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ASSESSING THE IMPACTS OF AN INCREASE IN WATER LEVEL ON WETLAND VEGETATION[1]

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Abstract. Three different approaches for assessing the impact of a permanent increase in water level on wetland vegetation were studied using a long-term, controlled, and replicated experiment. These three approaches were: (1) digitized vegetation maps derived from aerial photographs; (2) vegetation data (species abundance, species diversity) from 10 permanent quadrats in each cell; and (3) Bray–Curtis similarity indices comparing the composition of the vegetation in permanent quadrats within a cell and among cells. This study was conducted in a 10-celled wetland complex in the Delta Marsh, Manitoba, Canada. There were three water level treatments: (1) the normal or mean regulated water level in the surrounding Delta Marsh, (2) the medium (30 cm above normal), and (3) the high (60 cm above normal). There were four, three, and three cells (ranging in total area from 6 to 8 ha), respectively, in each treatment. The vegetation in all cells had been reestablished with a drawdown just prior to this study. To reduce cell-to-cell variation, we adjusted the indicators derived from vegetation maps from 1985 through 1989 by subtracting the mean values of the same indicators in 1979 and 1980, after 15–16 yr of normal water level conditions. The adjusted percentage of a cell covered with open water increased significantly and two other adjusted indicators, the number of vegetation types and the number of multispecies vegetation types, decreased significantly in the flooded treatments. The percentage of a cell covered with sparse emergent vegetation and percentage covered with standing litter did not differ significantly among treatments. In permanent quadrats, species richness, total shoot density of the emergent species, and the Shannon diversity index showed significant treatment effects: all three declined in the flooded treatments. The Simpson's index, however, did not show a treatment effect. When Bray–Curtis similarity indices comparing the vegetation either among permanent quadrats within a cell or for the same permanent quadrat in a cell among years were used, either within-cell vegetation heterogeneity or ongoing successional changes in the vegetation made it impossible to detect treatment effects.

Key words: Delta Marsh; emergent vegetation; flooding; freshwater wetlands; prairie wetlands; similarity indices; species diversity.

INTRODUCTION

Many factors can confuse, confound, or invalidate studies of the impact of a disturbance on the composition and structure of vegetation, including: (1) local differences or site characteristics (e.g., the percentage of an area at a certain elevation or with a certain soil type); (2) the number and complexity of the environmental gradients (e.g., soil fertility, soil moisture, or elevation gradients); and (3) succession. The most reliable method for coping with these confounding factors in impact studies is a controlled, replicated experiment with suitable temporal and spatial controls (Green 1979, Westman 1985, Eberhardt and Thomas 1991). There have been, however, very few field impact studies that have used a controlled, replicated experimental design. Two other crucial features of impact studies are the suitability of the approaches used to detect an impact and the suitability of the different measures that are used to determine the composition and structure of vegetation. Our study is unique in that it used a controlled experiment to assess both the utility and the reliability or robustness of three common approaches (vegetation maps, vegetation data collected in permanent quadrats, and similarity indices) and several associated vegetation measures or indicators for detecting the impact of a permanent water level increase on wetland vegetation undergoing succession.

The distribution of species and plant communities within a wetland is primarily a function of water depth (Spence 1982). A long-term change in water level, particularly an increase, can result in dramatic changes in wetland vegetation. Species, communities and, in extreme cases, nearly all emergent vegetation can be eliminated (Millar 1973, van der Valk 1981,1991, Sjoberg and Danell 1983, Bukata et al. 1988, Wallsten and Forsgren 1989). With the exception of experimental studies of individual wetland species (e.g., Lieffers and

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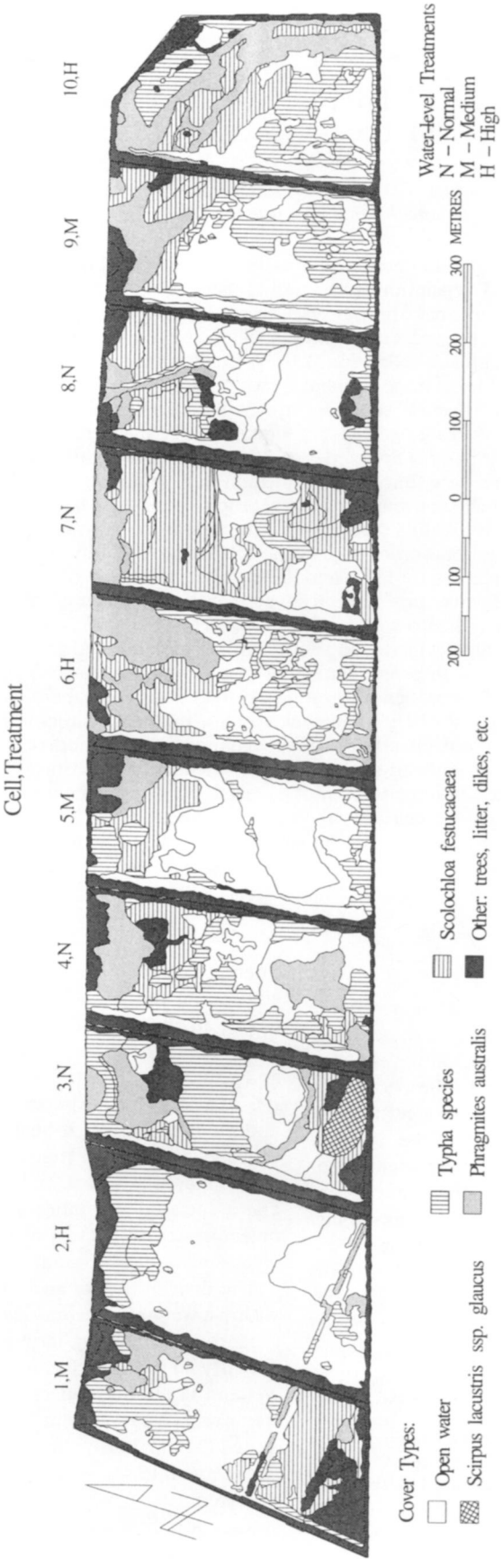

