

## CONSTRAINTS ON THE ESTABLISHMENT OF PLANTS ALONG A FLUCTUATING WATER-DEPTH GRADIENT

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**Abstract.** We used simulation modeling to investigate the relative importance of current environmental conditions and factors affecting establishment of different plant species on the formation of vegetative zonation patterns. We compared the results from a series of six models that incorporated increasing amounts of information about key factors affecting species' ability to adjust to water-level fluctuations. We assessed model accuracy using aerial photographs taken of a 10-yr field experiment, in which 10 wetlands were flooded to 1 m above normal water level for 2 yr, drawn down for 1 or 2 yr, and reflooded for 5 yr to three different water levels (normal, +0.3 m, +0.6 m). We compared each model's ability to predict relative areal cover of five dominant emergent species and to recreate the spatial structure of the landscape as measured by mean area of monospecific stands of vegetation and the degree to which the species were intermixed.

The simplest model predicted post-treatment species distributions using logistic regressions based on initial species distributions along the water-depth gradient in the experimental wetlands. Subsequent models were based on germination, rhizomatous dispersal, and mortality functions implemented in each cell of a spatial grid. We tested the effect on model accuracy of incrementally adding data on five factors that can alter the composition and distribution of vegetative zones following a shift in environmental conditions: (1) spatial relationships between areas of suitable habitat (landscape geometry), (2) initial spatial distribution of adults, (3) the presence of ruderal species in the seed bank, (4) the distribution of seed densities in the seed bank, and (5) differential seedling survivorship.

Because replicated, long-term data are generally not available, the evaluation of these models represents the first experimental test, of which we are aware, of the ability of a cellular-automaton-type model to predict changes in plant species' distributions.

Establishment constraints, such as recruitment from the seed bank, were most important during low-water periods and immediately following a change in water depth. Subsequent to a drop in water level, the most detailed models made the most accurate predictions. The accuracy of all the models converged in 1–2 years after an increase in water level, indicating that current environmental conditions became more important under stable conditions than the effects of historical recruitment events.

**Key words:** *cellular automaton; community; dispersal; environmental gradient; establishment constraints; logistic regression; seed bank; spatial model; spatial pattern; water depth; wetlands; zonation.*

### INTRODUCTION

Environmental gradients can be a dominant factor controlling the distribution of plants, and vegetation zones perpendicular to these gradients, coenoclines, are readily apparent in many landscapes (von Humboldt and Bonpland 1807, as cited in McIntosh 1985; Shreve 1922, Whittaker 1960, Whittaker and Niering 1965). Although patterns such as the upper limit of trees on mountain slopes or the concentric rings of vegetation along the shores of a lake are apparently simple, the composition of coenoclines is the outcome of complex interactions between abiotic conditions and differential rates of propagule dispersal, seed germination, seedling

mortality, and adult mortality among species (Grubb 1977, van der Valk and Welling 1988).

If species are not limited in their ability to become established in areas of suitable habitat, community composition will primarily reflect current environmental conditions. However, recruitment and dispersal limitations impinge on the ability of many species to respond to environmental change. Specifically, the ability of species to become established in new locations can be constrained by factors such as the spatial relationships between areas of suitable habitat (landscape geometry), distribution of refugial adults, competition with ruderal species, availability of viable seed in the seed bank, and seedling survivorship. These establishment constraints create a lag period during which species distributions reflect historical recruitment events rather than current environmental conditions (Werner and Platt 1976). This lag period may persist for hundreds of years if a site has few residual plants or prop-

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agules and is spatially isolated from sources of propagules (Godwin 1923, Stahelin 1943, Peet 1981).

What forces control the distribution of species along an environmental gradient? This question is difficult to address using empirical methods alone, because of the logistical difficulties and costs associated with landscape-scale experimental manipulations. For this reason, experimental work has typically focussed on local-scale processes, such as the direct effects of environmental conditions on the plant demography. For example, in freshwater wetlands, researchers have described the effects of flooding on seed survivorship in the seed bank (Poiani and Johnson 1989), recruitment from the seed bank (Keddy and Ellis 1985, Keddy and Constabel 1986, Seabloom et al. 1998), and adult growth and mortality (McKee et al. 1989, Squires and van der Valk 1992). Community responses to environmental change have also been studied at the mesocosm scale (Weiher and Keddy 1995*b*).

Because of the lack of landscape-scale experiments, there is a disparity in scale between our empirically based understanding of local ecological processes, which often operate on short time-scales, and development of broader, landscape-scale patterns, which are often produced over time scales of a decade or greater (Levin 1992, Moloney et al. 1992, Wiegand et al. 1998).

Simulation modeling can provide a critical link between local and landscape-scale processes. In cases where the only available data relate to local processes, a simulation approach provides a means to predict landscape-scale patterns. Conversely, in cases where the landscape-scale responses are known, simulation models provide a means to isolate the relative importance of the factors that potentially control the landscape-scale response of species to changing environmental conditions.

Interpretation of modeling results can be problematic, because different modeling strategies vary in their accuracy, realism, and generality (Levins 1966). However, the differential accuracy of models based on different assumptions can provide insight into biological processes (e.g., Murdoch 1994, Hilborn and Mangel 1997, Kendall et al. 1999). For this study, we developed a series of models that incorporated increasing amounts of information about key stages in the formation of vegetation zonation patterns in freshwater wetlands following a shift in water depth. We used relative model accuracy as a means of identifying the strongest determinants of species distributions by comparing predictions from a series of increasingly complex models.

We assessed the predictive ability of each model using data from a 10-yr experiment examining the effects of fluctuating water levels on vegetative composition of 10 wetlands at Delta Marsh in Manitoba, Canada (Murkin et al. 1985, 2000). These data are uniquely suited to studying effects of shifting environmental gradients, because model predictions can be tested against

data produced by an unusually long, replicated experiment. In addition, a single environmental gradient (i.e., water depth) is the strongest environmental factor controlling the distribution of adult wetland plants (Walker and Coupland 1968, Spence 1982) making it easier to simulate the effect of the environment on species' distributions (Palmer 1992).

Our simplest model, the niche model, used water depth as the sole predictor of the distribution of four plant species within the Delta Marsh wetland complex. The niche model is based on a series of logistic regressions developed by de Swart et al. (1994).

Subsequent models, referred to collectively as spatially explicit models, incorporated constraints on species' abilities to respond to changes in water depth in the form of rule-based germination, rhizomatous dispersal, and mortality functions implemented in each cell of a spatial grid. For this reason, colonization in the spatially explicit models was constrained by life-history characteristics, such as life-span, capacity for rhizomatous spread, and seed-bank density. This is in contrast to the niche model, where establishment was controlled solely by local environmental conditions rather than propagule availability.

An accurate landscape-scale model must reconstruct landscape composition and physiognomy (spatial arrangement of landscape types), because both characteristics have strong effects on ecological processes (Dunning et al. 1992). We compared each model's ability to predict relative areal cover of five dominant emergent species. We also compared the models' ability to simulate landscape physiognomy using two metrics: mean area of monospecific stands of vegetation (patch size) and the degree of interspersion among these patches (contagion). In this paper, we will present the results of our comparisons of these models and interpret the increased predictive ability in each of the increasingly data-rich models as being indicative of relative importance of the (1) current water-depth gradient, (2) landscape geometry (i.e., spatial relationships between areas of suitable habitat), (3) colonization from refugial stands of adults, (4) composition of the seed bank, (5) spatial patterning of the seed bank, and (6) differential germination responses to water depth.

While there are many wetlands models in the literature, few of them focus on plant community dynamics. Our modeling work is an extension of the few community-level wetland models that have been developed. The spatially explicit models we developed are extensions of the qualitative model of wetland succession developed by van der Valk (1981) in which the presence of species in a wetland is predicted based on three simple life-history features: adult life-span, propagule longevity, and propagule establishment requirements. This general approach has also been used by other researchers to model wetland plant community dynamics in response to water level fluctuations (Poiani and Johnson 1993, Ellison and Bedford 1995). Our modeling

work expands on these earlier efforts in that it models the distribution of individual species rather than functional groups (e.g., ruderals) and is validated using replicated experimental data.

We use a large-scale replicated experiment to validate our models. Because replicated, landscape-scale data are generally unavailable, (Kareiva and Andersen 1988), our evaluation of the models with establishment constraints is the first experimental test of the ability of a cellular-automaton-type models to predict landscape-scale changes in plant-species distributions.

