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Abstract

"Natural" waterfowl habitat management (Weller 1981) involves the use of natural forces (e.g., water levels, muskrat activity) to develop a mosaic of native plant communities, i.e., a habitat complex. Such a complex is designed to provide the nutritional and structural requirements for not only waterfowl, but also for a large variety of migratory bird and nongame species (Fredrickson and Taylor 1982). Natural management is less costly, more permanent, more esthetically pleasing, and provides more resources for wildlife than do standard agronomic practices (Fredrickson and Taylor 1982). Because natural marsh management is primarily the application of ecological principles, the successful development of a habitat complex requires a conceptual grasp of vegetation dynamics and a detailed understanding of the biological and physical factors that produce vegetation changes in wetlands.

Disciplines

Botany | Ecology and Evolutionary Biology | Terrestrial and Aquatic Ecology

Comments

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Vegetation Change and Seed Banks in Marshes: Ecological and Management Implications

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Introduction

"Natural" waterfowl habitat management (Weller 1981) involves the use of natural forces (e.g., water levels, muskrat activity) to develop a mosaic of native plant communities, i.e., a habitat complex. Such a complex is designed to provide the nutritional and structural requirements for not only waterfowl, but also for a large variety of migratory bird and nongame species (Fredrickson and Taylor 1982). Natural management is less costly, more permanent, more esthetically pleasing, and provides more resources for wildlife than do standard agronomic practices (Fredrickson and Taylor 1982). Because natural marsh management is primarily the application of ecological principles, the successful development of a habitat complex requires a conceptual grasp of vegetation dynamics and a detailed understanding of the biological and physical factors that produce vegetation changes in wetlands.

Vegetation Dynamics in Wetlands

Plant communities in wetlands are typically described as distinct zones or bands of vegetation that follow shoreline contours (Stewart and Kantrud 1972, Cowardin et al. 1979). Actually, individuals of different plant species are distributed independently along environmental gradients, with each species surviving under a specific set of environmental conditions (Swindale and Curtis 1957, Mandossian and McIntosh 1960, Beschel and Weber 1962, Raup 1975, van der Valk and Davis 1976a).

As environmental conditions change, plant species are redistributed as some populations are eliminated and others become established along the new environmental gradient. This "resorting" of vegetation is a function of recruitment from buried seed reserves (van der Valk and Davis 1978), buried vegetative propagules (Lieffers and Shay 1982), and the dispersal of propagules (Hall et al. 1946).

Once established, wetland vegetation can change both qualitatively, i.e., floristically, and quantitatively, i.e., species' abundance and physical structure. For these reasons, van der Valk (1984) has separated vegetation change into three separate phenomena: succession (the establishment of new populations or the extirpation of existing populations), maturation (the growth of individuals in established populations), and fluctuation (the year-to-year changes in density or size of individuals within established populations).

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All attributes of vegetation change (i.e., succession, maturation, fluctuation) are the result of changes within individual populations of the species which make up the wetland community. Therefore, the key to understanding and predicting vegetation change is a knowledge of the life-history characteristics of the species in the vegetation, since life-history features determine how each population will respond to the physical-chemical environment, competition, herbivory, and disease.

Life history characteristics that are potentially important for predicting vegetation change include: seed production, dispersal, longevity, and germination requirements; growth form and life span; and growth rate under different environmental conditions. When life-history information is combined with information about the biological and physical factors that cause vegetation change (for reviews, see Kadlec and Wentz 1974, Hutchinson 1975, Davis and Brinson 1980, Olson 1981, Ogaard et al. 1981), more reliable predictions about vegetation dynamics can be made.

This approach was first demonstrated by Hall et al. (1946) who used information on seed germination, seed dispersal, and water tolerance of wetland species to devise management regimes to control vegetation in Tennessee reservoirs. Other studies of wetland successions (Kadlec 1962, Harris and Marshall 1963, Weller and Spatcher 1965, Meeks 1969, Weller and Fredrickson 1974, van der Valk and Davis 1978, 1979) have also documented the importance of characterizing life-history features. The utility and predictive power of this approach make it a powerful tool for wetland managers.