FIG. 1. The major vegetation classes in the 10 cells of the MERP complex in 1987. Cells are numbered in order from west to east. Flooding treatments were randomly assigned.

Shay 1981, Squires and van der Valk 1992), available information on the impact of an increase in water level on wetland vegetation is based primarily on field observation of natural or man-made water level changes (Millar 1973, van der Valk and Davis 1978) or of water level changes in reservoirs (Dudgeon 1983, Nilsson and Keddy 1988).

Specifically, we monitored the vegetation in 10 cells in the experimental wetland complex of the Marsh Ecology Research Program (MERP) in which water levels were kept at normal and 30 or 60 cm above normal for five consecutive years. The emergent vegetation in all cells in the MERP complex had been eradicated by flooding the cells to 1 m above normal, and it was reestablished during a 1- or 2-yr drawdown prior to this study (Murkin and Murkin 1989). Thus, the vegetation in all three treatments was in an early successional stage at the start of the study. Because the marsh complex was created by diking a part of the Delta Marsh, each cell has a unique basin morphometry. Nevertheless, all cells contain about the same elevation range and initially had the same vegetation types.

Three approaches were used to assess the impact of raising water levels on the vegetation: (1) vegetation maps that were digitized and analyzed using a geographic information system, (2) vegetation data from 10 permanent quadrats in each cell, and (3) similarity indices that were used to compare the overall composition of vegetation among permanent quadrats within a cell in a given year and among years for each quadrat.

Study Site

The 10 cells of the Marsh Ecology Research Program (MERP) were constructed in 1979 within the Delta Marsh, Manitoba, Canada (50°11′ N, 98°19′ W). These 10 rectangular cells are contiguous (Fig. 1), and each had a total area of 6–8 ha. Their northern boundary is the sand ridge that separates the Delta Marsh from Lake Manitoba, and their other three boundaries are dikes. Their long axes run north–south, i.e., perpendicular to the sand ridge (Fig. 1). Each cell is equipped with a water control structure and an electric pump, which were used to maintain water levels at the designated treatment level for a cell during the experiment. Additional information about the MERP cells can be found in Murkin et al. (1985) and Murkin and Murkin (1989).

Each cell encompasses the entire elevation gradient (≈1.5 m) and, when constructed, had all of the major vegetation zones found in the Delta Marsh. In 1979 and 1980, the uppermost zone, the upland zone, was dominated by a mixture of terrestrial grasses and forbs and in some cells contained patches of trees. This zone normally was not flooded except during wet years. The grasses *Scolochloa festucacea* and *Phragmites australis* dominated the next two zones. Both of these monodominant zones were normally inundated in the spring. Monodominant zones of *Typha glauca* and *Scirpus lacustris* ssp. *glaucus* dominated the lower end of the emergent zone. These two zones were normally flooded all year, except for the upper end of the *Typha* zone, which was flooded only during the early part of the growing season. At the lowest elevations in the cells, the vegetation was dominated by a mixture of submersed species with *Potamogeton pectinatus* usually the most abundant. On the vegetation maps, this last zone is designated open water. Additional information on the vegetation in the Delta Marsh can be found in Walker (1959, 1965) and on the vegetation in the MERP cells can be found in Welling et al. (1988*a*, *b*), van der Valk and Welling (1988) and van der Valk et al. (1989). Nomenclature follows Scoggan (1978–1979).

Water levels in Lake Manitoba and the Delta Marsh, which is connected to Lake Manitoba by several channels, have been regulated by dams on Lake Manitoba since the early 1960s. Since that time, the mean water level in the marsh has been at an elevation of ≈247.5 m, designated the normal water level hereafter. Prior to the regulation of water levels, the lake and adjacent marsh had undergone cyclical changes in water levels over a period of ≈20 yr in response to changes in annual precipitation (Walker 1959, 1965). During wet years, water levels rose to 248.5 m and, during dry years, dropped to 247.0 m (Anonymous 1974).

