RESPONSE OF A WETLAND VASCULAR PLANT COMMUNITY TO DISTURBANCE: A SIMULATION STUDY[1]

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Abstract. We developed a spatial computer simulation model of the vascular plant community of a freshwater wetland in south-central Wisconsin. This model, based on the aggregation of an unwieldy collection of species into a manageable number of functional "species-types", is used to investigate the responses of wetland plant communities to anthropogenic disturbance that resulted in alterations in wetland hydrology. The results of the model are in general (rank-order) agreement with 7 yr of observed changes in vegetation structure of a sedge meadow and shallow marsh adjacent to a 1000-MW coal-fired power plant near Portage, Wisconsin. Sensitivity analysis of the model revealed that functional species' responses to disturbance depended most heavily on seed germination and dispersal characteristics, a result predicted qualitatively by the wetland succession model of van der Valk (1981). Although analyses of the model presented here appear to verify the model, validation of the model will depend on the collection of similar long-term data sets at disparate sites. This model may be of use in predicting the consequences of anthropogenic disturbance on other freshwater wetlands.

Key words: cellular automata; community structure; disturbance; functional groups; hydrology; simulation model; wetlands.

INTRODUCTION

Models, either qualitative or quantitative, often are used to test ideas about ecological community structure and to generate hypotheses that can be tested experimentally. Qualitative, or conceptual, models provide a concise representation of an investigator's ideas, hypotheses, or results. Quantitative models often are used to scrutinize the effects of variation in a specific parameter(s), particularly when experimental manipulations are difficult because of temporal, regulatory, or other logistical constraints. Such models also help streamline research efforts by focusing attention on critical processes structuring communities.

Quantitative models come in two general forms: analytical models that are amenable to direct mathematical solution (such as Lotka-Volterra models, or some linear differential equation models), and models that as a result of their formulation, complexity, or assumptions are addressable only through computer simulation. The latter type of models may represent, for example, numerical solutions to unsolvable systems of differential equations, or may be designed explicitly as simulation models.

An example of this class of models is cellular automata, "grid" models in which cells within a large grid have states determined by general system parameters and by the states of neighboring cells (Ulam 1962, von Neumann 1966, Farmer et al. 1984, Wolfram 1986). The distinctive features of such models are that (a) space, time, and the state of each cell in the grid are treated discretely, (b) each cell may assume any of a number of specified states, and (c) at each iteration of the model, the state of each cell is updated according to its current state, the states of its neighboring cells, and a set of fixed transition rules that may be deterministic or probabilistic (Phipps 1992, Molofsky 1994). Cellular automata are spatial, individual-based models that can account for community-level patterns. Such models have been used in biological investigations to examine the dynamics of virus assembly, cell–cell interactions, embryonic development, population dynamics, and community and ecosystem structure (reviewed by Farmer et al. 1984, Wolfram 1986, Molofsky 1994). Silvertown et al. (1992) summarize more recent use of cellular automata as models of various plant population processes and construct such a model to explore the effect of spatial pattern and configuration of competing species on the outcome of competition among terrestrial grasses. Colasanti and Grime (1993) recently developed a cellular automaton model based on rules derived from plant strategy theory (Grime 1977) to simulate vegetation dynamics on gradients of resource concentration and disturbance.
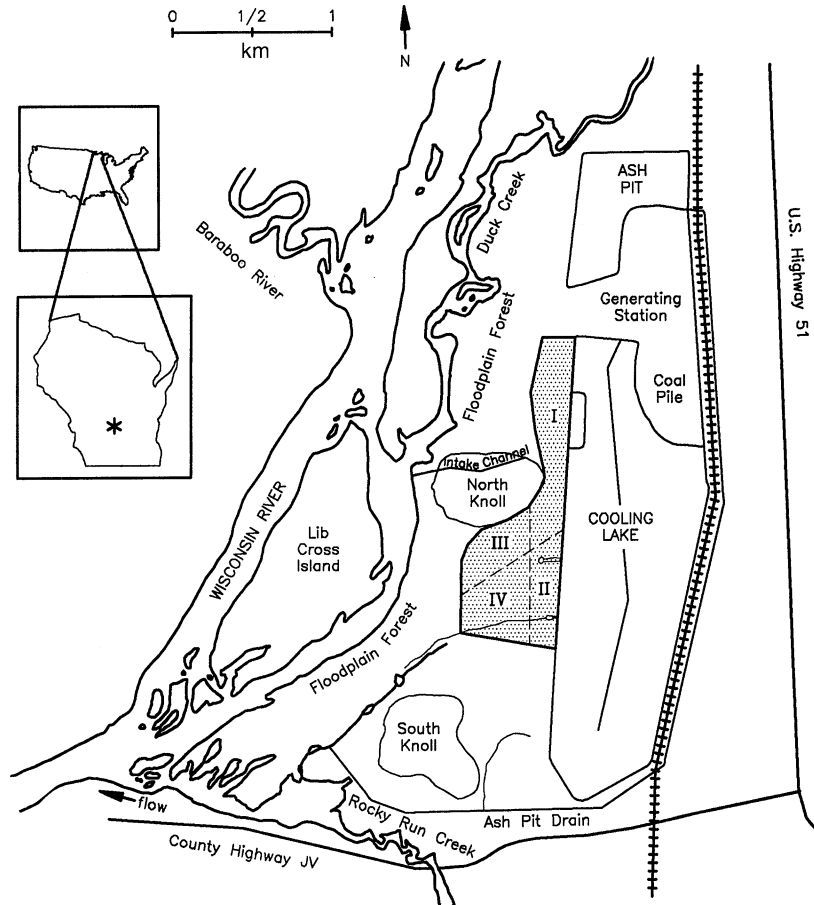
Here, we present the results from a cellular automa-