To predict vegetation change for a particular wetland, two sets of information are needed: (1) the potential flora of the wetland, and (2) the life-history type of each species. The potential flora includes all species found growing in the wetland, plus all additional species represented as seeds and propagules in the soil. Life-history information may be gleaned from the literature (Sculthorpe 1967, Kadlec and Wentz 1974, Hutchinson 1975, Herner and Co. 1980, see also the Information and Retrieval Service of the Aquatic Weed Program, University of Florida, Gainesville, FL 32611), or from long-term field studies (Hall et al. 1946, Connelly 1979, Fredrickson and Taylor 1982). However, much of the information needed for a particular wetland can be obtained by examining its' seed bank.

Seed Bank Studies

Seed bank studies involve collecting surface sediment samples from the marsh and exposing subsamples of each sample to conditions similar to those of an exposed mud flat and to those of a flooded wetland. The number of seedlings of each species (whose seeds germinated under the simulated drawdown and submersed conditions) are recorded after a suitable amount of time has passed, usually several months. Further information on the collection, preparation, and treatment of seed bank samples can be found in a review by Roberts (1981), and papers by van der Valk and Davis (1978) and Pederson (1981).

Van der Valk (1981) used seed bank information to develop a qualitative model for predicting wetland succession. Plant species were classified into life-history types on the basis of: (1) life span, (2) propagule longevity, and (3) propagule establishment requirements. This information was used to construct successional sequences (under different environmental regimes) for prairie glacial marshes and a fringe papyrus swamp (van der Valk 1981) and for a shallow southern lake (van der Valk 1980). In all cases, the model predicted changes which did actually occur in the field.

Although van der Valk's model is qualitative (it only predicts which species will be

present and does not predict their relative abundance), additional insight into potential vegetation response can be obtained by a more detailed analysis of seed dispersal and the spatial variation in the composition of the seed bank.

Seed Banks of Wetlands

In prairie pothole marshes, there is relatively little within-marsh variation in the composition of the seed banks (van der Valk and Davis 1976b). However, in other types of wetlands, there is considerable spatial variation in the location, size, and composition of buried seed reserves.

Seed Distribution in the Delta Marsh

Figure 1 summarizes data from a seed bank study (Pederson 1983) of the Delta Marsh (a large lacustrine wetland) located on the southern end of Lake Manitoba in Manitoba, Canada. The distribution of buried germinable seeds (calculated from numbers of seedlings which grew from substrate samples) is plotted against elevation in Figure 1 (species are grouped according to life-history types). The transition zone between aquatic and terrestrial habitats is located between elevations 247.4 m to 247.7 m.

Regardless of dispersal or life-history type, highest seed concentrations were located in soil samples from the shoreline zone and very few seeds were located in samples from open water areas. 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), and reflects the fact that the Delta Marsh is a littoral wetland not subject to extreme fluctuations in water levels; i.e., open water areas are always flooded even during periods of low water, and a seed bank is never developed.

Seed Dispersal in the Delta Marsh

Shoreline seed accumulations are caused by water movement depositing seeds along drift lines. This is illustrated in Figure 2, which shows the elevational distribution of seed rain for one year. Seed rain for all emergent species (whether they produced large seeds or light wind-dispersed seeds) and from submergent species was highest in shallow water areas of the shoreline zone. Few seeds were collected in seed traps located in deeper water. Similar dispersal patterns in other wetlands were documented by Hanson (1918), Hall et al. (1946), and Smith and Kadlec (1978), who observed that shoreline emergent communities (e.g., cattails and bulrushes) effectively trap both water- and wind-dispersed seeds.

Annual species contributed very little to the seed rain (Figure 2). This reflects the low occurance of these species in the present vegetation (Table 1). However, annuals and other "disturbance" species (e.g., *Scirpus validus* and *Scirpus maritimus*) are well-represented as viable seeds in the seed bank (Table 1). This implies that a quite different environment once occurred in the marsh.