Methods

Experimental design

All the MERP cells were flooded to 1 m above normal (i.e., 248.5 m) for 2 yr to simulate high water conditions during wet years and then were drawn down to 0.5 m below normal (i.e., 247.0 m) for 1 or 2 yr. In each cell, the existing upland and emergent vegetation was killed during the flooded years and new vegetation recruited from the seed bank during the drawdown years (Welling et al. 1988*a*, *b*). Because there is almost no recruitment of emergent species during the 2nd yr of a drawdown (Welling et al. 1988*b*), cells with a 1-yr and a 2-yr drawdown had similar vegetation in 1985. In our analyses, the two cells with a 1-yr drawdown (cells 3 and 7), which were both in the normal water level treatment, have been lumped with the two other cells (cells 4 and 8) in the normal water level treatment.

In 1985, at the end of the drawdowns, the cells were reflooded to one of three water depths: the mean regulated water level in the Delta Marsh (247.5 m), designated the normal treatment; 30 cm above normal (247.8 m), the medium treatment; and 60 cm above normal (248.1 m), the high treatment. There were four cells in the normal treatment (cells 3, 4 ,7, and 8) and three in the medium (cells 1, 5, and 9) and high (cells 2, 6, and 10) treatments. Reflooding treatments were assigned randomly (Fig. 1). The water level in each cell was kept at the appropriate level by pumping water

from the surrounding marsh into the cell as needed. These water level treatments were maintained for 5 yr (1985–1989).

Vegetation maps

Each August, false-color, infrared aerial photographs were taken at an altitude of 610 m above the ground with a 70-mm camera equipped with a 50-mm lens and a Wratten B and W orange 16 filter. The film used was Kodak 2443 Infrared (ASA 100). Each year all vegetation types in a cell were first delimited on a 20 × 20 cm color print of the aerial photograph of that cell. Each vegetation type in each cell was checked in the field to determine its dominant species and/or other features (standing litter, algal mats, open water, etc.). Vegetation maps of each cell were drafted by the Cartography Division of Ducks Unlimited Canada, Winnipeg, Manitoba. These vegetation maps were corrected for distortion, placed in a relative coordinate system, and digitized using a Data Copy scanner and Word Image Processing System (Version 1.70) software.

The areas of all vegetation types in a cell were determined using ISOIL software developed by the Land Use Analysis Laboratory of Iowa State University (Beavers 1991). Five potential vegetation indicators derived from the digitized vegetation maps were investigated. Three of these are structural indicators that indicate how much emergent plant cover or standing litter are present in a cell: (1) area covered with open water, i.e., completely free of emergent vegetation or standing litter; (2) area covered with sparse emergent vegetation, i.e., where the emergent plant cover was $<50\%$; and (3) area covered by standing litter. The other two are vegetation diversity indicators: (1) total number of vegetation types and (2) number of multispecies vegetation types, i.e., dominated by two or more species. Areas within 5 m of the periphery of each cell were excluded in our analyses of the vegetation maps to avoid sampling areas disturbed when the cells were constructed. To adjust for these cell-to-cell differences in basin morphometry, the mean values for the five indicators in 1979 and 1980 were subtracted from their corresponding 1985–1989 values. The adjusted indicators were analyzed using a two-way analysis of variance with repeated measures (Ott 1988).

All statistical analyses were done using the SAS GLM procedure (SAS 1989). Conservative degrees of freedom were used for all F tests involving repeated measures (Geisser and Greenhouse 1958). Because there are correlations among successive measurements made on the same cell (i.e., the time treatment [year] could not be randomized), correlations among successive measurements result in a distribution of F values that is flatter than that found in standard tables. To remove this bias, the degrees of freedom used in the analysis of variance of repeated measures effects can be adjusted in a variety of ways (Ott 1988). In our analyses, we divided by the degrees of freedom for all effects involving repeated measures by the degrees of freedom for years. These conservative degrees of freedom reduce the probability that calculated F values exceed the values in standard tables. Because the adjustment that we made in degrees of freedom is the most extreme that is normally used in a repeated-measures ANOVA, our statistical analyses were very conservative, and only strong treatment effects would be found significant. Since this is a comparative study of ways of assessing impacts, a conservative analysis made it possible to determine what were the best approaches for detecting, and the most robust indicators of, flooding impacts. All tests of significance were done at the 0.05 level.

Vegetation data

Permanent quadrats were established in each cell during the drawdown period. Each cell was divided into five equal zones from north to south, and two permanent quadrats were randomly placed in each zone. This stratified-random-sampling regime was used to ensure that the elevation gradient in each cell was adequately sampled. No permanent quadrats were placed within 5 m of the edge of a cell. Permanent quadrats were 2 × 2 m and were divided into four triangular 1-m^2 subquadrats by running a wire around the edges and along the diagonals of the quadrat. This permanent-quadrat design was chosen because it minimized damage to the vegetation inside the two sampled subquadrats (because two of their sides were adjacent to unsampled subquadrats). Each July from 1985 to 1989, the number of shoots of each emergent species was counted in the northern and southern triangular subquadrats of each permanent quadrat, and the percentage cover of each submersed and free-floating species was also estimated using the cover–abundance scale in van der Valk and Davis (1978). Thus, an area of 2 m^2 was sampled in each permanent quadrat, and all species diversity, shoot density, and shoot cover data are presented on a 2-m^2 basis.

