Vegetation Change in a Freshwater Wetland: A Test of *a priori* Predictions

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Abstract: We examined predictions about the vegetation composition of two experimental wetland cells when they were drawn down in 1983. Two approaches were used to make these predictions: extrapolations from vegetation maps and the van der Valk (1981) model of wetland vegetation dynamics. Both sets of data used to make these predictions were collected in 1980 before the emergent vegetation in the cells was destroyed by raising the water level to 1 m above normal. By comparing digitized vegetation maps from 1983 with those from 1980, we determined which vegetation types were present during the drawdown in areas dominated by different preflooding vegetation types. We predicted that each preflooding vegetation type would have only one corresponding drawdown vegetation type. Our prediction was wrong for three of the most widespread preflooding vegetation types. Areas dominated by each of these types in 1980 developed two different vegetation types during the drawdown. When both cells were considered together, the van der Valk (1981) model, which used the 1980 seed bank data as its primary input, predicted successfully all species that would be present during the 1983 drawdown with a density of one or more seedlings per 10 m^2. However, within an elevation range or within areas dominated in 1980 by a particular vegetation type, qualitative predictions were less reliable. Even when both cells were considered together, quantitative predictions of average seedling densities were generally too high for most emergent and wet meadow species and too low for most annuals. Within an elevation zone or preflooding vegetation type, discrepancies between predicted densities and actual densities were even larger. These discrepancies seemed to be due primarily to differences between environmental conditions in the field in 1983 and in the shelter where the seed bank study was done in 1980.

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INTRODUCTION

Ecologists often seem more concerned with the interpretation and explanation of phenomena or processes than with making predictions about their future states. This seems to be particularly true for community ecologists. Yet the ability to predict is one of the hallmarks of science. Successful predictions confirm that ecologists understand what controls community composition; unsuccessful predictions indicate that our ideas require revision.

The strongest type of prediction that can be used to test our understanding of a phenomenon or process is an *a priori* prediction (i.e., a prediction made prior to an independent study that tests the prediction). In many published ecological studies, it is difficult to determine whether the predictions or hypotheses examined were made before or after the study. *A posteriori* predictions or hypotheses obviously are of little, if any, value in establishing the reliability of concepts.

In this paper, we predicted the composition of vegetation (i.e., species and their densities) at a site after a major disturbance had eliminated the previous vegetation. Specifically, we examined the recolonization of freshwater wetlands during a drawdown after the emergent vegetation was destroyed by flooding. The destruction of all or most of the emergent vegetation by high water and/or muskrats in wetlands in the northern prairie region is a regular and well-documented phenomenon (Walker, 1959, 1965; Weller and Spatcher, 1965; Weller and Fredrickson, 1974; van der Valk and Davis, 1978). A drawdown, a period without standing water, is required to reestablish emergents in these wetlands (Walker, 1959, 1965; Harris and Marshall, 1963; Weller and Fredrickson, 1974; van der Valk and Davis, 1978).

Our objective was to evaluate how well the vegetation during a drawdown in a northern prairie wetland could be predicted using two different approaches: maps of preflooding vegetation and van der Valk's (1981) model of allogenic succession in wetlands. We conducted our study in an experimental marsh complex in the Delta Marsh, Manitoba, Canada. The emergent vegetation in the cells of this complex was eliminated by raising the water level by 1 m for 2 years. After this high water period, the cells were drawn down. We evaluated how well the vegetation during the first year of the drawdown (1983) was predicted using these two approaches and the preflooding data collected in 1980.

If the vegetation type that develops in an area during drawdown is a function of the previous type, then all that is needed to predict the drawdown vegetation type is a preflooding vegetation map. During drawdown, it is not likely that vegetation types will be similar in composition to preflooding vegetation types because of the presence of annuals (van der Valk and Davis, 1978). Thus all we could predict *a priori* was that each preflooding vegetation type would give rise to one distinct drawdown vegetation type. It was not possible to predict drawdown vegetation type.

In prairie wetlands nearly all of the recruitment of emergent species that occurs during drawdowns is from seed banks (van der Valk and Davis, 1978). A model to predict which species should become established on exposed mud flats in freshwater wetlands has been developed by van der Valk (1981). It predicts that mean seedling densities of species that will become established during a drawdown are equal to their mean densities in seed bank samples examined under drawdown conditions.