Fig. 1. Location and schematic map of the study site showing landscape features, facilities of the Columbia Electric Generating Station, and location of sampling area (shaded) with location of the four impact zones (Roman numerals) within the sampling area. The 40 sample transects, 50 m apart, were oriented perpendicular (281° E of N) to the west boundary of the cooling lake.

ton model designed to investigate the response of a freshwater vascular plant community to anthropogenic disturbance. Although wetland models are common in the ecological literature (reviewed by Mitsch et al. 1982, Costanza and Sklar 1985), virtually all of these models examine strictly nutrient or energy budgets of wetlands and rarely consider population- or community-level processes (see van der Valk 1981, Hanson et al. 1990, and Poiani and Johnson 1993 for notable exceptions). Based on 7 yr of vegetation data from a southern Wisconsin sedge meadow, beginning in a relatively undisturbed state in 1974 and continuing through a sustained disturbance (described briefly below, and in detail in Bedford [1980]), we created a simulation model to examine how plant species with different morphological, life history, and seed dispersal and germination characteristics respond to alterations in hydrology. Our model is related to the conceptual model of van der Valk (1981) in that we explicitly examine life history attributes and successional processes. We elaborate on this conceptual picture of wetlands by quantifying species characteristics and, using computer simulations and sensitivity analyses (Dale et al. 1988, Gladstein et al. 1991), examine how variation in these characteristics affects the response of wetland plant communities to severe disturbance.

BACKGROUND

The data set that provides the inspiration for this model is described in detail in Bedford (1980). The data are from a long-term study (1974–1980) of a sustained disturbance (sensu Bender et al. 1984) to a 60-ha section of sedge meadow and shallow marsh on the site of the Columbia Electric Generating Station in south-central Wisconsin, 4 km south of Portage, Wisconsin (43°33' N, 89°27' W; Fig. 1). The climate in this region is continental. Weather varies seasonally with a mean annual temperature of 6.5 ± 0.89°C, a mean summer maximum of 25.7 ± 0.94°C, and a mean winter minimum of −12.9 ± 2.06°C. The average frost-free period extends from about 1 May to 30 September. Annual precipitation averages ≈760 mm, with

more than half of it falling between May and September (Wang and Soumi 1957, 1958).

The Columbia Generating Station consists of two 527-MW coal-fired electric power generating units, a 200-ha cooling lake, a 28-ha ashpit, a 16-ha coal pile, and other associated facilities (Fig. 1). The adjacent wetlands form part of a regional groundwater discharge area and occupy a former channel of the Wisconsin River that lies within its current floodplain. A layer of peat 1–3 m thick overlies a thin layer of organic clay and silt, which in turn is underlain by alluvial sands with clay lenses. Bedrock of Upper Cambrian sandstones and Pre-Cambrian granites occurs at 125 m below the surface (Andrews and Anderson 1979). In 1971, prior to the initiation of construction activities, 545 ha of the site were classified as non-forested wetland: sedge meadow (340 ha), emergent aquatics (183 ha), and lowland shrub communities (22 ha) (Curtis 1959, Wisconsin Department of Natural Resources 1973). Prior to plant operations, the study area (Fig. 1) was dominated by long-lived rhizomatous perennials. Ninety-eight percent of all sampled quadrats contained such species. The numerically and spatially dominant species were *Calamagrostis canadensis*, *Carex lacustris*, *C. stricta*, and *C. rostrata*, which occurred respectively in 52, 61, 45, and 34% of the sampled quadrats. No quadrats were unvegetated, seedlings of the perennials were rare, and annual species were sparse (occurring in 26% of the sampled quadrats) (Bedford 1980).

Between 4 November 1974 and 2 January 1975, ≈200 ha of this wetland were filled, following construction of 5 m high dikes or by flooding, to form a cooling lake for the generating station. The first electric generating unit began operation in April 1975, at which time heated water began discharging to the cooling lake (Andrews and Anderson 1978, 1979). Heat output to the lake increased in spring 1978 when the second unit began operation (Andrews and Anderson 1979). Once the cooling lake was filled, water from the cooling lake leaked into the adjacent wetland (Andrews and Anderson 1978, 1979). Four broadly-defined disturbance zones were distinguished based on gradients of change in the amount of leakage and the dissipation with distance of the heat associated with the leakages (Bedford 1980; Fig. 1): two areas (impact zones I and II) where both water levels and water temperature changed; an area with water level increases but no significant changes in temperature (impact zone III); and an area with less change in water depth and no significant change in water temperature (impact zone IV). Changes in water depth in the four impact zones are shown in Fig. 2. In the model presented here, we focus on responses by the plant community only to changes in water depth, not to changes in temperature (e.g., impact zone III).

In the summer and fall of every year from 1974 through 1978, the fall of 1979, and the summer of 1980,
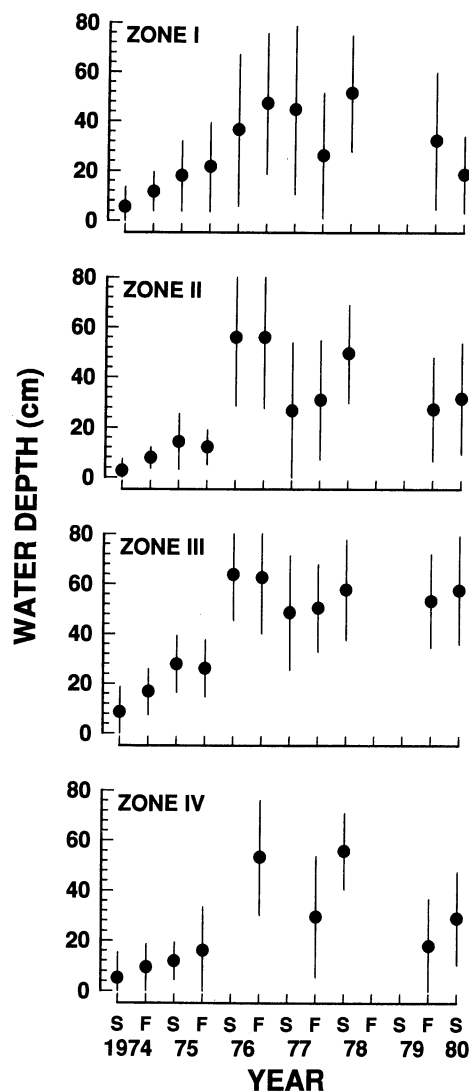