## METHODS

### *Study system*

Model parameterization and verification were based on data from a long-term experiment conducted within Delta Marsh, Manitoba, Canada as part of the Marsh Ecology Research Program (MERP, see Walker 1959 and 1965, Murkin et al. 1985, 2000, Welling et al. 1988). Experimental wetlands were constructed in 1979 by partitioning off a portion of Delta Marsh into 10 contiguous, rectangular cells ranging in size from 5.5 to 7 ha. For 20 yr prior to wetland construction, water levels at Delta Marsh were artificially maintained near 247.5 m above mean sea level (AMSL) producing water depths of up to 4.8 m in the experimental wetlands. Throughout the rest of the paper, elevations will be relativized to a normal flooding level of 0 m, by subtracting 247.5 m from the original AMSL elevations.

For all but one treatment (normal 1), water levels were maintained for 1 yr at 0 m, followed by 2 yr of flooding (+1 m) and a 2-yr draw-down period (−0.5 m). The next 5 yr were a recovery period characterized by three water-level treatments: normal (0 m), medium (+0.3 m), and high (+0.6 m). The normal treatment was subdivided into two treatments: normal 1 and normal 2. Normal 1 differed from other treatments by starting the experiment with 2 yr at 0 m and having only one draw-down year. There were two replicates of normal 1 and normal 2 and three replicates of medium and high.

Nomenclature follows Gleason and Cronquist (1991) throughout. *Phragmites australis* (Cav.) Trin., *Scolochloa festuacea* (Willd.) Link, *Typha × glauca* Godr. will be referred to by their generic epithets. Exposed mudflats in the system were dominated by a guild of species representing a complex of mudflat annuals, e.g., *Atriplex patula* L., *Aster laurentianus* Fern., *Chenopodium rubrum* L., *Ranunculus scleratus* L., and *Rumex maritimus* L. (Welling 1987). The mudflat annual species were represented as a single guild (mudflat annuals) in our simulations.

### *Maps construction*

Digital surface elevation and vegetation maps were constructed for each experimental wetland as a part of MERP (Murkin et al. 1985, 2000). The vegetation maps

served as the baseline against which we compared model predictions, and the elevation maps were used to calculate water depth at each point in the wetland given the current water level. We converted surface elevation maps (consisting of ARC/INFO polygon coverages; Environmental Systems Research Institute 1991, de Swart et al. 1994) into a grid of 3 × 3-m cells in which each cell was assigned the mean elevation for the cell area. Vegetation maps for the years 1979–1989 were made from low-level (610 m) aerial photographs taken in August (van der Valk et al. 1994). Homogeneous stands of vegetation were delimited on the photographs, assigned a value based on the dominant adult plant species after on-site validation, and digitized as ARC/INFO polygon coverages (de Swart et al. 1994). We converted ARC/INFO vegetation coverages into a grid composed of 3 × 3-m cells, the same resolution as the original aerial photographs (de Swart et al. 1994). The resulting cells corresponded exactly to the cells in the topographic grids. We excluded areas within a 5-m buffer zone placed around dikes and borrow pits from the analysis.

### *Model simulations*

Simulations used two types of models: the niche model based on logistic regressions and the spatially explicit model based on a cellular automaton structure (Table 1). All models were written in the ANSI C language (Kernighan and Ritchie 1988), compiled using the MIPSpro compiler with SGI scientific math libraries, and run on the IRIX 6 operating system (Silicon Graphics, Inc., Mountain View, California, USA). The source code and detailed parameter descriptions are available in *Ecological Archives* (see Supplement).

The niche model was used to make predictions about the distributions of four plant species (*Phragmites*, *Scolochloa*, *Typha*, and *Scirpus acutus* Muhl.) and the unvegetated areas in the Delta Marsh experimental wetlands as a function of water depth. For each year of the experiment, we used logistic regressions to calculate the probability of each species (or the unvegetated cover class) occurring in each of the 3 × 3-m grid cells of each wetland basin. We then selected the cover class of each cell, empty or occupied by species *i*, by a random draw, where the probability of selecting cover class *i* equaled  $p_i$  (Eq. 1).

The logistic regression models used in the niche model were developed by de Swart et al. (1994) using data from the 1980 growing season (Fig. 1). These regression take the basic form of the quadratic function

$$\ln\left(\frac{p_i}{1-p_i}\right) = f(x) = b_{i0} + b_{i1}x + b_{i2}x^2 \quad (1)$$

where  $p_i$  is the conditional probability of species *i* being present given water depth *x*, and  $b_{ij}$  is the *j*th regression coefficient for species *i*. The distributions of *Phragmites* and *Typha* were complex, and their models are based on a series of smooth quadratic splines.

TABLE 1. Summary of simulations of the Delta Marsh experiment.

Model name	Model type	Information included in simulations			
		Initial adult distributions	Ruderal species	Seed density	Seedling density
Niche	logistic	no	no	no	no
Basic spatial	spatial	no	no	no	no
Initial adult distribution	spatial	yes	no	no	no
Seed bank composition	spatial	yes	yes	no	no
Relative seed density	spatial	yes	yes	yes	no
Complete spatial	spatial	yes	yes	yes	yes

*Notes:* Models were based either on logistic regressions or were grid-based, spatially explicit models. The niche model used only current water depth to predict species distributions. The sole difference between the basic spatial model and the niche model was the incorporation of the effects of the unique spatio-temporal context of a grid cell (i.e., the spatial relationship between suitable habitat types). The initial adult distribution model was initialized with the observed adult distributions in each wetland at the start of the experimental water level manipulations. The seed bank composition model added two ruderal species (mudflat annuals and *S. validus*) that were very rare at the start of the experiment but common in the seed bank. The relative seed density model was initialized with seed densities that reflected the elevational density pattern from seed bank data. The complete spatial model was initialized with seed densities that reflected seedling recruitment.

Our application of these logistic regression models differed from de Swart in several ways. de Swart et al. (1994) did not explicitly model the probability of areas being unvegetated. We fit a logistic regression model to the original MERP vegetation and elevation data used by de Swart et al. (1994) that predicted the conditional probability of a cell being unvegetated,  $p_0$ , given water depth  $x$  as

$$\ln\left(\frac{p_0}{1-p_0}\right) = f(x) = 1724.5 - 6.977x. \quad (2)$$

The models that incorporated establishment constraints were based on a flexible family of spatially explicit

models, cellular automaton, or interacting particle system models (Wolfram 1984a, b). These models have had widespread use in biological (e.g., Wolfram 1984a, b, Ermentrout and Edelstein-Keshet 1993) and ecological (e.g., Molofsky 1994) applications. Cellular-automaton models have also been used in other freshwater wetland systems (e.g., Poiani and Johnson 1993, Ellison and Bedford 1995).

Cellular automaton models take the form of an  $n$ -dimensional lattice or grid that divides the spatial and temporal components of a system into discrete units (Durrett and Levin 1994). Individual cells exist in a fixed number of discrete states, e.g., cells may be oc-

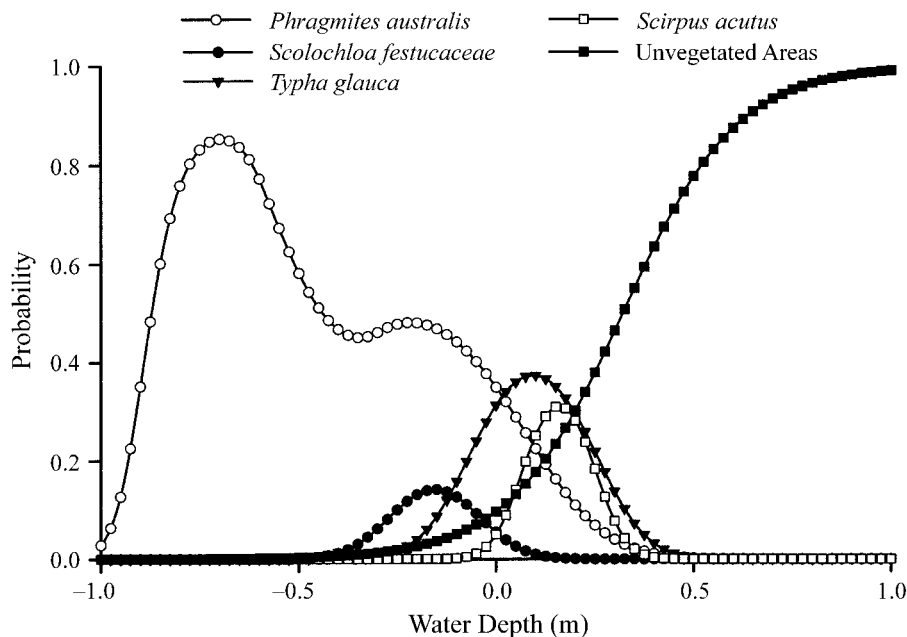


FIG. 1. Probability of occurrence of four perennial emergent plant species along a water-depth gradient, as predicted by de Swart et al. (1994), using logistic regression models. Each model estimates the probability of finding stands of adult plants or an unvegetated site at a given water depth, based on the distribution of the species in the wetlands in 1980 after 20 years of stable water levels.

