blackwell, Oxford.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of Northeastern United States and adjacent Canada. Van Nostrand Reinhold Co., New York. 810 pp.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York. 892 pp.

Harris, S. W., and W. H. Marshall. 1963. Ecology of water level manipulations on a northern marsh. Ecology 44:331-343.

Haslam, S. M. 1973. Some aspects of the life history and autecology of Phragmites communis Trin. A review. Pol. Arch. Hydrobiol. 20:79-100.

Hutchinson, G. E. 1975. A treatise on limnology. Vol. III. Limnological botany. John Wiley and Sons, New York. 660 pp.

Isley, D. 1944. A study of conditions that affect the germination of *Scirpus* seeds. Cornell Univ., Agric. Exp. Stn. Memoir 257. 15 pp.

Kadlec, J. A., and W. A. Wentz. 1974. State-of-the-art survey and elevation of marsh plant establishment techniques: induced and natural. 2 vols. NTIS (National Technical Information Service), Springfield, Virginia.

Kelley, A. D., and V F. Burns. 1975. Dissemination of weed seeds by irrigation water. Weed Sci. 23:486-493.

Leck, M. A., and K. J. Graveline. 1979. The seed bank of a freshwater tidal marsh. Am. J. Bot. 66:1006-1015.

Lieffers, V. J., and J. M. Shay. 1982. Distribution and variation in growth of *Scirpus maritimus* var. *paludosus* on the Canadian prairies. Can. J. Bot. 60:1938-1949.

Linde, A. F. 1969. Techniques of wetland management. Wisc. Dept. Nat. Res. Research Rept. No. 45. 156 pp.

Love, A., and D. Love. 1954. Vegetation of a prairie marsh. Bull. Torr. Bot. Club 81:16-34.

Macaulay, A. J. 1973. Taxonomic and ecological relationships of *Scirpus acutus* Muhl. and *S. validus* Vahl. (Cyperaceae) in southern Manitoba. Ph.D. Dissertation. University of Manitoba, Winnipeg, Manitoba. 212 pp.

Major, J., and W. T. Pyott. 1966. Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13:253-282.

McAtee, W. L. 1925. Notes on drift, vegetation balls, and aquatic insects as a food product of inland waters. Ecology 6:288-302.

McNaughton, S. J. 1968. Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*. Ecology 49:367-369.

Meeks, R. L. 1969. Effect of drawdown date on wetland plant succession. J. Wildl. Mgt. 33:817-821.

Moore, J. M., and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Can. J. Bot. 55:2408-2412.

Muenscher, W. C. 1936. Storage and germination of seeds of aquatic plants. Cornell Univ., Agric. Exp. Stn. Bull. 652. 17 pp.

Pederson, R. L. 1983. The distribution of buried seed populations in the Delta Marsh, Manitoba, Canada. Part I. Ph.D. Dissertation. Iowa State University, Ames, Iowa. 97 pp.

Roberts, H. A. 1981. Seed banks in soils. Advances in Applied Biology 6:1-55.

Schafer, D. E., and D. O. Chilcote. 1970. Factors influencing persistence and depletion in buried seed populations. Crop Sci. 10:342-345.

Sifton, H. B. 1959. The germination of light-sensitive seeds of Typha latifolia. Can. J. Bot. 37:719-739.

Smith, A. L. 1973. Life cycle of the marsh grass, Scolochoa festucacea. Can. J. Bot. 51:1661-1668.

Smith, L. M. 1983. Effects of prescribed burning on the ecology of a Utah marsh. Ph.D. Dissertation. Utah State Univ., Logan, Utah. 172 pp.

Smith, L. M., and J. A. Kadlec. 1983. Seed banks and their role during drawdown of a North American marsh. J. Applied Ecol. 20:673-684.

Smith, S. G. 1967. Experimental and natural hybrids in North American Typha (Typhaceae). Am. Mid. Nat. 78:257-287.

Staniforth, R. J., and P. B. Cavers. 1976. An experimental study of water dispersal in Polygonum spp. Can. J. Bot. 54:2587-2596.

Steward, R. E., and H. A. Kantrud. 1972. Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Geology Surv. Prof. Pap. 585-D. 36 pp.

Thompson, K. 1978. The occurrence of buried viable seeds in relation to environmental gradients. J. Biogeogr. 5:425-430.

Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67:893-921.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.

van der Valk, A. G., and C. B. Davis. 1976. The seed banks of prairie glacial marshes. Can. J. Bot. 54:1832-1838.

van der Valk, A. G., and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.

van der Valk, A. G., and C. B. Davis. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. Aquatic Botany 6:29-51.

van der Vegte, F. W. 1978. Population differentiation and germination ecology in Stellaria media (L.) Vill. Oecologia (Berl.) 37:231-245.

Walker, J. M. 1959. Vegetation studies on the Delta Marsh, Delta, Manitoba. M.S. Thesis. Univ. of Manitoba, Winnipeg. 203 pp.

Walker, J. M. 1965. Vegetation changes with falling water levels in the Delta Marsh, Manitoba. Ph.D. Thesis. Univ. of Manitoba, Winnipeg. 272 pp.

Watkinson, A. R. 1978. The demography of a sand dune annual, Vulpia fasciculata. II. The dynamics of seed populations. J. Ecol. 66:35-44.

Whigham, D. F. 1979. The distribution of seeds, seedlings, and established plants of Arrow Arum (Peltandra virginica (L.) Kunth) in a freshwater tidal wetland. Bull. Tor. Bot. Club 106:193-199.

Whipple, S. A. 1978. The relationship of buried, germinating seeds to vegetation in an old-growth Colorado subalpine forest. Can. J. Bot. 56:1505-1509.

Yeo, R. R. 1964. Life history of common cattail. Weeds 12:284-288.

GENERAL SUMMARY

The goal of this research was to elucidate the role of seed banks in vegetation dynamics of the Delta Marsh, Manitoba (a large lacustrine marsh). There are sizable reserves of buried seeds beneath the plant communities of the Delta Marsh with the largest concentrations of seeds located in the shoreline zones. There is also a large potential for seed dispersal to colonize new available habitat. Many species which are represented in the seed bank are not present in the contemporary vegetation.

Vegetation change in the Delta Marsh is dependent on three factors: buried disseminule and seed reserves ("seed bank"), vegetative reproduction from existing plants ("bud bank"), and disseminule dispersal into the community ("seed rain"). The importance of the seed bank, bud bank, and seed rain to vegetation dynamics will vary according to the environmental factors which act on the individual seeds, ramets, and plants. The relatively stable environment recently created in the Delta Marsh by the control of water levels has produced conditions where perennial species are favored and reproduction is primarily accomplished by vegetative means. This change has also resulted in a decrease in species diversity and a diminished role of the seed bank in vegetation dynamics. If water levels in the marsh were allowed to fluctuate to the degree and duration that historically occurred, the role of seed banks in vegetation change would increase dramatically.

LITERATURE CITED

Cook, R. 1980. The biology of seeds in the soil. Pages 107-129 in O. Solbrig, ed. Demography and evolution in plant populations. Blackwell, Oxford.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deep water habitats of the United States. FWS/OBS-79/31. Office of Biological Services, Fish and Wildlife Service, U.S.D.I., Washington, D.C. 103 pp.

Dix, R. I., and F. E. Smeins. 1967. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. Can. J. Bot. 45:21-58.

Dodd, J. D., and R. T. Coupland. 1966. Vegetation of saline areas in Saskatchewan. Ecology 47:958-968.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York. 892 pp.

Millar, J. B. 1973. Vegetation changes in shallow marsh wetlands under improving moisture regime. Can. J. Bot. 51:1443-1457.

Roberts, H. A. 1981. Seed banks in soils. Advances in Applied Biology 6:1-55.

Steward, R. E., and H. A. Kantrud. 1972. Vegetation of prairie potholes, North Dakota, in relation to quality of water and other environmental factors. U.S. Geology Surv. Prof. Pap. 585-D. 36 pp.

Thompson, K. 1978. The occurrence of buried viable seeds in relation to environmental gradients. J. Biogeogr. 5:452-430.

Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67:893-921.

van der Valk, A. G., and C. B. Davis. 1976. Changes in composition, structure, and production of plant communities along a perturbed wetland coenocline. Vegetatio 32:87-96.

van der Valk, A. G., and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335.

Walker, B. H., and R. T. Coupland. 1968. An analysis of vegetation environment relationships in Saskatchewan sloughs. Can. J. Bot. 46:509-522.

Watkinson, A. R. 1978. The demography of a sand dune annual, *Vulpia fasciculata*. II. the dynamics of seed populations. J. Ecol. 66:35-44.

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