FIG. 2. Water depth (quadrat means ± 1 SD) for the four disturbance zones before (1974) and after (1975–1980) filling of the cooling lake.

water depth and marsh vegetation were surveyed to assess changes in the composition and structure of the vegetation. Note that sampling began before the power plant began operations. Water depth was measured and all vegetation was counted (number of stems) and identified within two 0.25-m² randomly-oriented circular quadrats at 50-m intervals along 40 permanently marked transects spaced 50 m apart. Percent cover of floating aquatic plants (e.g., *Lemna minor*) was estimated if these species were present. Because the permanent transects were established before the impact zones were defined, the total number of quadrats per impact zone differed (impact zone I: 50 quadrats; II: 112; III: 106; IV: 98). Logistical constraints (time, money, and weather) limited the actual number of quadrats sampled each year. A total of 169 species were

encountered in the samples. Nomenclature follows Gleason and Cronquist (1991); plant voucher specimens were deposited in the Madison Herbarium, University of Wisconsin (WIS). Complete descriptions of the survey technique and vegetation are presented in Bedford (1980).

For modelling purposes, 169 species are unwieldy. We therefore grouped these species into a smaller number of "species types" or functional groups. In studies of species-rich communities, aggregation of species into functional groups was pioneered by Raunkaier (1934) and Dansereau (1951), and is a common approach to understanding processes responsible for large-scale vegetation structure (e.g., Rogers 1983, Bouchard et al. 1987, Floret et al. 1987, Smith and Huston 1989). In our model, species groupings are based on morphology, life history, and seed dispersal characteristics (Table 1). Our model can accommodate up to 10 different functional "species", each of which is defined by a combination of 10 life history characteristics. With some exceptions (e.g., *Typha, Carex, Potamogeton, Polygonum*), life history data are unavailable for most wetland species. We used available data on wetland seed banks and seed germination ecology (Ungar and Riehl 1980, Parker and Leck 1985, Farmer and Spence 1987, Leck and Simpson 1987, McGraw 1987, Welling et al. 1988*a, b,* Gerritsen and Greening 1989, Leck 1989, McIntyre et al. 1989*a, b,* Poiani and Johnson 1989, Streng et al. 1989), wetland plant growth and response to flooding (Grace and Wetzel 1981*a, b,* Farmer and Spence 1987, Heathcote et al. 1987, Talbot and Etherington 1987, Talbot et al. 1987, Waldren et al. 1987*a, b,* Donovan et al. 1988, Grace 1989, Carter and Grace 1990) and other environmental gradients (Keddy 1984, Shay and Shay 1986, Shipley et al. 1989, Poiani and Johnson 1993), and our own observations on wetland species to define the functional groups. The groupings that we came up with fit easily into functional group categories of wetland plants described independently by Boutin and Keddy (1993). We refer to our simulated functional "species" simply as species throughout the remainder of this paper to avoid wordiness.

THE MODEL

Model description

The wetland is simulated as a 100 × 100 cell grid, which allows spatial effects to be incorporated explicitly. Spatial effects considered here include local variation in seed dispersal, growth patterns, death, and water level (analogous to local topography). At any time, a given cell can be occupied by at most a single stem (ramet) of a growing plant. Seeds of all species types can occupy each cell's seed bank. Seedlings can recruit only into empty cells. Seeds, however, can land on and occupy the seed bank of occupied cells. The model structure also permits neighborhood competitive inter-
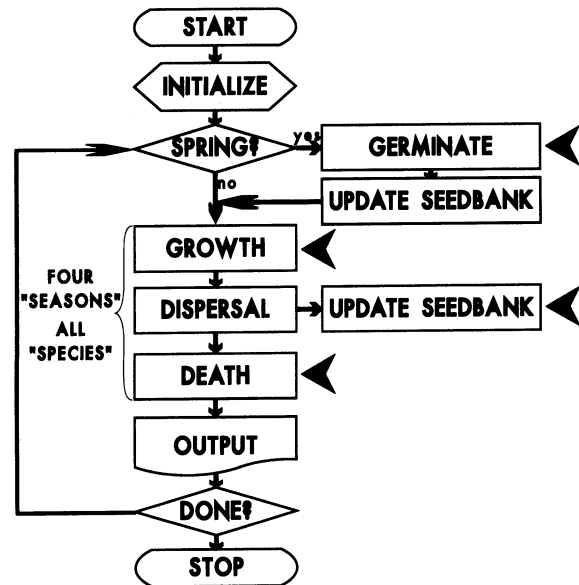

FIG. 3. Simulation model structure. Arrow points indicate subroutines where water level can have significant effects.

actions between species occupying adjacent cells (cf. van Tongeren and Prentice 1986, Silvertown et al. 1992). For the simulation runs described here, such competitive interactions are not included, as most ecological treatments of wetland community structure discount the importance of competition (reviewed by Mitsch and Gosselink 1986, but see Grace and Wetzel 1981*a,* Bertness and Ellison 1987, Grace 1987 for exceptions). We emphasize, however, that preemption of cells by plants is itself a form of competition (cf. Chesson and Warner 1981, Comins and Noble 1985). Preemption is known to have significant impacts on wetland community structure (Bertness and Ellison 1987, Grace 1987).