Vegetation History in the Delta Marsh

Since seed banks contain a historical record (in the form of viable seeds) of past vegetation change (van der Valk and Davis 1979), additional insights about vegetation dynamics of a wetland can be gained by examining the composition of seeds at different depths in the substrate.
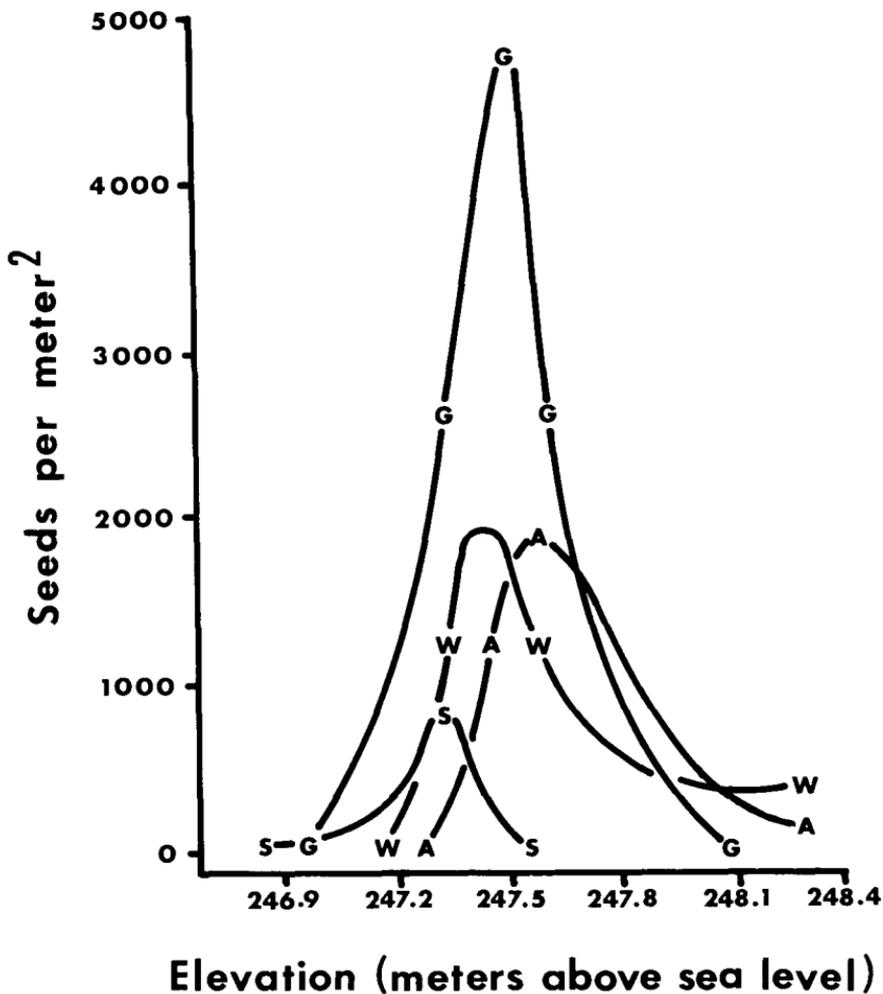
Figure 1. Distribution of buried seed populations along an elevational gradient in the Delta Marsh, Manitoba.

G = Seeds of emergent perennials (*Carex atherodes, Scirpus* spp., *Scolochloa festucacea*) which produce large seeds (achenes or grains).

W = Seeds of emergent perennials (*Phragmites communis, Typha* spp.) which produce small wind-dispersed seeds.

A = Seeds of annuals (*Aster brachyactis, Atriplex patula, Chenopodium rubrum, Ranunculus sceleratus, Rumex maritimus*).