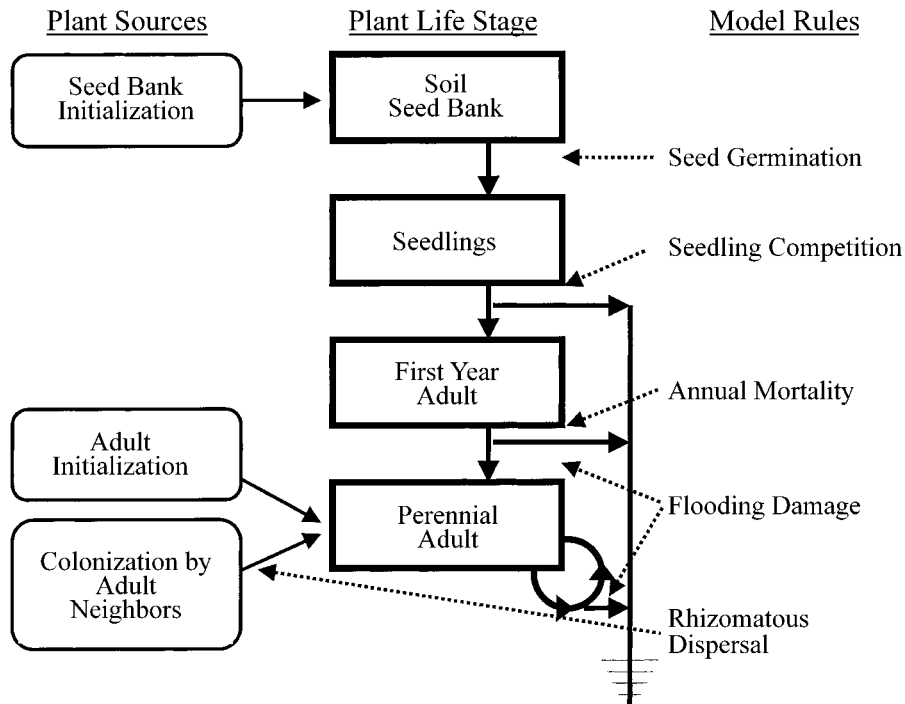


FIG. 2. Schematic diagram of the model structure for a single cell of the spatial wetland vegetation model. Individuals can exist in one of four life stages: dormant seeds (soil seed bank), seedlings, first-year adult, or perennial adult. Five sets of rules govern the movement from one stage to the next. A single adult species may exist in each cell. Dotted arrows indicate the locations in the model where transition probabilities are governed by specific sets of rules. Adults become established in one of three ways: (1) initialization routines that establish the seed bank density of each species and the adult species in each cell at the outset of a model run, (2) the invasion of a cell by a neighboring adult through rhizomatous growth, or (3) recruitment from the soil seed bank.

cupied or empty (Molofsky 1994). Individual cells change states based on a rules that evaluate the state of the cell and its neighbors in the lattice during the previous time step.

As in the niche model, these models predicted the dominant species in each  $3 \times 3$ -m cell of the experimental wetlands, with water depth playing a large role in determining species distributions. In contrast to the niche model, these models explicitly accounted for the spatial and temporal relationships among individual cells. As a consequence, the current state of a cell in the spatially explicit models was the result of a unique set of historical events that took place in the cell itself and the surrounding grid. An adult plant not only had to tolerate its current environmental conditions, it also had to pass through a series of environmental filters, i.e., historical water depths, that could remove species based on historical conditions (Drake 1991, Weiher and Keddy 1995a, b).

Within each cell, plants could exist in one of four stages: dormant seeds, seedlings, first year adults, and perennial adults (Fig. 2). Five sets of rules (see Appendix) governed the probability that individual plants would move from one stage to the next (Fig. 2). These rules were applied to each cell in the spatial grid during each annual time step. Multiple species of dormant

seeds and seedlings could coexist in a single cell of the spatial model, but only a single adult species could persist. The dominant adult species represented a monospecific stand rather than a single individual.

A species could become the dominant adult in one of three ways (Fig. 2): (1) it was the dominant species at the start of the simulation and remained so, (2) it colonized an empty cell from a neighboring cell via rhizomatous growth, or (3) it germinated from the soil seed bank and survived through the seedling stage and into adulthood.

An adult in a cell could exist in one of two states: reproductive or dormant. A reproductive stand had the capacity to spread into neighboring cells through rhizomatous growth if the neighboring cell was unoccupied. Reproductive stands were also more resistant to flooding damage than dormant stands. These rules reflect the biological response of plants to flooding; active growth and sexual reproduction cease fairly rapidly in adult plants under flooded conditions (McKee et al. 1989, Squires and van der Valk 1992, van der Valk et al. 1994), although mortality does not generally begin until second year (Millar 1973, van der Valk and Davis 1980, van der Valk et al. 1994).

The behavior of species in the spatial model was determined through the following demographic char-



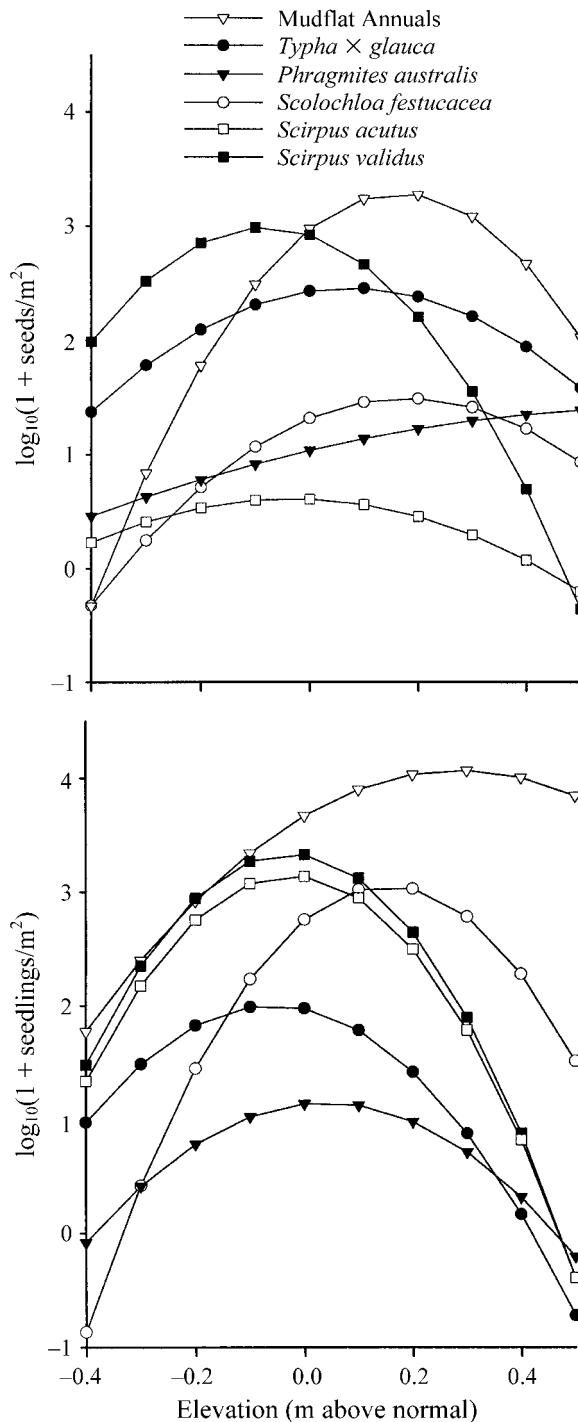


FIG. 3. Regression models of the change in seed and seedling density along an elevation gradient in 10 experimental wetlands. Regressions are based on mean densities at 0.1-m intervals for seeds (Pederson 1983) and seedlings (Welling 1987). The  $r^2$  and  $P$  values for the seed density models are as follows: mudflat annuals ( $r^2 = 0.90$ ,  $P < 0.01$ ), *Phragmites australis* ( $r^2 = 0.67$ ,  $P = 0.02$ ), *Scolochloa festucacea* ( $r^2 = 0.74$ ,  $P = 0.01$ ), *Scirpus validus* ( $r^2 = 0.91$ ,  $P < 0.01$ ), *Typha x glauca* ( $r^2 = 0.62$ ,  $P = 0.03$ ), and *Scirpus acutus* ( $r^2 = 0.85$ ,  $P < 0.01$ ). The  $r^2$  and  $P$  values for the seedling density models are as follows: mudflat annuals ( $r^2 = 0.82$ ,  $P < 0.01$ ),

acteristics: germination rates, rates of rhizomatous spread, survivorship, reproductive state of adults, and life span. Life span was a fixed characteristic, and species were either annual or perennial. All other demographic traits were affected by water depth (see Appendix). Seed production and seed dispersal were not explicitly modeled, however these processes did not play a significant role over the time frame of the study, because the single draw-down period was the only major opportunity for seed germination.