The general structure of the model is illustrated in Fig. 3. This model is similar to models developed by Karlson (1981), Karlson and Jackson (1981), and Karlson and Buss (1984) to study community dynamics of hard-substratum benthic marine communities, Hobbs and Hobbs (1987) to study the effects of small-scale disturbances in grassland communities, and Poiani and Johnson (1993) to study the impact of climate change on prairie wetlands.

Temporally, each simulation "year" is divided into four "seasons" (spring, summer, fall, winter). Seeds of seed bank species germinate only in the spring; the seed bank species that germinates in any given cell is selected at random (uniform distribution) weighted by the number of seeds of that species present in the seed bank. Seeds persist in the seed bank for a fixed number of years, depending on the species type (e.g., Galinato and van der Valk 1986, Poiani and Johnson 1988, 1989). Each species is assigned a specific season of maximal growth. This season is the only season in

TABLE 1. Species grouping characteristics, and combinations of characters for the four functional "species" used in the simulations. The last two lines of the table give a real wetland species closely analogous to the funcitonal "species", and the functional classification for each species according to the independent classification of Boutin and Keddy (1993).

| Character | Functional "species" group | | | |
	1	2	3	4
Lifespan	Perennial	Perennial	Annual	Perennial
Morphology	Spreading	Caespitose	⋯	Spreading
Means of proliferation	Rhizomes	Rhizomes	⋯	Bulbils
Growth rate	Fast	Slow	⋯	Fast
Primary growing season	Summer	Summer	Summer	Summer
Seed dispersal distance (c_1)	Far (5)	Far (2)	Far (10)	Far (1)
Seed persistence in seed bank (yr)	1	1	3	2
Germination requirement	Under water or drawdown	Drawdown	Drawdown	Under shallow water or drawdown
Change in growth rate with water level (c_2)	Linear decrease (0.2)	Linear decrease (1)	Threshold (N/A)	Linear decrease after threshold depth reached (0.5)
Change in death rate with water level (c_3)	Exponential increase (1)	Exponential increase (4)	Threshold: dies when water level higher than surface (N/A)	Exponential increase after threshold depth reached (2)
Closest real analogue	*Typha latifolia*	*Carex stricta*	*Bidens* spp.	*Cicuta bulbifera*
Comparable functional classification of Boutin and Keddy (1993)	Matrix perennials: clonal dominant	Interstitial perennials: tussock interstitial	Ruderal: obligate annual	Interstitial perennials: clonal interstitial

which growth of that species occurs in the model. For annual species, seedlings germinate in the spring, and persist throughout the year (barring seasonal death, a random process). All annual species die in the winter. For perennial species, seedlings germinate in the spring and reproduce vegetatively during their defined season of growth. Fast- and slow-growing species differ in their rates of colonization of adjacent cells. Slow-growing species can occupy only one adjacent cell during growth, while fast-growing species can occupy more than one. This distinction between fast- and slow-growing species can be considered analogous to real differences in rate of growth or ramet proliferation. The direction of growth is chosen randomly (uniform distribution) from one of the eight cardinal directions as clonal wetland species whose growth forms have been studied normally do not display directional growth (Metcalfe et al. 1986 and references therein). If the cell chosen for lateral growth is already occupied by the same or another species, then it cannot be occupied by the growing species. This decision-rule simulates preemption competition; other forms of competition can be incorporated in the model, but are not analyzed here. Perennial species overwinter in the cells they occupy by the end of the fall season. In the absence of water level changes, seasonal death of both annuals and perennial ramets occurs with fixed probability throughout the year.

Seed dispersal occurs in the season following maximal growth under the assumption that growth and reproduction are often temporally exclusive activities in wetland plants. Seed dispersal in the simulations described here occurs locally to the parent plant, with the number of seeds dispersed into adjacent squares determined according to a truncated gamma distribution (Mendenhall et al. 1981). We used this distribution, rather than the inverse power distribution suggested by Okubo and Levin (1989), because the degree of right (positive) skewness of the gamma distribution can be easily controlled by parameter selection. The number of seeds (s) dispersed a distance r cells from the parent plant (ramet) is then given by:

$$s = \frac{c_1 \cdot e^{(\alpha-1)} \cdot \ln(r) \cdot e^{r/\beta}}{e^\alpha \cdot \ln(\beta) \cdot \alpha!} \tag{1}$$

where α and β are distribution parameters (set here at $\alpha = 2$, $\beta = 1$ to give a positively-skewed probability distribution whose maximum $\gg 0$) and c_1 is a species-specific scaling constant (Table 1) that is directly proportional to the expected number of viable seeds produced. In the runs presented here, the distribution is truncated at three cells distance for species with dispersal "near" to the parent plant and seven cells distance for species with "far" dispersal (Table 2). We only consider primary dispersal of seeds in the model, although secondary dispersal of seeds by water currents is of known importance in wetlands (e.g., Payne and Mann 1981, Schneider and Sharitz 1988). In the densely vegetated sedge meadow simulated here, such secondary dispersal may be less important in determining plant distribution.

In this study, we consider only disturbance due to

TABLE 2. Basic values for variable parameters used in simulations and ranges of parameters examined in sensitivity analyses. See *The Model: Model description* for functions used to relate probabilities of growth and death to water level.