S = Seeds of submergent aquatics (*Potamogeton pectinatus, Utricularia vulgaris, Zannichellia palustris*).
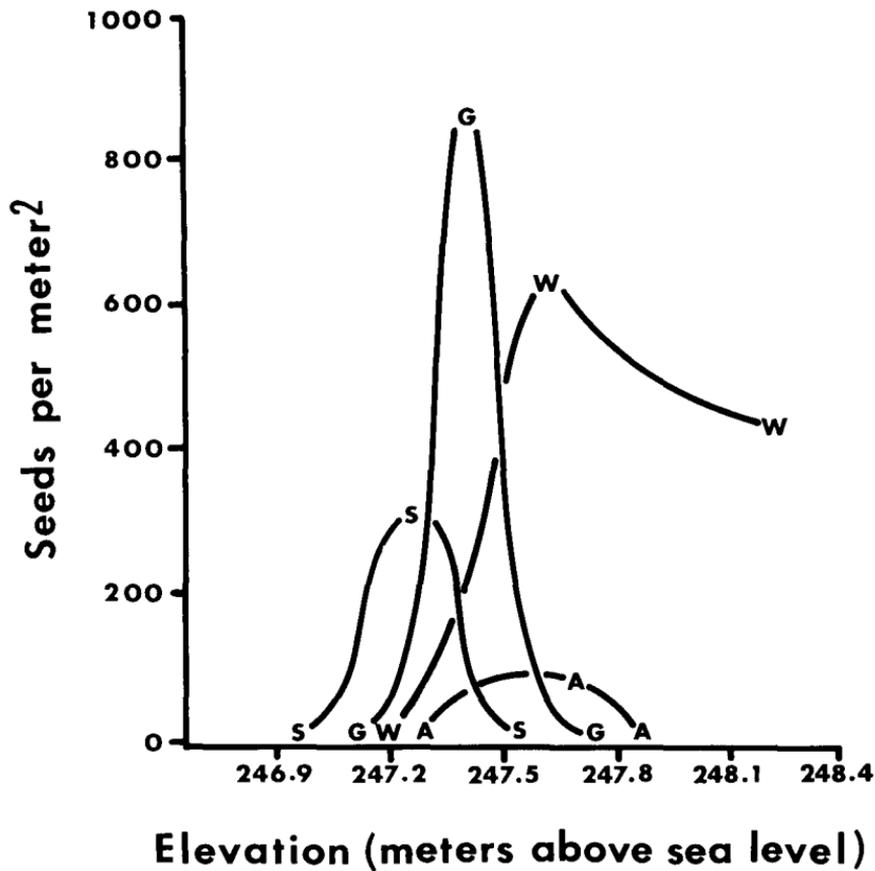
Figure 2.   Distribution of seed rain (calculated from seeds collected in seed traps over a period of one year) along an elevational gradient in the Delta Marsh, Manitoba.

G = Seeds of emergent perennials (*Carex atherodes, Scirpus* spp., *Scolochloa festucacea*) which produce large seeds (achenes or grains).

W = Seeds of emergent perennials (*Phragmites communis, Typha* spp.) which produce small wind-dispersed seeds.

A = Seeds of annuals (*Aster brachyactis, Atriplex patula, Chenopodium rubrum, Ranunculus sceleratus, Rumex maritimus*).

S = Seeds of submergent aquatics (*Potamogeton pectinatus, Utricularia vulgaris, Zannichellia palustris*).

Table 1.   Relative frequency ($n = 250$ points) of representative species in the Delta Marsh vegetation and in soil samples (seed bank). Data taken from Pederson 1983.

Species	% Frequency in existing vegetation (1979)	% Frequency in the seed bank (1980)
Annuals		
Aster brachyactis	0	25
Atriplex patula	1	23
Chenopodium rubrum	11	65
Ranunculus sceleratus	18	53
Rumex maritimus	1	25
Emergent Perennials		
Carex atherodes	15	28
Phragmites communis	43	38
Scirpus acutus	26	8
Scirpus maritimus	0	22
Scirpus validus	0	74
Scholochloa festucacea	24	28
Typha spp.	34	91

Table 2 illustrates seed profiles of soil cores taken from a *Typha glauca* community in the Delta Marsh. Annuals *(Chenopodium rubrum, Ranunculus sceleratus, Rumex maritimus)* and certain perennials *(Scirpus validus, Scirpus maritimus)* all exhibited their highest seed densities in the lower sections (4–8 centimeter depth) of the soil cores. Conversely, largest seed accumulations of *Typha* spp. and *Zannichellia palustris* occurred in the upper 4 centimeters of the soil core. This seed distribution profile suggests the site was once much drier (large seed accumulations from annual species), then became wetter and was dominated by *Scirpus* spp. In recent history, there has been a diminished seed input from annuals, and *Typha* has replaced *Scirpus* as the dominant vegetation on the site. The sequence of seed accumulation in the upper soil profile suggests a recent period of relatively stable water levels in the Delta Marsh, which in fact has occurred.