We used data from two contiguous cells specifically to examine how well preflooding vegetation maps can predict vegetation types during drawdown and how well the van der Valk (1981) model predicts the species densities (1) for two cells taken together, (2) for three elevation ranges within these cells, and (3) for areas dominated by different preflooding vegetation types. We examined predictions within elevation ranges and areas with different preflooding vegetation types because their seed banks were different (Pederson, 1983).

MATERIALS AND METHODS

Study Site

The Marsh Ecology Research Program (MERP) complex is located in the Delta Marsh in south-central Manitoba, Canada. The experimental complex consists of ten contiguous cells created by diking off a section of the Delta Marsh. Each experimental cell is rectangular and covers an area of approximately 5 ha. These cells are used to study the impact of cyclical changes in water levels on prairie wetlands (Batt et al., 1983; Murkin et al., 1985). During such a cycle, high water periodically eliminates most of the emergent vegetation, and a subsequent period of low water allows emergents to reestablish on exposed mud flats. The last such cycle in the Delta Marsh was described by Walker (1959, 1965). These cycles have since been eliminated because of water level controls imposed on Lake Manitoba in 1961 (Manitoba Department of Mines, Resources, and Environmental Management, 1974).

In 1980, when the seed bank sampling was done and aerial photographs were taken for the preflooding vegetation maps, the cells were connected to the main marsh. During the next 2 years, the cells were flooded 1 m above normal depth, killing most of the emergents. Emergents survived primarily in shallow water along the peripheries. Because areas within 10 m of peripheral dikes or ditches were not considered to be part of a cell, these surviving emergents were not sampled. In 1983, the cells were drawn down by pumping their water levels to 50 cm below normal.

The vegetation of the MERP complex was similar to that of the whole Delta Marsh. From the highest to the lowest elevation, it consisted of a series of bands: upland vegetation, *Scolochloa festucacea* or *Phragmites australis*, *Typha glauca*, *Scirpus lacustris* ssp. *glaucus*, and open water with submersed aquatics. The two cells chosen contained all the major vegetation types found in the complex. More detailed information on the vegetation of the Delta Marsh can be found in Walker (1959, 1965), Love and Love (1954), Pederson (1981, 1983), Pederson and van der Valk (1985), Shay and Shay (1986), Welling (1986), and van der Valk (1986).

Vegetation Maps

In August 1980 and 1983, false color infrared aerial photographs were taken of the experimental marsh complex from an elevation of 610 m above ground level with a 70-mm camera equipped with a 50-mm lens and a Wratten B and W orange 16 filter. The vegetation of both cells was mapped using 20-cm × 20-cm prints of each marsh. Each vegetation type that could be distinguished was investigated in the field and its dominant species recorded. Vegetation maps were drafted by the cartography section of Ducks Unlimited Canada in Winnipeg, Manitoba, and digitized by the Land Use Analysis Laboratory of Iowa Sate University. The smallest area or section that could be distinguished on the digitized vegetation maps was 3 m × 3 m. A topographic map with 10-cm contour intervals of each marsh was also digitized.

By combining information from the 1980 and 1983 vegetation maps, the vegetation transition in each 3-m × 3-m section of both cells was determined. A transition relates the vegetation type in a section in 1980 to the type present in the same section in 1983; e.g., *Phragmites* to *Phragmites* indicates that *Phragmites*-dominated vegetation occupied this section in both years. We predicted that for every vegetation type recognized in 1980, there would be a unique corresponding vegetation type in 1983 (i.e., every section with a particular vegetation type in 1980 would undergo the same vegetation transition). Vegetation transitions were examined within three elevation ranges or zones to determine if transitions were dependent on past environmental conditions (water regimes): Zone I, low elevations that are flooded when water levels are normal (<247.5 m AMSL); Zone II, mid-level elevations that are seasonally flooded (247.5 to 247.8 m); and Zone III, high elevations that are rarely flooded (>247.8 m). In 1980, Zone I was covered mostly with open water and *Typha* vegetation types; Zone II with *Typha* and *Phragmites*; and Zone III with *Phragmites* and upland. The number of sections (i.e., the area that underwent a particular vegetation transition in both cells) was calculated and expressed as a percentage of the total number of sections in a zone.