Parameter	Basic value	Range in sensitivity analyses
Vegetative growth		
Rhizomatous: fast spreading	grow 2 cells/season	grow 2–8 cells/season
Rhizomatous: slow caespitose	grow 1 cell/season	grow 1–2 cells/season
Tuberous: fast spreading	grow 3 cells/season	grow 1–3 cells/season
Seed dispersal		
"Far" from parent plant	7 cells distant	4–13 cells distant
Seed production	weighted by c_1 (see Table 1)	unchanged
Seed longevity in seed bank	1, 2, or 3 yr	contrast with exponential decay
Seed germination	identical among species	
Death rate	0.01/season	0.005–0.1/season
Responses to flooding		
Probability of growth	linear decrease with depth	species-specific variance in c_2
Probability of death	exponential increase with depth	species-specific variance in c_3

flooding. In this model, flooding occurs from a point source within the wetland. Although this does not represent the range of possibilities by which a wetland could be flooded, it does mimic in broad strokes the flooding process observed at the Columbia site. In the model, a randomly chosen cell is flooded, and adjacent cells flood in subsequent seasons. From a starting value of water depth = 0, depth in each cell would increase at a rate of 1 unit every 2 seasons once that cell was adjacent to an already flooded cell. After 25–50 simulated years, the entire grid would be under water to some degree. Seed germination is related to water depth by a species-specific germination parameter (Table 1) that determines whether or not a species can germinate in a cell with a given water level. Seeds of species that can germinate only during periods of drawdown will not germinate in a given cell if the water depth in that cell > 0. Similarly, species that germinate only during flooded conditions will not germinate in a given cell if its water depth = 0. Species that can germinate regardless of the presence or absence of water will germinate as long as the cell's water depth is < 20 units. Plant growth rate remains the same regardless of water depth, but the probability that a plant grows at all decreases linearly with increasing water depth:

$$\text{Probability of growth} = c_2 \cdot (1 - 0.02 \cdot \text{water depth}). \quad (2)$$

The probability of plant (ramet) death increases with increasing water depth according to the following function:

$$\text{Probability of death} = c_3 \cdot 0.013 \cdot e^{0.017 \cdot \text{water depth}} \quad (3)$$

where c_2 and c_3 are species-specific constants relating water depth to growth and death rates (Table 1). The function relating water depth to probability of growth assumes that if a plant will grow at all, it will grow in a predictable way (i.e., the rate and direction of growth do not change), but that with increasing water depth the likelihood of any growth declines as a linear function of water depth. Many plants show a roughly linear reduction in growth rate and leaf size in response to

flooding (e.g., Kozlowski et al. 1991, Squires and van der Valk 1992). In our simulations we did not deal with leaf size, and a linear reduction in growth rate is roughly equivalent to a linear reduction in the probability of growth into adjacent cells when only a single ramet can occupy a cell. Similarly, the function relating water depth to mortality assumes that once established, a plant (ramet) is able to survive even as conditions deteriorate (i.e., water depth increases), but eventually conditions are so unfavorable that death occurs with high probability (e.g., Kozlowski et al. 1991). This phenomenon can be modelled easily with an exponential function. Eq. 3 gives a background probability of death of ≈0.01 per ramet per year and the scaling parameter (c_3) is directly proportional to flood tolerance. The relative differences between functional species' scaling parameters c_1, c_2, and c_3 (Eqs. 1–3), not their absolute values, determine the relative performance of each functional species in the model.

The model was written in Turbo-Pascal 3.0 (Borland International 1986) for use on International Business Machines (IBM) PC and PS/2 class computers. Random number generation routines are from Turbo-Rand (Loesl, Ltd. 1986) using standard multiplicative congruential methods (Knuth 1981). Copies of the model (source or compiled code) are available on request from the senior author.

Model execution

For each model run described below, the wetland grid was seeded with four species (=functional groups: Table 1) placed in random positions with relative abundances similar to those seen for analogous species in the Columbia wetland prior to the disturbance. The results presented below are from simulations run for 75 computer "years". Computer years should not be construed as real calendar years; rather, knowledge of the biology of the system permits an appropriate relationship between model "time" and real time. Model results are illustrated as the percent cover (percent of cells occupied) of each species type, because these data

are comparable most closely with the data taken by Bedford (1980).

Sensitivity analyses

We examined the sensitivity of the model to changes in the basic growth, dispersal, seed bank decay, and ramet death parameters. The basic parameters and the ranges examined in the sensitivity analyses are presented in Table 2. The ranges of parameters used in these analyses were chosen to exceed, by at least a factor of 4, the ranges for these parameters found in real situations after appropriate relative scaling for the size of the grid. We contrasted fixed duration of seeds in the seed bank with an exponential seed decay function because many investigators have found that seeds follow an exponential decay rate in the soil (reviewed by Fenner 1983). Seed production was varied by species type simply by varying the scaling parameter c_1 in Eq. 1. Growth and death relationships with water depth were examined by varying c_2 and c_3 of Eqs. 2 and 3, respectively (Table 2).

Sensitivity analyses were performed using a vectorized Fortran-77 version of the model (identical in all respects to the Pascal version) compiled using the VS Fortran version 2.4 compiler on Cornell University's IBM 3090 array-processor supercomputer.

RESULTS

Sample runs

We present results from three sample simulation runs in Fig. 4. Using the basic values for all parameters (Table 2), the annual species (functional species 3) shows a rapid decline with increasing water level (Fig. 4A). Species 1 and 4 are rapidly-growing perennial species with seeds that can germinate both under moderately flooded conditions and during drawdown. These species show an initial slow rate of increase in abundance following flooding, but their rates of increase quicken through time (Fig. 4A). Species 2 initially increases in abundance following the disturbance while water level is low, but declines slowly in abundance as water level increases. These results illustrate the substantial inertia of the system following the disturbance. This inertia is a consequence of the vegetative growth of the perennial species. The annual, unable to colonize new cells except by seed, shows a much more rapid response to disturbance. By the end of this simulation run, however, the two latter species have declined to extinction; the wetland has become a shallow, Typha-dominated lake.