The initial distribution of adults in each simulation was either determined by a random draw weighted by the logistic equations that comprise the niche model or set as the distribution of dominant plant species as the Delta Marsh experimental wetlands during 1980 (see Appendix). Initial seed density was either set as the mean total density divided by the number of species or based on estimates obtained from three sources: Pederson (1983) and Welling (1987) for annuals and van der Valk and Welling (1988) for perennials (see Appendix, Fig. 3).

*Processing of simulated vegetation maps*

We processed the simulated vegetation maps so as to make them as comparable as possible to the aerial photographs. In the aerial photographs, relatively large areas were classified by their dominant vegetation, resulting in a simplification of the original data made up of finer scale patterns of coexisting species. We used a two-stage process to develop vegetation maps from model output. First, the models were run at a fine scale of resolution ( $3 \times 3$ -m cells). Second, we used a simple smoothing algorithm to eliminate small, isolated stands that would not have been visible on aerial photographs. The algorithm selected the most common single value (adult species) in each  $3 \times 3$  array of cells to represent the corresponding  $9 \times 9$ -m grid cell. In the case of a tie, selection was made by a single, evenly weighted, random draw.

*Methods of analysis*

Our measure of the accuracy of model  $k$  for wetland  $j$ ,  $A_{jk}$ , is the multivariate similarity between the vegetation cover observed in the aerial photographs that predicted by a given model. This similarity measure was developed specifically for proportional data, where all variables sum to 1 (Manly 1986) and is calculated as:

$$A_{jk} = 1 - \frac{\sum_{i=0}^n |o_{ijk} - p_{ijk}|}{2} \tag{3}$$

*Phragmites australis* ( $r^2 = 0.80$ ,  $P < 0.01$ ), *Scolochloa festucacea* ( $r^2 = 0.76$ ,  $P < 0.01$ ), *Scirpus validus* ( $r^2 = 0.81$ ,  $P < 0.01$ ), *Typha x glauca* ( $r^2 = 0.65$ ,  $P = 0.03$ ), and *Scirpus acutus* ( $r^2 = 0.80$ ,  $P < 0.01$ ).

based on the proportion of the experimental wetland ( $o_{ijk}$ ) or model wetland ( $p_{ijk}$ ) occupied by a cover class;  $i = 0$  represents unvegetated cells and  $i = 1-6$  represents the six different cover types that could dominate a cell. The dummy variable  $j$  represents the individual wetland being considered, and the dummy variable  $k$  represents the model being considered.

If  $A_{jk}$  equals 0, there is no overlap in any of the  $n + 1$  proportions, and the model is always wrong when predicting presence or absence of all cover classes. A value of 1.0 indicates that each of the  $n + 1$  proportions is equal, and the model fit is perfect.

We repeated all analyses using two additional similarity metrics to ensure that the results were robust to metric choice. The second metric (Manly 1986) is calculated as

$$A2_{jk} = \frac{\sum_{i=0}^n o_{ijk} p_{ijk}}{\sqrt{\sum_{i=0}^n o_{ijk}^2 \sum_{i=0}^n p_{ijk}^2}} \quad (4)$$

The third metric (Krebs 1989) is calculated as

$$A3_{jk} = \sum_{i=0}^n \text{minimum}(o_{ijk}, p_{ijk}). \quad (5)$$

All results were qualitatively similar regardless of the metric, so we will only discuss results calculated as in Eq. 3.

In order to assess the relative performance of the various models across the 10 replicate wetlands, we had to account for the variation in model accuracy attributable to the effects of individual wetlands. In a single year,  $A_{jk}$  can be represented by the equation

$$A_{jk} = \mu + w_j + m_k + \varepsilon \quad (6)$$

in which  $\mu$  is the overall mean accuracy,  $w_j$  is the effect of wetland  $j$ ,  $m_k$  is the effect of model  $k$ , and  $\varepsilon$  is the error. We normalized model accuracy by subtracting the mean accuracy for each wetland such that

$$A_k = A_{jk} - A_j. \quad (7)$$

Specifically, we compare normalized accuracy,  $A_k$ , among the models by plotting the means and standard errors for each model in each year.

In these analyses, we did not make corrections for autocorrelation between measurements made in consecutive years. A correction for nonindependent samples, such as Bonferroni or Dunn-Sidak, would increase the acceptance region of the null hypothesis and would make tests of equivalence less stringent (Sokal and Rohlf 1995).

We compared the spatial pattern in the aerial photographs and simulated landscapes using two metrics: mean patch size and contagion. A contagion value of 100 indicates that cover classes are much more likely to be adjacent to identical classes, while a value of 0

indicates that there are no differences in adjacencies between classes. Contagion,  $C$ , is calculated as

$$C = 1 + \frac{\sum_{i=1}^m \sum_{l=1}^m \left[ P_i \left( \frac{g_{il}}{\sum_{l=1}^m g_{il}} \right) \right] \left[ \ln(P_i) \left( \frac{g_{il}}{\sum_{l=1}^m g_{il}} \right) \right]}{2 \ln(m)} \times 100 \quad (8)$$

where  $P_i$  is the proportion of the wetland covered by vegetation class  $i$ ,  $g_{il}$  is the number of adjacencies between cover class  $i$  and  $l$ , and  $m$  is the number of vegetation classes in the wetland. We used FRAGSTATS (McGarigal and Marks 1994) to calculate the mean contagion and mean patch size (i.e., mean area of monospecific, contiguous stands of vegetation) in each of the 10 wetlands during that last year of the experiment (1989). In this analysis, we wanted to discern differences in distribution patterns of vegetation and excluded unvegetated areas from pattern analyses.

All analyses and data management were conducted using SAS version 6.11 (SAS Institute 1989).

## RESULTS

Although among-run variability in the niche model was nearly nonexistent, there was variability in the predictions among runs of the other models with identical initial conditions and parameter sets. We calculated the variance among 10 replicate model runs to examine the amount of variability that arose through the stochastic components of model initialization and the demographic components of germination, seedling competition, dispersal, and mortality. We found that there was little variability in proportion of a wetland covered by each species among the 10 replicate runs. The largest standard deviation in the proportion of a wetland covered by any cover class in any year was 0.031, indicating that the area incorporated in the model wetlands is large enough to show strong ergodic behavior in overall dynamics, producing similar results among replicate runs.

### Predictions of landscape composition

Prior to alteration of flooding levels, *Phragmites*, *Scolochloa*, *Typha*, and *Scirpus acutus* Muhl. accounted for nearly all of the emergent vegetation in the Delta Marsh wetland complex. The two years of flooding killed most of the emergent vegetation in the wetland cells, though some plants persisted in shallow areas and elsewhere as dormant roots (Squires and van der Valk 1992, van der Valk 1994; Fig. 4). The draw-down period produced a large seedling recruitment event dominated by *Scirpus validus* Vahl. and mudflat annuals. Flooding during the recovery period largely eliminated the mudflat annuals, *Scirpus validus*, and *Scolochloa* (Fig. 4). *Typha* increased its dominance during this period through rhizomatous dispersal (Fig. 4).