In permanent quadrats, four indicators were examined: species richness, total shoot density or cover, Shannon's index, and Simpson's index. Diversity indices for the emergent and submersed species in each quadrat were calculated separately because we expected emergent and submersed species to respond differently to an increase in water level.

In the statistical analysis of vegetation indicators derived from permanent quadrat data, cells were the experimental units because water level treatments were randomized at this level. Within each cell there were five zones that covered the elevation gradient. These zones were treated as subplots. Thus, the experiment had a split-plot design with repeated measures. The GLM procedure in SAS was used to calculate the ANOVAs. Emergent and submersed vegetation data were analyzed separately. Conservative degrees of freedom

TABLE 1. Two-way, unbalanced ANOVA model with repeated measures used to test for water level treatment (TRT), cell (CL), and year (YR) effects for five variables from the vegetation map data and for the within-year Bray–Curtis (BC) similarity index values. *F* values are given except for the CL(TRT) and YR × CL(TRT) treatment effects, for which mean squares are given. Degrees of freedom (df) in parentheses are conservative degrees of freedom (defined in *Methods: Vegetation maps*) used for *F* tests involving repeated measures.

Source	df	Open water (%)	Sparse cover (%)	Litter cover (%)	Total veget. types†	Multispecies types†	BC index‡
TRT	2	13.3*	3.8	1.8	14.0*	46.6*	3.3
CL(TRT)	7	337	135	131	43.9	14.3	0.013
YR	(1)	12.9*	4.6	3.9	4.4	5.4*	5.8*
YR × TRT	(2)	1.5	0.9	1.9	1.2	1.9	0.4
YR × CL(TRT)	(7)	149	120	20.9	14.1	12.8	0.0021

* *F* value greater than expected when $\alpha = 0.05$.
† Total number of vegetation types or number of multispecies vegetation types in a cell.
‡ Within-year BC similarity index.

(Geisser and Greenhouse 1958) were used for all *F* tests involving repeated measures.

Similarity indices

Euclidean distance, relative Euclidean distance, and Bray–Curtis similarity indices (Ludwig and Reynolds 1988) were calculated for the emergent vegetation in permanent quadrats within a cell or among cells. These similarity indices gave nearly identical results, and only the Bray and Curtis index values have been included. All similarity indices were calculated using SAS and the formulae in Ludwig and Reynolds (1988). Similarity index data were analyzed in two ways.

First, Bray–Curtis similarity indices were calculated comparing all permanent quadrats within a cell. These are designated as the within-year similarity values. The half matrix of similarity values generated by comparing each permanent quadrat with every other permanent quadrat in a cell contained 45 entries. The mean of these 45 Bray–Curtis similarity values and their frequency distribution was used to characterize the uniformity of the vegetation in a cell in a given year and for the entire cell among years. A two-way analysis of variance with repeated measures was used to analyze these means (Table 1). This is the same ANOVA model used to analyze the vegetation maps.

Second, Bray–Curtis similarity indices were calculated comparing the composition of the emergent vegetation in each permanent quadrat in 1985 with that in the same quadrat in 1986, 1987, 1988, and 1989. These are designated the among-year similarity values. These Bray–Curtis indices were calculated using SAS and analyzed using a split-plot with repeated measures model with the GLM procedure in SAS. This is the same ANOVA model used for the analyses of the vegetation data.

RESULTS

Vegetation maps

Of the three structural measures of the state of the vegetation (adjusted percentage of a cell covered with open water, litter, or sparse emergent vegetation) obtained from the vegetation maps, only the percentage of a cell covered with open water showed a statistically significant treatment effect (Table 1). It was not until the 3rd yr of flooding (1987) that the amount of open water in the medium and high treatment cells was significantly greater than in the normal treatment cells. By 1989, cells in the medium and high treatment had ≈40% more area covered with open water than cells in the normal treatment (Table 2).

Both the adjusted total number of vegetation types and the adjusted number of multispecies vegetation types showed a significant treatment effect (Table 1). By 1989, both were highest in the normal treatment (Table 3). The mean adjusted total number of vegetation types and mean adjusted number of multispecies

TABLE 2. Mean adjusted* percentage of a wetland cell covered with open water, litter, or sparse emergent vegetation on vegetation maps of cells in the normal ($n = 4$), medium ($n = 3$), and high water level ($n = 3$) treatments from 1985 through 1989.