Results from the simulation run shown in Fig. 4A are compared in Fig. 5 with measured abundances of Typha latifolia, Carex stricta, summer annuals, and Cicuta bulbifera at the Columbia site in impact zone III (the area affected most severely by flooding, but not affected significantly by increased water temperature). Based on iterative examination of simulated re-
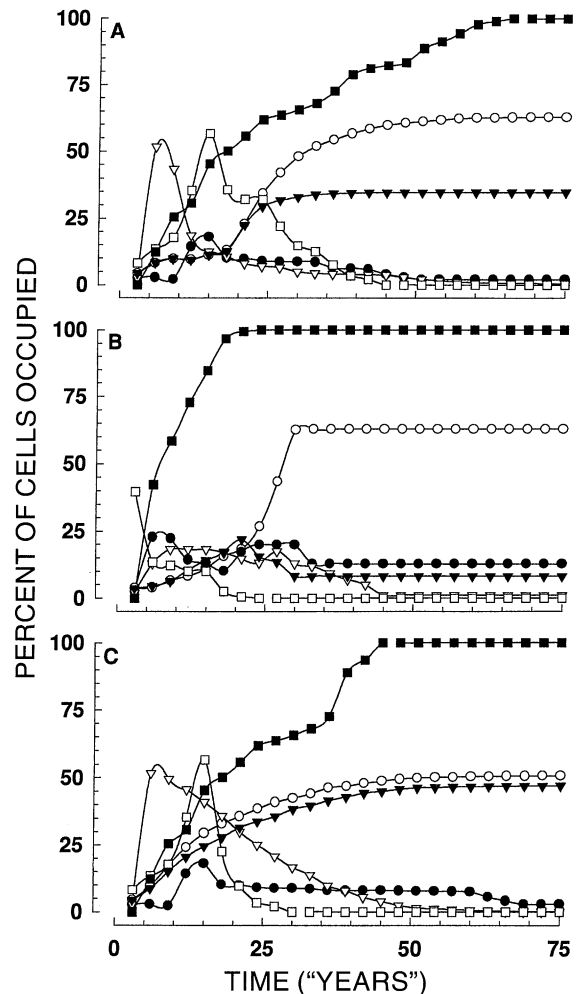

FIG. 4. Temporal changes in abundance of functional species during three sample runs. Symbols: ○ Functional species 1; ● Functional species 2; ▽ Functional species 3; ▼ Functional species 4; □ Unflooded bare space; ■ Flooded cells. See Tables 1 and 2 for parameter sets.

sults with real data, one real calendar year was most highly correlated with 15 simulated years. Consequently, in Fig. 5, observed data from 1974 correspond to simulated data from year 0, observed data from 1975 correspond to simulated data from year 14, etc. Spearman rank-order correlation coefficients indicated good agreement between predicted and observed ranked abundances of Typha ($r_S = 0.9$), Carex ($r_S = 0.6$), and Cicuta ($r_S = 0.8$) (Fig. 5). Differences in absolute predicted abundance relative to real abundance results from the fact that in the model only one stem can occupy a single cell, while observed data are mean number of stems per 0.25-m² quadrat. Model predictions were not well related to actual abundances of summer annuals ($r_S = -0.7$) (Fig. 5), although the extreme variability of summer-annual abundances (annual coefficient of variation in mean number of plants/quadrat ≥ 350%) at the Columbia site make comparisons to
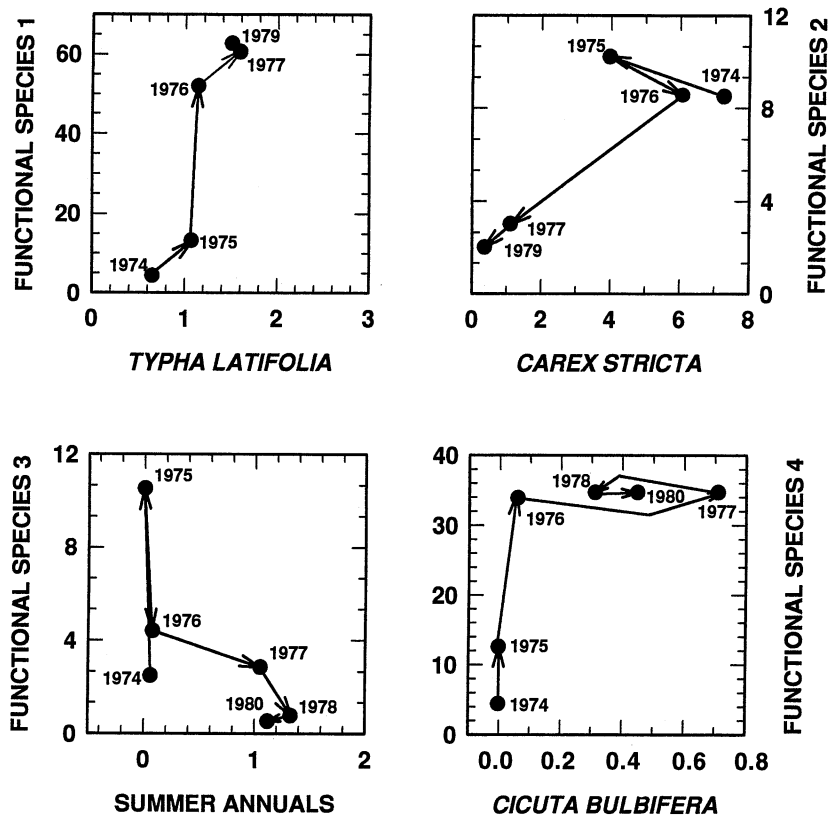
FIG. 5. Comparison of model results (species abundance, from Fig. 4A) with data from the Columbia site. The x-axis is observed mean number of stems per 0.25-m² sampled quadrat, and the y-axis is the percent of cells occupied in the model grid by each functional species. Data for *Typha* and *Carex* are from censuses conducted in impact zone III (Fig. 1) in the fall of 1974–1977 and 1979 (sampling, in successive years: 52, 58, 64, 106, and 70 quadrats), while data for the annuals and *Cicuta* are from censuses conducted in the summers of 1974–1978 and 1980 (52, 59, 64, 106, 106, and 102 quadrats in the respective years). Corresponding model predictions are separated by intervals of 15 simulated years. Functional species 1, 2, and 4 are compared with their closest real analogues (*Typha latifolia, Carex stricta,* and *Cicuta bulbifera,* respectively). Functional species 3 is compared with pooled stem counts of the five most abundant species of summer annuals (*Bidens cernua, B. corona, Impatiens capensis, Pilea pumila, Rorippa palustris*) because of the overall low abundances of any individual summer annual species.