Seed Bank Sampling

In June 1980, seed bank samples were collected at 25 sites within each cell. These sites were selected using a stratified random design and their elevations were determined using a level transit. Each sample of a 30-cm × 30-cm × 5-cm block of soil was screened to remove all rhizomes, tubers, and large pieces of litter and was placed in a shallow plastic flat. These flats were placed in an outdoor shelter in a randomized design and watered with well water daily to keep the surface of the samples moist. From June through September, seedlings were counted and removed as soon as they could be identified. Voucher specimens for all species were deposited in the herbarium of the Delta Waterfowl and Wetlands Research Station. The nomenclature is based on Scoggan (1978-1979).

The elevation range over which seed bank samples were collected was divided into three zones similar to those used with the vegetation maps, except that the boundary between Zone I and II is set at 247.4 m AMSL.

Permanent Plots

Ten permanent, 2-m × 2-m plots were located in a stratified random design in each cell in June 1983. Each plot was divided into four triangular quadrats by stringing wire diagonally between the opposite corner posts and around its perimeter. The number of seedlings or shoots of each species was counted in the northern and southern quadrats during June, July, and August 1983. The elevation of each permanent plot was obtained using a level transit, and the type of vegetation that dominated the plots prior to the high water years was determined by examining the remaining standing and fallen litter. Litter of all the emergent species in the cells was still present in large quantities after 2 years of flooding (van der Valk, 1986).

RESULTS

Predictions from Vegetation Maps

In 1980, there were seven vegetation types in the cells that occupied 97, 95, and 100% of the area in elevation Zones I, II, and III, respectively (Table 1). Three of these seven types (open water, *Scirpus lacustris* spp., and

TABLE 1

Vegetation Transitions from 1980 (Preflooding) to 1983 (Drawdown) in Three Elevation Zones*

Vegetation transition		
Vegetation 1980	Vegetation 1983	Relative area, %
	Zone 1 (<247.5 m AMSL)	
Open water	No vegetation	24
Open water	Annuals	16
Typha	Annuals	47
Scirpus	Annuals	8
Scirpus	No vegetation	2
Other transitions		3
	Zone II (247.5 m to 247.8 m)	
Carex	Annuals	16
Phragmites	Annuals	20
Phragmites	*Phragmites*	2
Scolochloa	Annuals	14
Typha	Annuals	43
Other transitions		5
	Zone III (>247.8 m)	
Carex	Annuals	19
Phragmites	Annuals	28
Phragmites	*Phragmites*	31
Upland	*Phragmites*	22

*The results are expressed as the percent of the area of each zone in which a transition occurred.

Phragmites) underwent two vegetation transitions. Areas covered by six vegetation types in 1980 had the same vegetation type in 1983 (annuals). Vegetation types found in two elevation zones (*Typha, Carex,* and *Phragmites*) underwent the same transitions in each zone.

Predictions from Model

All 18 species predicted to occur in these cells were found in 1983 (Table 2). Actual seedling densities, however, often differed from predicted densities, and were one order of magnitude lower or higher for 6 of the 18 species.

TABLE 2

Predicted and Actual Mean Seedling Densities (per 10 m^2) During the Drawdown in 1983 in Both Experimental Cells

Species	Predicted density, n=50	Actual density, n=20
	Emergents	
Scirpus lacustris	2500	730
Typha glauca	4200	780
Scolochloa festucacea	170	64
Phragmites australis	42	5
Scirpus maritimus	25	8
Carex atherodes	75	770
	Annuals	
Atriplex patula	33	7000
Aster laurentius	25	47
Chenopodium rubrum	83	360
Ranunculus sceleratus	250	27
Rumex maritimus	330	28
	Wet meadow perennials	
Lycopus asper	75	1
Mentha arvensis	83	2
Stachys palustris and *Teucrium canadense*	33	72
Sonchus arvensis	17	15
Cirsium arvense	49	13
Urtica dioica	17	59

When predictions were made for a particular elevation zone, they were even less reliable (Table 3). In Zone I, only five species were predicted, but nine were found, including five annuals, none of which were predicted. In Zone II, 16 species were predicted. All 16 were found, plus one additional species. Fifteen species were predicted in Zone III, but only nine were actually found, plus one species not predicted.