The accuracy of all models showed qualitatively similar dynamics over time. Accuracy remained high dur-

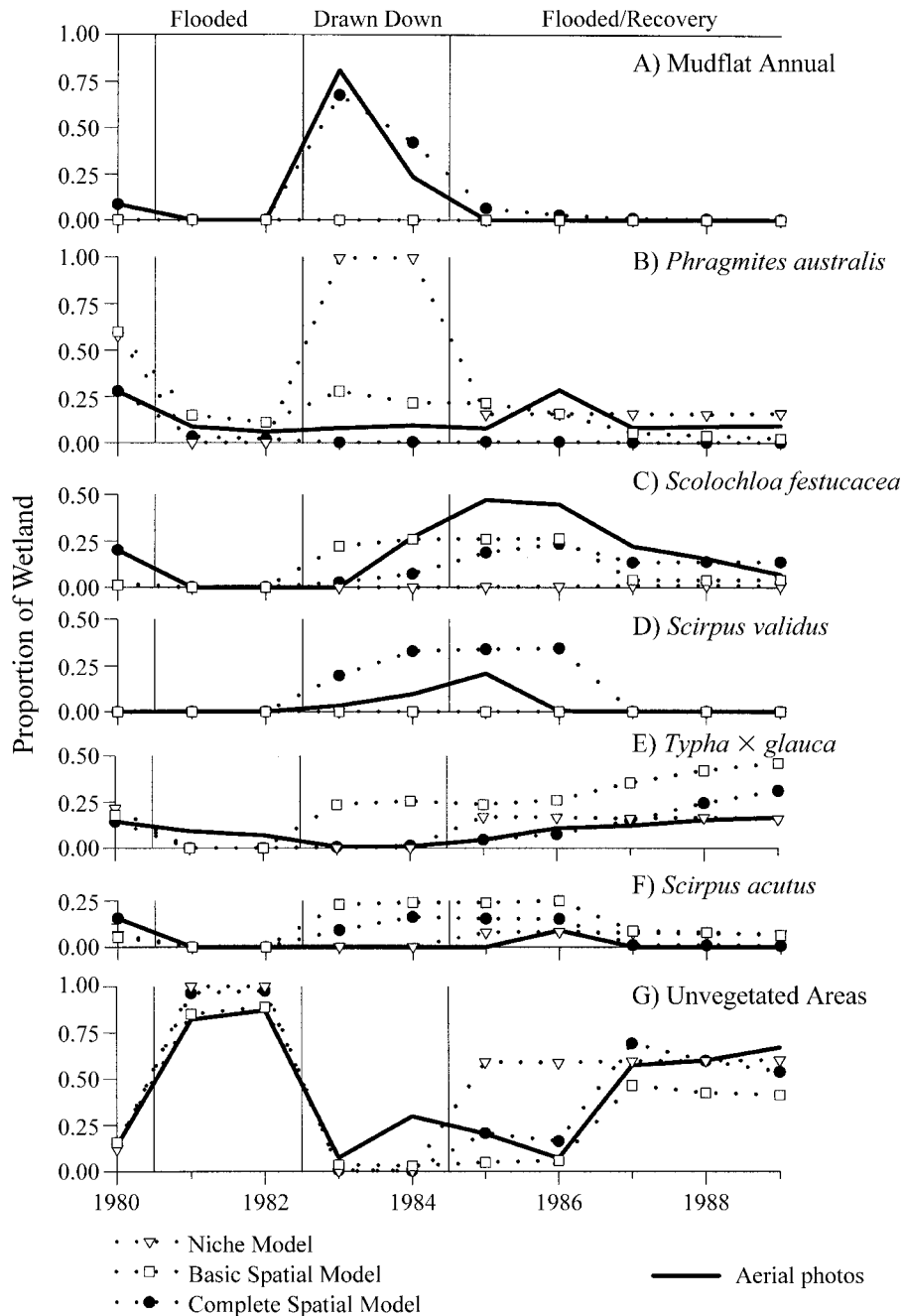


FIG. 4. Temporal change in vegetative composition over 10 yr in the three wetlands in the Delta Marsh experimental wetland complex that were assigned to the medium treatment. Vegetative composition is summarized for seven cover classes: (A) mudflat annuals, (B) *Phragmites australis*, (C) *Scolochloa festuacea*, (D) *Scirpus validus*, (E) *Typha* × *glauca*, (F) *Scirpus acutus*, and (G) unvegetated areas. The wetland water levels were normal (0 m) in 1980, flooded (+1 m) in 1982, drawn down (−0.5 m) in 1984, and flooded again (+0.3 m) from 1985 to 1989. Predicted and observed values are presented as the mean proportion of each cover class in the three wetlands. Predicted values are model estimates, and observed values are calculated from aerial photographs of the wetlands.

ing flooded periods, dropped rapidly in the draw-down period, and increased during the last five years of the experiment when water levels were held constant (Fig. 5). While this overall pattern was similar, the models differed in their relative accuracy. The niche model

always had the lowest accuracy until the last three years during the stable water conditions of the recovery period (Fig. 6). In general, the addition of increasingly detailed data increased model accuracy. Although, the addition of adult distribution data did not improve mod-



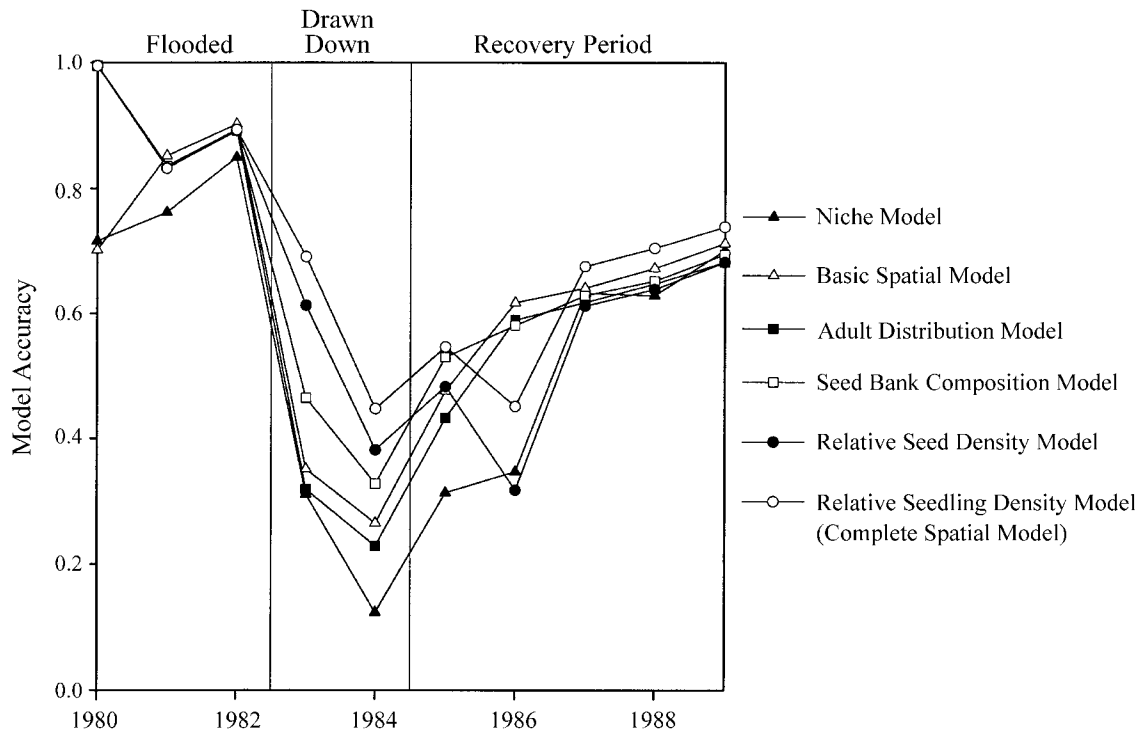


FIG. 5. Temporal change in the overall accuracy of six models estimating the vegetative composition in ten experimental wetlands. Each model incorporates all of the detail of the previous model plus an additional factor that further constrains dispersal. (1) Niche model: Adult distributions were predicted using logistic regression models based on species distribution in relation to water depth. (2) Basic spatial model: Species' colonization abilities are constrained by the explicit landscape geometry imposed by this grid-based model. (3) Adult distribution model: Initial distributions in the simulation are based on actual adult distributions in each wetland at the start of the experimental water level manipulations. (4) Seed bank composition model: Two ruderal species (mudflat annuals and *S. validus*) were added to the seed bank. (5) Relative seed density model: Initial seed densities in the simulations reflect elevational gradients in density based on seed bank data. (6) Relative seedling density model (complete spatial model): Initial seed densities in the simulation reflected seedling recruitment rates rather than seed density. Each point is the mean accuracy for 10 experimental wetlands.

el accuracy (i.e., the basic spatial model was at least as accurate than the adult distribution model; Fig. 5).