model output more difficult than comparisons with the less variable and more abundant long-lived perennials.

In the second sample run, the relative difference between the fast- and slow-growing rhizomatous species (species 1 and 2) was increased from a factor of 3 to a factor of 5. The results of this change were evident only on species 1 (the fast-growing perennial) and the annual. Figure 4B illustrates that while the responses of species 2 and 4 to water level increase were qualitatively similar to their responses in the first sample run, an increase in the growth rate of species 1 resulted in a more rapid rate of its increase and a more rapid rate of decline of the annual species. As a consequence of its increased growth rate, species 1 could fill more rapidly those cells vacated by the death of species 3 and preclude seedling recruitment by the annual into nearby cells that were not yet flooded. This result also is in good rank-order agreement ($r_S = 0.9$) with the trend of increasing dominance by *Typha latifolia* observed in areas of the Columbia wetland subject to

moderate increases in water level and in water temperature, a factor known to increase growth rates at low levels (Adriano et al. 1980).

In the final sample run presented (Fig. 4C), the relative difference in growth rates between the slow- and fast-growing rhizomatous perennials was restored to the original value (factor of 3). However, the season of growth of the slow-growing caespitose perennial (species 2) was changed from summer to spring. All other basic model parameters were left intact (Table 2). In this run, the dynamics of the annual species (species 3) were similar to the first run. The temporal shift to an earlier growing season by species 2 resulted in a decrease in its rate of decline following flooding (longer time to extinction) and a concomitant slowing in the rate of increase of species 1 and 4, the fast-growing perennials (Fig. 4C). We interpret this result to represent preemption of space early in the growing season by a perennial species that effectively excludes invasion by later-growing species (e.g., Grace 1987). It is
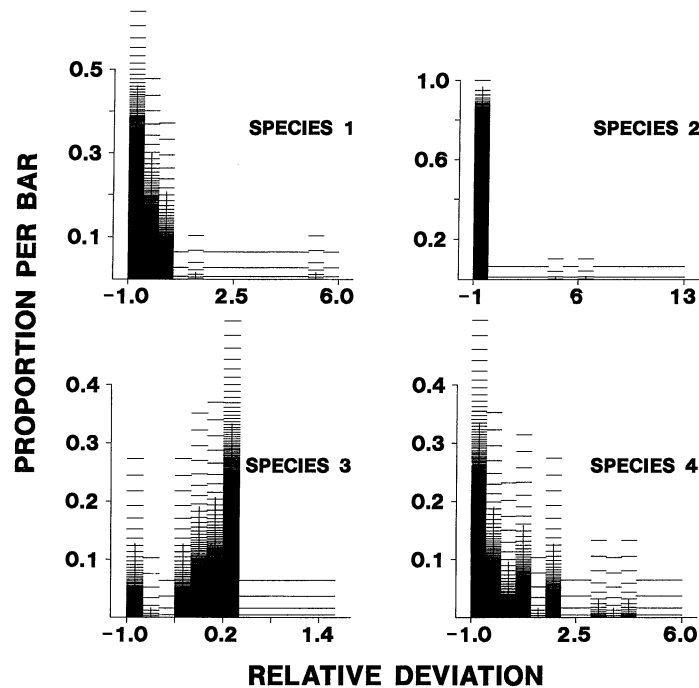
FIG. 6. Frequency distribution of results (difference in species percent cover between runs of the model under the experimental and the basic parameter values) from sensitivity analyses under "dry" conditions. Data are shown as a "fuzzy" histogram (fuzzygram, sensu Haber and Wilkinson 1982, Wilkinson 1990), which superimposes a probability distribution on each bar. The height of the vertical line in the center of each bar is the actual height of the bar in the sample ($n = 64$ model runs). The amount of space between successive horizontal lines of a single bar is derived from an arcsine-transformed estimate of the expected proportion of a similarly-sized replicate sample that would fall within a given interval. Intervals with large sample sizes have relatively solid bars, while intervals with small sample sizes have fuzzy bars. Intuitively, one should have higher confidence in results that fall within intervals with sharper bars than within fuzzier ones. Wilkinson (1990) describes in detail the construction of fuzzygrams, and Haber and Wilkinson (1982) discuss in depth their interpretation.

nonetheless true that in "real" situations, such early growing species may senesce in time for later-growing species also to use the same space. Such dynamics are not incorporated into the model in its present form.

The results of the three sample runs illustrate that while the overall qualitative dynamics of the system are relatively insensitive to changes in some of the parameters, small changes in a single parameter of one species can produce quantitative and qualitative changes in the temporal paths that each species follows. A more detailed investigation of the results of simultaneous changes in multiple parameters is presented in the next section.