Treatment	1985	1986	1987	1989	1989	Mean
			Open water			
Normal	−14	−13	−6.6	−6.1	2.4	−7.5
Medium	−3.7	−4.0	16	29	44	16
High	5.3	2.7	29	37	40	23
Mean	−5.1	−5.7	11	17	26	8.6
			Litter			
Normal	−2.1	−2.0	0.3	−1.8	0.3	−1.1
Medium	−0.3	−0.3	14	12	5.3	6.2
High	3.5	0.8	4.3	4.3	3.8	3.4
Mean	0.1	−0.7	5.6	4.3	2.9	2.4
			Sparse emergent vegetation			
Normal	2.3	0.8	23	17	11	11
Medium	15	11	38	28	14	21
High	8.0	13	13	14	14	13
Mean	7.9	7.5	25	19	13	14

* Values were adjusted by subtracting the percentage of a cell covered by open water, litter, or sparse emergent vegetation in 1980 from their values in 1985–1989.

TABLE 3. Mean adjusted* number of vegetation types and multispecies vegetation types, i.e., with two or more co-dominants, that were visible on vegetation maps of wetland cells in the normal ($n = 4$), medium ($n = 3$), and high water level ($n = 3$) treatments from 1985 through 1989.

Treatment	1985	1986	1987	1988	1989	Mean
Total number of vegetation types						
Normal	8.3	6.3	12	17	7.8	10
Medium	1.3	−1.3	2.7	2.7	0.7	0.9
High	−0.3	−0.3	1.7	−0.3	−2.3	−0.3
Mean	3.6	2.0	6.2	7.6	2.2	4.3
Number of multispecies vegetation types						
Normal	8.5	10	17	22	12	14
Medium	1.7	0.0	4.7	4.7	1.7	2.5
High	3.3	5.0	6.0	4.7	2.0	4.2
Mean	4.9	5.6	9.9	11	5.9	7.5

* Values were adjusted by subtracting either the number of vegetation types or multispecies vegetation types in 1980 from their values in 1985–1989.

TABLE 5. Mean number of emergent species and submersed and free-floating species in vegetation data collected in permanent quadrats (2 m²) in the normal ($n = 40$), medium ($n = 30$), and high ($n = 30$) water level treatments from 1985 through 1989.

Treatment	1985	1986	1987	1988	1989	Mean
Emergent species						
Normal	7.3	5.5	3.6	4.1	3.6	4.8
Medium	5.8	4.1	2.5	2.1	1.9	3.3
High	4.7	3.0	1.5	0.9	0.9	2.2
Mean	6.1	4.3	2.6	2.6	2.3	3.6
Submersed and free-floating species						
Normal	0.6	1.3	1.5	1.3	1.3	1.2
Medium	0.4	1.9	2.0	1.8	1.7	1.5
High	0.5	2.3	2.4	2.6	2.4	2.0
Mean	0.5	1.8	1.9	1.8	1.8	1.5

types declined in the 1st yr of flooding in the medium and high treatments and changed little after that.

Vegetation data

The results of the ANOVAs for the diversity indices are summarized in Table 4. Mean species richness (Table 5), shoot density (Table 6), and Shannon's index (Table 7) of emergent vegetation were all significantly lower in the medium and high water level treatments than in the normal treatment (Table 4). In all three treatments, there was a significant year effect (Table 4). There was no treatment or year effect for the Simpson's index (Tables 4 and 8).

Although for submersed and free-floating species there was no treatment effect for the number of species (Table 4), there was a treatment effect for total cover and Shannon's index. Both were lower in the medium and high water level treatments (Tables 6 and 7). There was a year effect for species richness (Tables 4 and 5), total cover (Tables 4 and 6), and Shannon's index (Tables 4 and 7). The mean number of species doubled from 1985 to 1986, but did not change significantly in subsequent years in any treatment (Table 5). As with the emergent vegetation, Simpson's index was unaffected by the water level treatments. There was, however, a year effect (Tables 4 and 8).

With the exception of emergent species richness, which declined with distance from the northern boundary, i.e., with increasing water depth, there was no statistically significant zone effect for any other emer-

TABLE 4. Split-plot, unbalanced ANOVA model with repeated measures¶ used to test for water level treatment (TRT) main-plot, cell (CL), zone (ZN) split-plot, and year (YR) effects used to analyze emergent and submersed vegetation data and the among-year Bray–Curtis (BC) similarity indices for emergent vegetation. F values are given except for the CL(TRT), CL × ZN(TRT), CL × YR(TRT), and CL × ZN × YR(TRT) treatment effects, for which mean squares are given.