At the start of the simulation, the models that started with simulated adult distributions had an accuracy close to 0.75 while the models that began with actual adult distributions, by definition, had perfect accuracy. During the subsequent two years of flooding, the spatial models were more accurate than the niche model in their prediction of large amount of open water (Figs. 4 and 6). The greatest disparity between the models occurred during the draw-down period when model accuracy was at its lowest. During the draw-down period, the complete spatial model was the most accurate (Fig. 6). The relative accuracy of the models converged during the stable conditions of the recovery period their level of accuracy was indistinguishable during the last three years of the experiment (Fig. 6).

The niche model was the least accurate during the draw-down period and the first two years of the recovery period (Fig. 5). Model accuracy was increased during the draw-down period by incorporating the effects of ruderal species, relative seed densities and distributions, and seedling densities. A single exception

to this pattern occurred in 1986 when the models that incorporated detailed seed and seedling data were less accurate than the other models due to an overestimation of the cover of *Scirpus validus* in 1986 (Fig. 4D).

The low accuracy of the niche model during the draw-down period was due to an overestimation of the extent to which *Phragmites* was present immediately following recruitment (Fig. 4). During the early recovery period the niche model also overestimated the open areas, because it did not incorporate the time lag caused by the gradual mortality of plants due to the flooded conditions.

We compared the effects of the experimental water level treatments on the accuracy of the niche model and the complete spatial model. During the last five years of the experiment, when there were differences among the treatments, the niche model accuracy was unaffected by the treatments (Fig. 7). Initially, the complete spatial model was less accurate in the high-water treatments and most accurate in the normal treatments (Fig. 7). This effect was caused by an overestimation of the proportion of open areas in the high water treat-

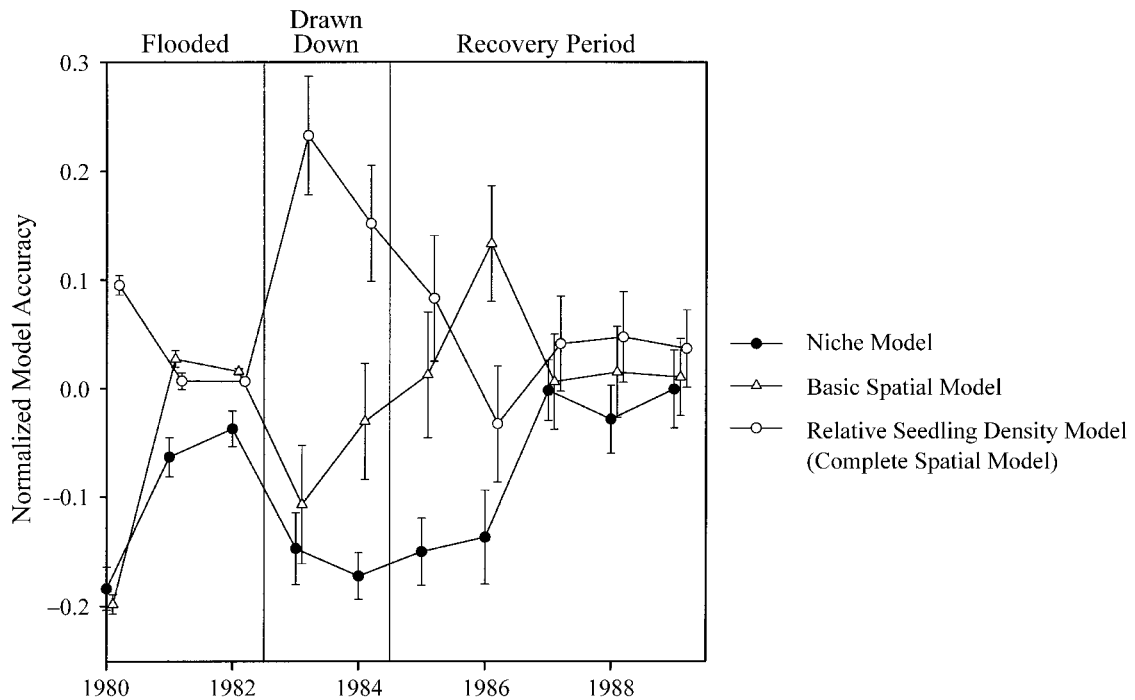


FIG. 6. Normalized accuracy of the niche, basic spatial, and complete spatial models' estimates of the vegetative composition in ten experimental wetlands. Accuracy is the similarity between the vegetation coverage predicted by a given model and the vegetation coverage in the aerial photographs (see Eq. 3). Accuracy is normalized by subtracting the mean accuracy for each wetland. The niche model makes predictions of adult distributions based solely on current water depth.

ments (Fig. 4). This treatment effect was not present in the last three years of the study.

#### *Predictions of landscape physiognomy*

We used paired *t* tests to compare patch area and contagion in simulated landscapes generated by the basic and complete spatial models. In paired *t* tests, mean patch area in the 1989 aerial photographs (1461 m<sup>2</sup>) did not differ from the mean patch area of the simulated landscapes produced by the basic spatial model (1104 m<sup>2</sup>,  $P = 0.11$ ) or the complete spatial model (1353 m<sup>2</sup>,  $P = 0.79$ ). Likewise, the patch contagion of the aerial photographs in 1989 (39.4) did not differ from the contagion in the simulated landscapes produced by the basic spatial model (41.0,  $P = 0.77$ ) or the complete spatial model (45.2,  $P = 0.30$ ).

#### DISCUSSION

In our analysis of the MERP experimental data, we found that constraints on species' ability to colonize suitable habitat created a several year lag-period during which species distributions were more strongly related to historical recruitment events than to the current environmental gradient. Species were constrained in their ability to respond to environmental change by landscape geometry and its inherent limits on species movement. In addition, species' dispersal was limited by their initial distributions and density in the seed bank

and their ability to colonize through vegetative dispersal.

Despite their initial importance, establishment constraints had only a transitory effect following water level changes. Eventually, the community began to converge on its original distribution relative to the water depth gradient (Fig. 5). The rate at which the original coenocline was re-established depended on the direction of the water level change. During the flooded period, the original coenocline was rapidly reestablished as indicated by the high accuracy of the niche model (Figs. 5 and 6). In wetlands, species distributions in flooded conditions are largely dependent on physiological tolerance of anoxic conditions (Squires and van der Valk 1992), which is a direct function of water depth.

In contrast, many species can colonize and survive in the mesic conditions present during a draw-down period (Seabloom et al. 1998), and community composition is driven by dispersal and colonization events. This was the case in the MERP wetlands, as indicated by the high accuracy of the spatially explicit models relative to the niche model (Fig. 6).

The accuracy of all models was low during the draw-down period. In our simulations, we did not have explicit seed-bank distribution data for individual wetlands and relied on the relationship between elevation and seed density (Fig. 3). To improve the overall ac-