Predictions of mean seedling density are less accurate within an elevation zone than for the cells overall (Tables 2 and 3). The mean total seedling density predicted for both cells is 8000 seedlings per 10 m^2; it was 10,000 seedlings per 10 m^2, i.e., 25% higher than predicted. In Zones I, II, and III, actual mean total seedling densities were 100% higher, 400% lower, and 1300% higher, respectively, than predicted.

Qualitative predictions made for areas with the same vegetation type in 1980 were not as reliable as those for the cells overall (Tables 2 and 4). In

TABLE 3

Predicted and Actual Mean Seedling Densities (per 10 m^2) in Three Elevation Zones During the 1983 Drawdown*

Species	Zone I Pred., n=16	Zone I Act., n=8	Zone II Pred., n=27	Zone II Act., n=9	Zone III Pred., n=7	Zone III Act., n=3
Emergents						
Scirpus lacustris	850	520	4,000	820	180	1,000
Typha glauca	400	1,800	7,200	86	860	0
Scolochloa festucacea	0	0	290	130	0	47
Phragmites australis	16	3	31	8	150	0
Scirpus maritimus	16	18	40	1	0	0
Carex atherodes	0	0	100	1,700	130	0
Annuals						
Atriplex patula	0	1	46	42	83	47,000
Aster laurentius	0	14	19	80	83	33
Chenopodium rubrum	0	260	1,300	520	840	150
Ranunculus sceleratus	0	3	430	57	240	0
Rumex maritimus	0	6	430	56	240	0
Wet meadow perennials						
Lycopus asper	0	0	140	2	12	0
Mentha arvensis	0	0	86	2	240	3
Stachys palustris and *Teucrium canadense*	0	0	28	10	150	450
Sonchus arvensis	0	0	9	29	110	13
Cirsium arvense	0	0	0	4	350	73
Urtica dioica	5	0	6	11	71	360

*Elevation Zone I is <247.4 m AMSL; Zone II is 247.4 to 247.8 m; and Zone III is >247.8 m.

former open water areas, five species were predicted to occur, but only three of these were found. One species not predicted was also found. In former *Typha* areas, nine species were predicted: all of these were found, plus eight more. Thirteen species were predicted in former *Scolochloa* areas: 11 were found, plus three more that were not predicted.

Quantitative predictions of seedling densities within areas dominated in 1980 by a particular vegetation type were also much poorer than those made for both cells (Tables 2 and 4). Actual mean total seedling densities in areas that were formerly open water, *Typha*, and *Scolochloa* are 400% lower, 100% lower, and 100% higher, respectively, than predicted densities.

DISCUSSION

Predictions from Vegetation Maps

Contrary to our *a priori* predictions made from the 1980 vegetation maps, all areas with a given vegetation type did not have the same vegetation type in 1983 (Table 1). Most of the vegetation types mapped in 1983 were dom-

TABLE 4

Predicted and Actual Mean Seedling Densities (per 10 m²) During the Drawdown in 1983 in Areas with Three Different Vegetation Types in 1980

	Vegetation type in 1980					
	Open water		*Typha*		*Scolochloa*	
Species	Pred., n=13	Act., n=3	Pred., n=9	Act., n=11	Pred., n=6	Act., n=3
			Emergents			
Scirpus lacustris	730	100	4,300	680	2,100	1,000
Typha glauca	370	27	14,000	320	850	0
Scolochloa festucacea	0	0	65	77	0	140
Phragmites australis	19	0	28	7	28	3
Scirpus maritimus	19	47	83	4	0	0
Carex atherodes	0	0	0	93	290	4,800
			Annuals			
Atriplex patula	0	0	9	30	28	47,000
Aster laurentius	0	0	0	67	69	63
Chenopodium rubrum	0	100	1,500	470	550	400
Ranunculus sceleratus	0	0	460	40	600	30
Rumex maritimus	0	0	460	47	600	3
			Wet meadow perennials			
Lycopus asper	0	0	0	1	180	3
Mentha arvensis	0	0	0	2	110	0
Stachys palustris and *Teucrium canadense*	0	0	0	6	42	350
Sonchus arvensis	0	0	0	5	41	80
Cirsium arvense	0	0	0	3	0	73
Urtica dioica	1	0	0	8	0	210