Since 1961 water levels in Lake Manitoba (and the Delta Marsh) have been stabilized by water control structures (Manitoba Department of Mines, Resources, and Environmental Management 1974). Stable water levels for the last two decades have resulted in a decrease in plant diversity in the marsh (which is reflected in the seed banks—Tables 1 and 2), and an increase in the importance of certain perennials (particularly *Phragmites communis*, which now covers 75 percent of the marsh area occupied by emergent vegetation—Bossenmaier 1968).

Seed Banks and Marsh Management

Smith and Kadlec (1983) used seed bank data in conjunction with soil data to recommend management options for saline wetlands in Utah. They noticed that when seed bank samples were covered with a few centimeters of water, soil salinities were much lower than in the drawdown samples. The lower salinity permitted seeds of more species to germinate in the submersed samples than the drawdown samples. This information

Table 2. Mean number (m^{-2}) of seeds found in 2 cm layers of soil (4 depths) from soil cores of *Typha glauca* communities in the Delta Marsh, Manitoba. Data adapted from Table 1−5 in Pederson (1983).

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

prompted Smith and Kadlec to recommend drawdowns which maintained very shallow water levels. This type of drawdown would still provide food resources for waterfowl and shore birds, permit submerged species to be retained, and discourage establishment of nuisance vegetation such as *Tamarix pentandra* (Smith and Kadlec 1983).

Management implications (derived from seed bank information) for the Delta Marsh indicate that the restoration of fluctuating water levels in the marsh would allow a diverse flora to develop from the seed bank. Table 3 outlines several predicted successional sequences for an open water community in the Delta Marsh. Although these predictions were made from seed bank data, similar vegetation sequences (Walker 1959, 1965) occurred during the last "natural" fluctuation of water levels (1954—1964).

In addition, the absence of large numbers of seeds in soil samples from the large bays indicates these areas may remain unvegetated if completely drained for management purposes. The location of large seed banks in the shoreline zone implies that partial drawdowns are probably the best option for promoting emergent vegetation.

The relationship of fluctuating water levels to vegetation diversity has been 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 Lake Manitoba 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 (Fredrickson and Taylor 1982).

Summary

This paper has shown that seed bank studies can be used to provide information on plant life-histories, 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, irrigation schedules) for different types of wetlands (e.g., palustrine, lacustrine, riverine, saline) to develop the vegetation potential of seed reserves.

Table 3. Predicted successional sequences under different environmental regimes in a shallow, open water community in the Delta Marsh, Manitoba. Adapted from seed bank data in Table 1-1 of Pederson (1983).

Dominant genera[a] in seed bank	Genera present in vegetation under different environmental regimes			
	After prolonged flooding and muskrat activity	After drawdown	Reflooding after drawdown	After prolonged flooding
Aster	—	Aster	—	—
Atriplex	—	Atriplex	—	—
Chenopodium	—	Chenopodium	—	—
Utricularia	Utricularia	—	Utricularia	Utricularia
Zannichellia	Zannichellia	—	Zannichellia	Zannichellia
Scirpus	—	Scirpus	Scirpus	—
Scolochloa	—	Scolochloa	Scolochloa	—
Typha	—	Typha	Typha	Typha

[a] *Aster, Atriplex,* and *Chenopodium* are mud flat annuals; *Utricularia* and *Zannichellia* are submerged aquatics; *Scirpus* and *Scolochloa* are perennial emergents intolerant of prolonged flooding; *Typha* is a perennial emergent tolerant of prolonged flooding.

Acknowledgements

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