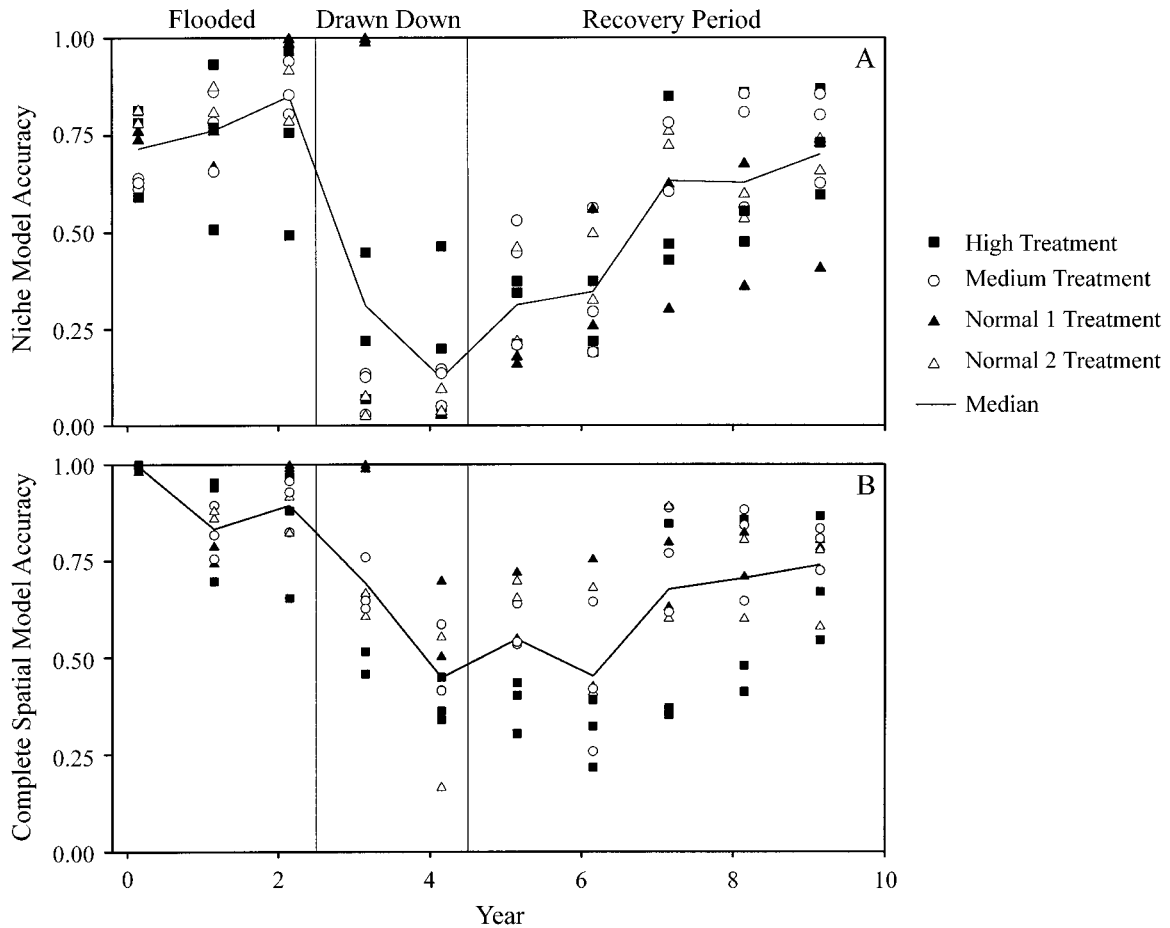


FIG. 7. Temporal change in the overall accuracy of the niche and complete spatial models in estimating the vegetative composition of ten experimental wetlands.

curacy of the model predictions, it may be necessary to collect more detailed seed-bank data rather than relying on seed-bank composition and elevation relationships to reconstruct spatial patterning. In addition, our seedling competition model was based solely on seed abundance. However, it is clear that water depth can have strong effects on community composition (Keddy and Ellis 1985, Keddy and Constabel 1986, Seabloom et al. 1998), and a more realistic model of seedling competition could also improve the predictive power of the spatially explicit models during the draw-down period.

#### *Modeling vegetation dynamics in a fluctuating environment*

The relative performance of the models we tested suggest some general recommendations for researchers attempting to model landscape-scale species distributions in stable and dynamic environments.

1. *A spatially explicit modeling approach may provide the most accurate predictions of species composition in dynamic landscapes.*—We found that the spatially explicit models made more accurate estimates of

vegetation change in dynamic environments than the niche model. The spatially explicit models also converged with the actual species distributions more quickly than the niche model following an environmental shift.

There is a caveat to this recommendation. While the basic spatial model was based on the same data as the niche model, the complete spatial model incorporated seed and seedling distribution data that may not be available in all systems. In addition, the absolute accuracy of the spatially explicit models was at its lowest when it provided the greatest relative improvement over the niche model. All the models were much less accurate during the recruitment events that occurred during the draw-down period (Fig. 5).

2. *Simple spatial models can accurately predict landscape physiognomy.*—Without the addition of any information beyond that contained in the niche model, the basic spatial model was able to predict mean patch area and contagion. The ability to predict spatial pattern is a distinct advantage over purely environmentally based statistical models, in which spatial pattern is largely determined by pixel size. Given an accurate

description of the spatial-autocorrelation structure prior to a manipulation, it may be possible to build statistically based models that accurately recreate spatial pattern. However, this approach would only succeed if the autocorrelation structure of the plant community was unaffected by environmental fluctuations.

3. *Simple niche models may provide accurate predictions of species composition after a period of stable environmental conditions.*—These models have two appealing properties: they rely on familiar techniques, such as linear or logistic regression; and they can be developed with little a priori knowledge of system processes, because they are phenomenological in nature.

Niche models are expected to perform best when environmental conditions are stable, because they assume species are at equilibrium with their environment, (de Swart et al. 1994). Nonetheless, they have been used to predict species' responses to environmental change (e.g., Barendregt et al. 1992). Our results indicate that these models will only make accurate predictions after a period of environmental stability. In contrast to the MERP wetlands, the length of time required before niche models will produce accurate results may be hundreds of years if reestablishment is limited by spatial isolation, depauperate seed banks, or preemption by exotic species (Godwin 1923, Møller and Rørdam 1985, Galatowitsch and van der Valk 1996).

#### *Plant community responses to dynamic environments*

Because species differ in their adult niche, environmental gradients that are associated with changes in resource levels or stress intensity can directly control both the total pool of species that have the potential to exist at a location (Liebig 1840, as cited in Kaiser et al. 1994; Shelford 1911, Shreve 1922, Gause 1932, van der Valk and Welling 1988) and the number of species that coexist at a given location along the gradient (Whittaker and Niering 1965). Accordingly, abiotic factors often have a large impact on the distribution of species in landscapes as is shown clearly by the frequency with which species are distributed in zones arrayed along single environmental gradients.

Nonetheless, abiotic conditions alone may not be accurate predictors of species distributions, especially in dynamic landscapes. Many species are very limited in their ability to move between locations, and order of species arrival at a site has been shown to have large effects on species distributions (Cornell and Lawton 1992, Caley and Schluter 1997, Tilman 1997) and community structure (Grace 1987, Robinson and Dickerson 1987, van der Valk and Welling 1988, Drake 1991). To the degree that species are limited in their ability to become established in areas of suitable habitat due to preemption or constraints on dispersal, their distribution will reflect historical recruitment events as well as the current environmental conditions.

In our modeling simulations, we examined the ef-

fects of five factors that can constrain species' recruitment: landscape geometry, the distribution of refugial adult plants, the presence of ruderal species in the seed bank, seed bank density and spatial patterning, and differential germination rates. We found that all of these factors, except the initial distribution of adults, increased the accuracy of the model predictions. We interpret this increase in accuracy as indicative the importance of these factors in determining species' distributions.

Each of these factors has been shown to affect the distribution and competitive abilities of plants in other studies. The geometry of a landscape has direct effects on species dispersal and colonization rates because it directly affects the ability of species to colonize areas of suitable habitat (Godwin 1923, Møller and Rørdam 1985). In fact, Palmer (1992) asserts that studies of species responses to environmental gradients that do not explicitly incorporate effects of landscape geometry are likely to be "seriously compromised." The spatial patterning of adult plants has also been shown to delay or, possibly, even forestall competitive exclusion in experimental (Harper 1961, van Andel and Nelissen 1981, van Andel and Dueck 1982, Marshall 1990, Thórhallsdóttir 1990) and modeling studies (Czárán and Bartha 1989, Silvertown et al. 1992). Ruderal species can often dominate a plant community in areas of high disturbance (Colasanti and Grime 1993), and the dynamics of these and other species are often determined by their relative abundance in the seed bank (Egler 1954, van der Valk 1981). Species-specific germination rates can change the composition of the pool of species in the seedling community from which adult plants are recruited (Grubb 1977, Seabloom et al. 1998).

Although establishment constraints were important initially, their effects were temporary, and all models had similar accuracy during stable conditions. The convergence of the environmentally based niche model with the spatially explicit models indicated the declining importance of establishment constraints under stable environmental conditions. This result is in contrast to the modeling work of Ellison and Bedford (1995) in which seed bank dynamics and seed dispersal patterns had lasting effects on composition of a freshwater marsh.

The discrepancy between our results and those of Ellison and Bedford (1995) are not surprising. While our results indicate that the effects of establishment constraints were transitory, it is unreasonable to expect historical effects to attenuate as rapidly as in the MERP wetlands in all biological systems. It is clear that recovery from major disturbances can take hundreds of years if preempting species are long lived or the habitat is very isolated and has a limited number of residual plants or propagules (Godwin 1923, Stahelin 1943, Peet 1981, Møller and Rørdam 1985). It is also evident in other systems that disturbance may drive a system

into an alternate stable state due to profound physical changes in the environment or competitive exclusion (van de Koppel et al. 1997, Turner et al. 1998). In these cases, the original coenocline will not be reestablished, because the original cohort of species can no longer persist at the site.

After the draw-down, the rate at which the original coenocline was reestablished in the MERP wetlands was probably atypically rapid, because the experimental wetlands are directly adjacent to a large marsh which can serve as a seed source. In addition, the length of the draw-down was sufficiently short that there was probably little loss of diversity in the soil seed bank (Wienhold and van der Valk 1988). Rather than establishing a typical rate, the MERP data illustrate that a coenocline composed of perennial species can be reestablished rapidly given sufficient propagule availability and in the absence of invasive exotic species.