Source of variation	df	Emergent vegetation: Total shoot density	Number of species	H† index	S‡ index	Among-year BC index§	Submersed and free-floating: Total shoot cover	Number of species	H† index	S‡ index
TRT	2	4.9*	16.6*	6.8*	2.6	0.2	6.0*	3.3	12.1*	0.7
CL(TRT)	7	94,427	8.81	0.26	0.19	0.14	34,356	4.75	0.19	0.29
ZN	4	1.4	3.8*	1.4	0.7	4.4*	0.6	1.7	2.6	1.6
TRT × ZN	8	1.7	1.9	1.1	1.1	0.2	1.0	1.3	0.7	1.7
CL × ZN(TRT)	28	46,441	5.88	0.36	0.089	0.60	12,624	1.79	0.19	0.18
YR	(1)	13.9*	103.5*	42.0*	2.3	44.4*	16.0*	19.7*	5.7*	12.5*
TRT × YR	(2)	0.4	0.7	0.7	0.9	0.8	3.7	1.5	2.3	0.8
CL × YR(TRT)	(7)	20,079	34.9	0.06	0.069	0.23	8,381	0.88	0.13	0.094
ZN × YR	(4)	2.9*	0.8	1.2	1.9	1.0	0.7	1.1	0.6	1.3
TRT × ZN × YR	(8)	0.9	0.7	0.6	0.7	0.9	0.7	0.8	1.0	1.4
CL × ZN × YR(TRT)	(28)	9,865	104	0.05	0.034	0.014	4,171	0.33	0.58	0.11

* F value is greater than expected when $\alpha = 0.05$.
† H = Shannon's diversity index.
‡ S = Simpson diversity index.
§ Among-year Bray–Curtis (BC) similarity index.
¶ Conservative degrees of freedom (defined in *Methods: Vegetation maps*), indicated by parentheses, were used for F tests involving repeated measures.

TABLE 6. Mean total shoot density of emergent and mean total percentage cover of submersed and free-floating species in the vegetation data collected in permanent quadrats (2 m^2) in the normal (n = 40), medium (n = 30), and high (n = 30) water level treatments from 1985 through 1989.

Treatment	1985	1986	1987	1988	1989	Mean
Total shoot density of emergent species						
Normal	310	370	200	240	200	260
Medium	280	260	140	140	120	190
High	220	190	68	58	46	120
Mean	280	280	140	150	130	200
Total cover of submersed and free-floating species						
Normal	13	26	63	74	44	44
Medium	5	58	110	140	86	80
High	10	72	130	200	175	120
Mean	10	49	99	130	96	77

gent or any submersed community characteristic examined.

Similarity indices

The mean within-year Bray–Curtis similarity index (Table 9) for a cell showed no treatment effect, but did show a year effect (Table 1). The percentage frequency distribution of Bray–Curtis indices within cells indicates that the number of times this index was <0.1 (usually 0) increased in all three treatments from 1985 to 1989. By 1989, 80% or more of the index values in the medium and high treatments were <0.1, vs. ≈60% in the normal treatment.

The mean among-year Bray–Curtis similarity index values (Table 10) also showed no treatment effect (Table 2). There was a year effect with the greatest decline in the mean among-year similarities occurring between 1985–1986 and 1985–1987 comparisons.

DISCUSSION

Over the 5 yr of our study, there was little change in the flora of the cells in any water level treatment. It was the abundance and distribution of species within a cell that were affected by higher water levels. The most striking impact of higher water levels was a large reduction in the percentage of a cell covered with emergent vegetation (by ≈40% on average in the medium and high treatments by 1989 [Table 2 and Fig. 1]). This loss of emergent cover was accompanied by an increase in the cover of submersed and free-floating species in all treatments (Table 5). These results are consistent with many previous studies of the impact of a long-term increase in water level on wetlands (Millar 1973, Bukata et al. 1988, Wallsten and Forsgren 1989). It was not until 1987, the 3rd yr of the study, that significant differences between the normal and higher water treatments occurred (Tables 2, 3, 5, and 6). This lag time in the response of emergent species to flooding is consistent with previous studies of prairie wetlands (Millar 1973, van der Valk and Davis 1978, Squires 1991, Squires and van der Valk 1992) which documented that it takes 2 or 3 yr of high water to eliminate susceptible emergent vegetation.

Green (1979) and Eberhardt and Thomas (1991) have reviewed the design of field impact studies. The preferred experimental design for such studies is a planned experiment with replication, such as this study. Nev-

TABLE 7. Mean Shannon's diversity index of emergent species, calculated using shoot density data, and of submersed and free-floating species, calculated using percentage shoot cover, from the vegetation data collected in permanent quadrats (2 m^2) in the normal (n = 40), medium (n = 30), and high (n = 30) water level treatments from 1985 through 1989.

Treatment	1985	1986	1987	1988	1989	Mean
Emergent species						
Normal	1.10	0.93	0.73	0.74	0.65	0.84
Medium	0.90	0.60	0.43	0.28	0.24	0.49
High	0.65	0.35	0.21	0.12	0.10	0.28
Mean	0.92	0.66	0.48	0.42	0.36	0.57
Free-floating species						
Normal	0.07	0.23	0.27	0.17	0.21	0.19
Medium	0.01	0.34	0.41	0.34	0.19	0.26
High	0.06	0.49	0.46	0.66	0.61	0.46
Mean	0.05	0.34	0.37	0.37	0.32	0.29

TABLE 8. Mean Simpson's diversity index of emergent species, calculated using shoot density data, and of submersed and free-floating species, calculated using percentage shoot cover, from vegetation data collected in the permanent quadrats (2 m^2) in the normal (n = 40), medium (n = 30), and high (n = 30) water level treatments from 1985 through 1989.