inated by annuals, and it was unclear which of the emergent species would eventually dominate. For example, it was not clear whether former *Typha* stands would consistently become *Typha* stands again or if they would become *Phragmites* or *Scolochloa* stands. Areas formerly dominated by *Typha* had a higher average density of *Typha* seedlings in 1983 than seedlings of most other emergents, but seedlings of *Scolochloa* and *Phragmites* were also present (Table 4). Although 1980 vegetation maps were not very useful in predicting what type of vegetation would develop in a particular area during the drawdown, they might prove to be more reliable predictors after the marshes are reflooded when the vegetation will be dominated by emergents again.

Predictions from Model

The van der Valk (1981) model, using data obtained primarily from seed bank studies prior to drawdown, predicted all the species that would be recruited with a density of more than one seedling per 10 m² during a drawdown. The model also predicted which emergent species would have the highest seedling densities in the cells, but it was less successful in predicting the densities of annuals (Table 2).

The composition of the vegetation was predicted to vary among elevation zones and this occurred (Table 3). Likewise, areas dominated by different vegetation types in 1980 were predicted to differ in composition following drawdown, and this was found to be the case (Table 4). However, predictions within an elevation zone or former vegetation type were less reliable, perhaps due to an inadequate number of samples in some instances. These predictions were made on the basis of very few seed bank samples, as few as three in the most extreme case. Likewise, as few as three permanent quadrats were used to estimate actual seedling densities in 1983.

There is also an indication, however, that some of the errors in predicting which species would be present at a given elevation range are due to differences in the composition of the seed bank between 1980 and 1983. At the lowest elevation range in 1983, five species of annuals were found and none of them were predicted to occur. In the next highest elevation range, these annuals were found in high densities and predicted to be there. As the water receded in 1983, seeds of these annuals may have been transported into the lower elevation range from above. This pattern is consistent with data collected by Smith (1983) on the movement of seed by water currents within a Utah marsh.

The disparity between predicted and actual densities is not due simply to inadequate sample size (Welling, 1986). Seed bank samples were exposed to a particular set of environmental conditions in the shelters in 1980 that differed from those on the exposed mud flats, particularly soil temperatures and soil moisture levels. Seed germination of emergents and annuals in these marshes is influenced by temperature regime (Galinato, 1985; Galinato and van der Valk, 1986). Differences in soil moisture (Harris and Marshall, 1963) and salinity (Galinato and van der Valk, 1986) also can have an impact on seed germination percentages of each of these species and on their recruitment from the seed bank. It seems that soil moisture conditions in the seed bank study favored the germination of seeds of emergents as compared to conditions in the field in 1983 which were more favorable for the germination of seeds of annuals.

The way the seed bank samples were handled could also influence the seedling densities. These samples were disturbed whenever seedlings were removed during the summer. This kept their surfaces more open than in the field and could have favored the recruitment of emergents (Meredith, 1985). Another factor not taken into account in seed bank studies is the presence of litter in the field which significantly reduced seedling recruitment in 1983 (van der Valk, 1986).

The van der Valk model also was tested by Smith and Kadlec (1985) in a saline marsh in Utah. They found that the model applied poorly to areas dominated by different emergent species. The original model, however, cannot be used in saline wetlands, since the impact of salinity on seed germination is not considered. The model can be easily adapted to saline wetlands if this information is available (Galinato and van der Valk, 1986). When the model is applied to freshwater wetlands, as in our study, it makes quite accurate qualitative predictions but unreliable quantitative predictions.

The failure of our quantitative predictions indicates that additional information is needed. By exposing seed bank samples to a greater range of relevant environmental conditions, it should be possible to improve the accuracy of quantitative predictions. Because it is impossible to predict *a priori* environmental conditions during a future drawdown, seed bank studies should concentrate on the impact of the potential range of environmental conditions (soil moisture, temperature, salinity, and so forth) that will be found in the field on recruitment from the seed bank for each species.

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