The restoration of prairie pothole wetlands in the midwestern United States provides an examples of wetland recovery in the absence of adequate sources of propagules. These wetlands are similar hydrologically and floristically to the MERP experimental wetlands. However, reflooded prairie pothole wetlands do not converge on predrainage floras as rapidly as the MERP wetlands. In a survey of 27 prairie pothole wetlands, Seabloom (1997) found that after five to seven years, restored wetlands had only 65% as many species as nearby natural wetlands.

Prairie pothole wetland basins have typically been drained for decades and are now isolated in a matrix of agricultural land relatively isolated from other wetlands, although large wetland complexes originally occupied 20–60% of the prairie landscape (Galatowitsch 1993). The current degree of isolation is certainly enough to slow colonization significantly and may be extreme enough to present a permanent dispersal barrier to some species (Galatowitsch and van der Valk 1996).

In addition to having fewer wetlands, the current midwestern landscape is dominated by aggressive exotic species. These species invade the upper zones of restored wetlands and may prevent the establishment of subsequently arriving species (Galatowitsch 1993). The occupation of available safe sites (*sensu* Harper 1977) by exotic species may represent a permanent barrier to continued colonization (Johnstone 1986). If this is the case, then vegetation in restored wetlands will not converge with that of natural wetlands, unless seeds or plants are introduced artificially.

We found that the importance of establishment constraints varied depending on the direction and magnitude of the environmental change. All of the models were able to accurately predict the shift to largely unvegetated conditions during the flooded period within a single year after the water level in the marshes was raised 1 m above normal. Similarly, the accuracy of all models converged during the recovery period. How-

ever, this convergence did not occur until the third year after reflooding.

The rapid convergence of model accuracy after severe flooding occurred because of the presence of a strong environmental gradient that overwhelmed the effects of establishment constraints on species distributions. In freshwater wetlands, flooding-induced anoxia causes physiological stress in most species of emergent plants, but species differ in their ability to tolerate the stress (McKee et al. 1989). In the MERP experiment, plant distributions following an increase in water level were controlled by tolerance of anoxia.

While the models converged more quickly in the flooded than the recovery period, flooding level during the recovery period did not affect the rate at which coenoclines were reestablished. This result is contrary to the findings of de Swart et al. (1994), who found the niche model to be most accurate in the normal flooding treatments. This disparity may be due to the differences in our assumptions about taxonomy and species coexistence. de Swart et al. (1994) combined *Scirpus acutus* and *Scirpus validus* due to the morphological similarity of the species, while we treated *Scirpus* species separately in our simulations. *Scirpus validus* was not present at the start of the experiment, and the original logistic regression for the *Scirpus* species reflects the distribution of *Scirpus acutus*. This regression model was subsequently used by de Swart et al. to predict *Scirpus* distributions during the recovery period that were dominated by *Scirpus validus* (Fig. 4). de Swart et al. (1994) also made independent predictions for each species and, in effect, allowed multiple species to coexist at a single location. In our simulations, only a single species could exist at a single point in space.

The different conclusions in the two studies may also have been statistical in nature. de Swart et al. treated individual elevation survey points within a wetland as replicates, while we treated entire wetlands as replicates. Because of the higher number of samples, the analyses of de Swart et al. had a higher apparent power. However, their analyses did not account for the inherent correlation among samples taken in a single wetland.

It was apparent from field observations that zonation patterns were most rapidly reestablished in the wetlands that were reflooded to the original water levels (A. van der Valk, *personal observation*). In particular, it was clear that most emergent, perennial species could not move upslope following an increase in water level (van der Valk 1994). Instead, the adjustment of the species to the new water levels occurred when open areas created by flooding mortality in stands of *Scolochloa* and *Scirpus validus* were invaded by higher elevation stands of *Typha*. These on-site field observations indicate that de Swart et al. (1994) may have detected a true biological effect of the flooding treatments on the rate of coenocline reestablishment.

In contrast to the cases in which water level in-



creased, the accuracy of the spatially explicit and niche models diverged during the draw-down period with the spatially explicit models becoming increasingly more accurate than the niche model. The divergence in model accuracy suggests that species distributions after a decrease in water levels were driven by factors such as the distribution of seed densities and seedling recruitment rates, as indicated by the higher accuracy of models that incorporated seed and seedling data. Unfortunately, the draw-down period was not long enough to determine if the accuracy of all the models would have converged after several more years, as occurred during the recovery period.

While the more biologically complex models did relatively better during the draw-down period, the absolute accuracy of all the models was at its lowest during this time. This low absolute accuracy is indicative of the stochastic nature of the processes controlling recruitment events. The difficulty of predicting recruitment events in wetlands is illustrated by the ten-year study of recruitment into a freshwater marsh plant community conducted by Leck and Simpson (1995) in which they found only weak correlations among species abundances as seeds, seedlings, and adults. In their annual dominated wetland system, Leck and Simpson found that there were large annual fluctuations in species composition even under a constant water regime. Poiani and Johnson (1993) identified their assumption of unlimited seed availability as a source of error in their model of wetland plant community responses to water-level fluctuations. Ellison and Bedford (1995) also found that the response of the annual species to water-level fluctuations was difficult to predict, presumably because their dynamics are driven wholly by seedling recruitment.

As in other systems, we found that the relative importance of biotic factors and environmental stress changes along the water depth gradient in the MERP wetlands. In the MERP wetlands environmental stress became increasingly important with increasing water depth. In intertidal communities, lower limits on species distributions can be controlled by biotic factors (e.g., competition for space), while the upper limits on their distributions are controlled by tolerance of environmental stresses (e.g., desiccation; Connell 1961). Similarly, transplant experiments have shown that many salt marsh species thrive in the more benign habitats of the marsh, but they are generally restricted by competition to harsher locations characterized by long periods of inundation or high salinity (Snow and Vince 1984, Pennings and Callaway 1992, García et al. 1993).

### *Conclusions*

We tested the effects of five factors controlling the reestablishment of a coenocline following a change in environmental conditions: (1) landscape geometry, (2) spatial arrangement of refugial adult stands, (3) the presence of ruderal species in the seed bank, (4) the

distribution of seed densities in the seed bank, and (5) differential germination and seedling survivorship. We found that each of these factors incrementally increased model accuracy during the draw-down period with the exception of the initial spatial arrangement of adults. The incremental effect of each factor on community composition may explain the difficulty in relating seed density to seedling and adult distributions (e.g., Leck and Simpson 1995), because seed density was only one among the many factors controlling the ultimate distribution of adults.

Our modeling results suggest that the presence of a strong environmental gradient will ultimately control the distribution of species in a community under stable conditions. However, many factors constrain the rate at which plants respond to shifting environmental conditions. Specifically, the effects of landscape geometry on species dispersal, the distribution of seeds in the soil, and the differential germination response of species to environmental conditions can all play a role in determining the rate at which the original coenocline reforms. Accordingly, the distribution of species in dynamic environments will reflect a continually shifting balance between current environmental conditions and historical recruitment events.

The transitory nature of establishment constraints in the MERP wetlands indicates that coenoclines can be reestablished rapidly in wetlands systems. However, given the isolation of many wetlands, their depauperate seed banks, and the presence of exotic species it is much more likely that the original coenocline will require many years to become reestablished, if the wetlands have not already entered a species-poor alternate stable state dominated by weedy exotic species. This conclusion indicates the importance of actively overcoming dispersal barriers by introducing desired species during wetland restorations.

Our results indicate that the response of wetland plant communities to environmental change depends on the direction and magnitude of the change. At one end of the continuum (flooded conditions), species distributions converged on the original coenocline after one or two years indicating that establishment constraints were not important. Conversely, when water levels were drawn down, there was no evidence of convergence on the original coenocline after two years indicating that stochastic recruitment events and other establishment constraints controlled species distributions. In the MERP wetlands, as in other systems, environmental gradients represent changes in the relative importance of abiotic and biotic forces on species distributions.

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#### APPENDIX

A description of the spatially explicit model used to simulate the effects of fluctuating water level on the distribution of freshwater plants, including the rules that govern model initialization, dynamic behavior, and data output is available in ESA's Electronic Data Archive: *Ecological Archives* E082-022-A1.

#### SUPPLEMENT

The source code and detailed parameter descriptions for the spatial model used to simulate the response of freshwater emergent plants to water-level fluctuations are available in ESA's Electronic Data Archive: *Ecological Archives* E082-022-S1.