Treatment	1985	1986	1987	1988	1989	Mean
Emergent species						
Normal	0.45	0.52	0.59	0.54	0.58	0.54
Medium	0.55	0.67	0.69	0.65	0.58	0.63
High	0.66	0.77	0.81	0.56	0.61	0.68
Mean	0.55	0.64	0.68	0.58	0.59	0.61
Submersed and free-floating species						
Normal	0.36	0.49	0.48	0.64	0.50	0.46
Medium	0.26	0.57	0.59	0.70	0.62	0.55
High	0.36	0.65	0.63	0.56	0.39	0.52
Mean	0.26	0.56	0.56	0.64	0.51	0.51

TABLE 9. Mean of the mean Bray–Curtis (BC) similarity index, comparing the similarity of the vegetation in the 10 permanent quadrats in each cell (n = 45 per cell), in the normal (n = 4 cells), medium (n = 3), and high (n = 3) water level treatments from 1985 through 1989. These similarity indices were calculated using emergent shoot density data only.

Treatment	1985	1986	1987	1988	1989	Mean
Normal	0.22	0.29	0.24	0.18	0.19	0.23
Medium	0.14	0.17	0.14	0.11	0.10	0.13
High	0.19	0.21	0.14	0.13	0.13	0.16
Mean	0.19	0.23	0.18	0.14	0.14	0.18

TABLE 10. Mean Bray–Curtis (BC) similarity index comparing the similarity of the vegetation in a particular permanent quadrat in each cell in 1985 to that in 1986, 1987, 1988, and 1989 in the normal ($n = 40$), medium ($n = 30$), and high ($n = 30$) water level treatments. These similarity indices were calculated using emergent shoot density data only.

Treatment	1985–1986	1985–1987	1985–1988	1985–1989	Mean
Normal	0.52	0.23	0.25	0.22	0.31
Medium	0.46	0.24	0.22	0.13	0.27
High	0.53	0.30	0.21	0.21	0.31
Mean	0.51	0.25	0.23	0.19	0.30

ertheless, five major problems can potentially invalidate or confound the results of such experiments: (1) site heterogeneity, (2) boundary effects, (3) a small number of replicates, (4) the suitability of the approaches used to detect treatment effects, and (5) the suitability of the various directly measured and calculated indicators of the state of the vegetation. The last two are interrelated and will be discussed together.

Cell heterogeneity

Cell heterogeneity was a problem, particularly with the indicators derived from vegetation map data and with the similarity indices. We were able to overcome this problem with relevant vegetation map indicators by subtracting from them the mean value of the indicator in 1979 and 1980. The 1979/1980 values of these indicators are assumed to represent steady-state values at a water level of 247.5 m above mean sea level, since water levels in Lake Manitoba and the connecting Delta Marsh had been regulated with a series of dams to keep them at that water level since the mid-1960s. This successfully adjusted for the effects of cell-to-cell differences on the experimental results.

Boundary effects

In this study, boundary effects were not a problem. The experimental cells were large, and all areas within 5 m of a boundary were eliminated when vegetation maps were analyzed. Likewise, permanent quadrats were located at least 5 m from any dike or borrow ditch, and their triangular shape (which eliminated investigator trampling on two sides) minimized damage caused by repeated sampling. Thus the vegetation data and similarity indices also were not affected by disturbances around either the cell or the permanent quadrats.

Number of replicates

Although the number of replicates per treatment was small in this study because of the cost of constructing and maintaining a cell, there were still more replicates than in most field studies (Eberhardt and Thomas 1991). Our results indicate that the experimental design was powerful enough to detect treatment effects using some approaches and indicators, but not all. Would increasing the number of replicates have significantly altered our results? We think not. The primary reason treatment effects were not detected in some cases was not the power of the experimental design, but the unsuitability or lack of relevance (in the sense of Green 1979) of one of the approaches, similarity indices, and some of the indicators used to characterize the vegetation.

Suitability of approaches and indicators

The vegetation map and vegetation data approaches were able to detect changes caused by flooding, while the similarity indices approach could not. Nevertheless, not all indicators derived from the vegetation maps or from the vegetation data proved to be suitable.

The vegetation map data analyses indicated that two adjusted indicators, percentage of a cell covered with litter and percentage covered with sparse emergent vegetation, did not show a treatment effect (Table 1). Although between 1986 and 1987, 20–30% of the emergent vegetation was killed in the medium and high treatments, no corresponding increase in percentage litter cover, particularly in the high treatment, occurred (Tables 2 and 3). This is because the two emergent species that had the greatest decline in abundance, *Scolochloa festucacea* and *Scirpus lacustris* ssp. *validus,* did not produce persistent standing litter. Their litter toppled quickly and was not detectable on the aerial photographs because it was largely under water. Sparse emergent vegetation in some years covered as much or more of the cells in the normal treatment as in the higher water level treatments (Table 3). Succession was opening up stands of emergent vegetation, and this confounding factor made it impossible to detect a treatment effect.

Our analysis of the vegetation data gave results that generally were comparable to that from the vegetation maps. The major change that occurred in the permanent quadrats was a decline in the abundance or local extirpation of emergent species (Tables 2, 3, 5, and 6). In addition, the permanent quadrat data provided information on the increase in abundance of submersed and free-floating species (Table 6). Changes in the submersed and free-floating vegetation, however, were strongly inversely correlated with changes in the emergent vegetation. Thus, submersed and free-floating vegetation data actually provided little additional information about the responses of wetlands to higher water levels compared to the emergent vegetation data.

Simpson's index showed no treatment response in spite of significant changes in total shoot density or cover of species in the permanent quadrats. In a statistical study of the power of various diversity indices to detect a change in the composition of a community, Heltshe and DiCanzio (1985) concluded that "... Simpson's index was not as responsive to changes in species abundances" and consequently was less powerful than the Shannon's index and the other two in-

dices that they examined. Also, ". . . Simpson's index is more responsive to dominant species . . . and is little influenced by changes in rare species" (Heltshe and DiCanzio 1985). The vegetation in the MERP cells throughout the study typically consisted of one, or occasionally two, dominant species plus some minor species irrespective of water level treatment. Simpson's index is not a relevant measure.

Of the other three indicators examined (species richness, total emergent shoot density, and Shannon's index), the first two showed a consistent and monotonic response to the three water level treatments (Tables 5 and 6). We agree with Green (1979) that directly measured indicators (e.g., species richness and density) are preferable to calculated indicators (e.g., species diversity indices) in quantifying the response of vegetation in impact studies. Because diversity indices do not contain information about species composition, two communities could have the same diversity index value and have no species in common. Green (1979) favors analyses of community impacts using similarity indices because they do use information about species composition.

Similarity indices in this study proved to be the poorest of the three approaches examined. There was no treatment effect for the mean within-year Bray–Curtis index values (Tables 1 and 9). Regardless of treatment, the cells in 1985 contained a variety of vegetation types ranging from wet meadow to open water; therefore, mean Bray–Curtis values for a cell were always low, even in the normal treatment. The insensitivity of this indicator to vegetation change in a cell can be seen by examining its value in the normal treatment. Although there were successional changes in the vegetation of cells in the normal treatment, these changes had little, if any, impact on the mean within-year Bray–Curtis index value (≈ 0.2) during the entire study (Table 9). The Bray–Curtis index has a value of 0 when two quadrats have no species in common, which occurred in the MERP cells when permanent quadrats at the higher elevations were compared with those at lower elevations or when one quadrat contained no vegetation. Consequently, because of the heterogeneous vegetation in the MERP cells, even the complete elimination of emergent vegetation from one or more permanent quadrats in a cell often had little or no impact on the mean index value for that cell. In short, because within-cell vegetation heterogeneity (spatial heterogeneity) makes it difficult or impossible to detect the elimination of emergents, the mean within-year Bray–Curtis similarity value is not a suitable indicator.

Within-cell heterogeneity can be reduced by estimating the abundance (e.g., mean shoot density) of each species in a cell from the permanent quadrat data. Similarities can then be computed for each pair of cells. (Because similarity indices are nonlinear distance functions, this also gets around the problem of how best to estimate mean similarities.) Because direct measures of the abundance of species, such as mean shoot density, were one of the two best indicators of a treatment response, it is unnecessary to calculate whole-cell similarity indices in order to test for a treatment effect.

Among-year Bray–Curtis index values also showed no significant treatment effect. With this approach, successional changes in the vegetation were detected, i.e., there was a significant year effect. These successional changes (temporal heterogeneity) made it impossible to detect a treatment effect. The use of among-year similarity indices to detect the impact of higher water levels on wetland vegetation is not recommended.

Recommendations

Vegetation data, particularly directly measured indicators such as total shoot density and species richness, from permanent quadrats were the best approach for detecting the impact of high water levels on wetland vegetation. This was the only approach that was robust enough to cope with both cell heterogeneity and succession.

Vegetation sampling with permanent quadrat requires more time and considerably more labor than constructing vegetation maps from aerial photographs. Permanent quadrats, however, yielded more detailed information about the vegetation (species richness and shoot density) that are directly affected by a change in water level (Squires 1991, Squires and van der Valk 1992). Similarity indices, which require additional calculations, proved to be unsuitable indicators because either temporal (successional) or spatial (within-cell) vegetation heterogeneity made it impossible to detect the main treatment effect, the local elimination of emergent vegetation. Vegetation data collected using permanent quadrats, however, cannot determine as well the spatial extent of a disturbance.

Indicators derived from vegetation maps were less reliable than those from vegetation data unless they could be corrected for site-to-site differences. Aerial photographs require less field sampling, but more post-field processing (digitization and computer manipulation of the digital images) before relevant information can be extracted. Maps provide less detailed information about the state of the vegetation within a cell, but clearly are superior for determining the area of a disturbance. The most reliable and informative approach to impact studies would be to use both vegetation maps and vegetation data collected using permanent quadrats.

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