Sensitivity analyses

Although virtually all simulation models (including this one) incorporate stochastic elements, these types of models are essentially deterministic. For this reason, as well as the significant cost of computer time, examining the sensitivity of simulation models to changes in model parameters is normally done without replication. That is, the model is run once for each possible combination of values of the parameters of interest. (In this case, to examine all possible combinations of the 8 parameters, each varied incrementally over the ranges

given in Table 2 required 2^8 runs just to examine the extreme values.) Therefore, although varying model parameters normally results in observable changes, assessing the statistical "significance" of such changes is not meaningful given the unreplicated design. In presenting the results, therefore, we illustrate relative deviations from the model run with basic parameter values (Fig. 4A) following changes in parameter values. Only results from extreme values are presented, for simulations run with and without disturbance (flooding). Deviations are given as the percent difference between the equilibrium, final percent cover of each species in the "experimental" run and the same measure in the "basic" run.

Frequency distributions of these relative deviations overlain with their probability distributions (fuzzygrams, sensu Haber and Wilkinson 1982, Wilkinson 1990) are illustrated in Figs. 6 and 7. In both the absence and presence of flooding, deviations from results of the basic runs (Fig. 4A) for all species were relatively small; the mean deviation for each species was generally $< \pm 60\%$ (in the absence of flooding: species 1: -35%; species 2: -56%; species 3: -84%; species 4: $+34\%$; with flooding: species 1: -55%; species 2: -58%; species 3: $+23\%$ [outliers removed]; species
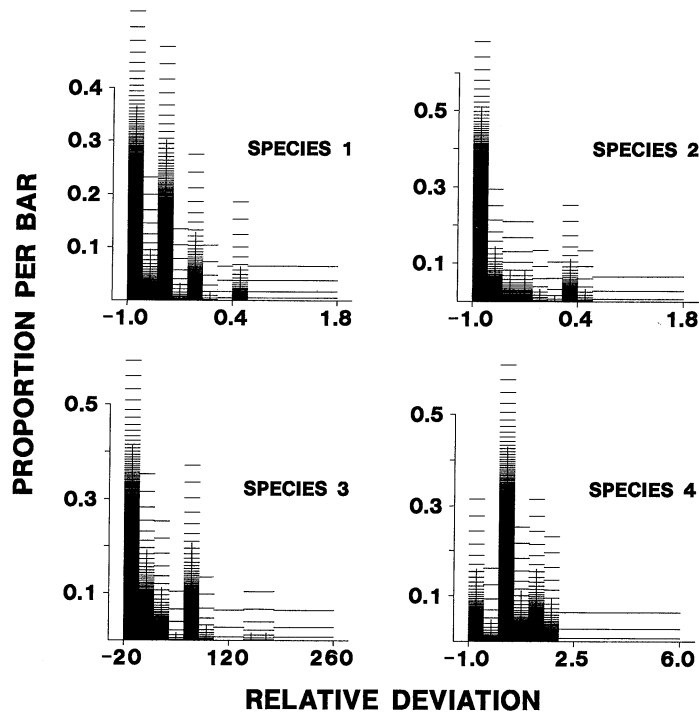
FIG. 7. Frequency distribution of results from sensitivity analyses under flooded conditions. Illustration and interpretation as in Fig. 6.

4: +36%). Deviations for each species were not symmetrically distributed around 0 (Figs. 6 and 7). This result reflects the inherent preemption competition built into the model. Since only one species can occupy a cell at any given time, if variance in a parameter or set of parameters favors a particular species, it will by necessity reduce the abundance of others. Because of this inherent covariance between the final abundances of each species, the absolute magnitude of the deviations shown in Figs. 6 and 7 is not as meaningful as the correlations between deviations of each species.

We examined in detail the correlations between the deviations of all possible pairs of species to determine if changes in particular parameters qualitatively altered the relative performance of each species with respect to the others. These results are best illustrated as matrices of scatterplots, which draw attention to overall pattern as well as to outliers—those points where changes in model input parameters significantly changed relationships between species (Figs. 8 and 9).

In the absence of flooding, significant positive correlations in deviations were seen between species 1 and 2, while significant negative correlations in deviations were seen between species 1 and 3, 2 and 3, and 3 and 4 (Fig. 8, Table 3). That is, in dry conditions, the more mesic perennial species dominate the system and replace (displace) the annual and the emergent aquatic analog. Similarly, under flooded conditions, significant positive correlations were seen between species 1 and 2, while significant negative correlations were again

seen between species 1 and 4, and between species 3 and 4 (Fig. 9, Table 4). In the context of a flooded wetland, this result clearly illustrates the replacement of less flood-tolerant perennials and mudflat annuals by more flood-tolerant emergent aquatics.

Runs that resulted in outliers, i.e., runs that if removed from the plots would alter the correlation coefficient significantly, are noted as larger symbols on the scatterplot matrices (Figs. 8 and 9). In both dry and flooded conditions, these outliers represent those runs with high values for seed dispersal distance, and a shift in the model from seed banks that diminish on a fixed schedule (1, 2, or 3 yr) to one that is diminished following a negative exponential. Variation in all other parameters resulted in deviations from the basic parameter values of <10%.

Under dry conditions, a shift from short-range dispersal to long-range dispersal underlies all but two of the extreme negative deviations for species 3, and the two positive deviations for species 4. The remaining two extreme deviations (negative for species 3 and positive for species 1 and 2) resulted from a shift to negative exponential decay of seeds in the seed bank. Under flooded conditions in the model, the pattern was reversed. Long-distance seed dispersal and exponential decay of seeds in the seed bank favored (extreme positive deviations) the annual (species 3) and the two less flood-tolerant perennials (species 1 and 2), and resulted in extreme negative deviations for the more flood-tolerant emergent aquatic (species 4).
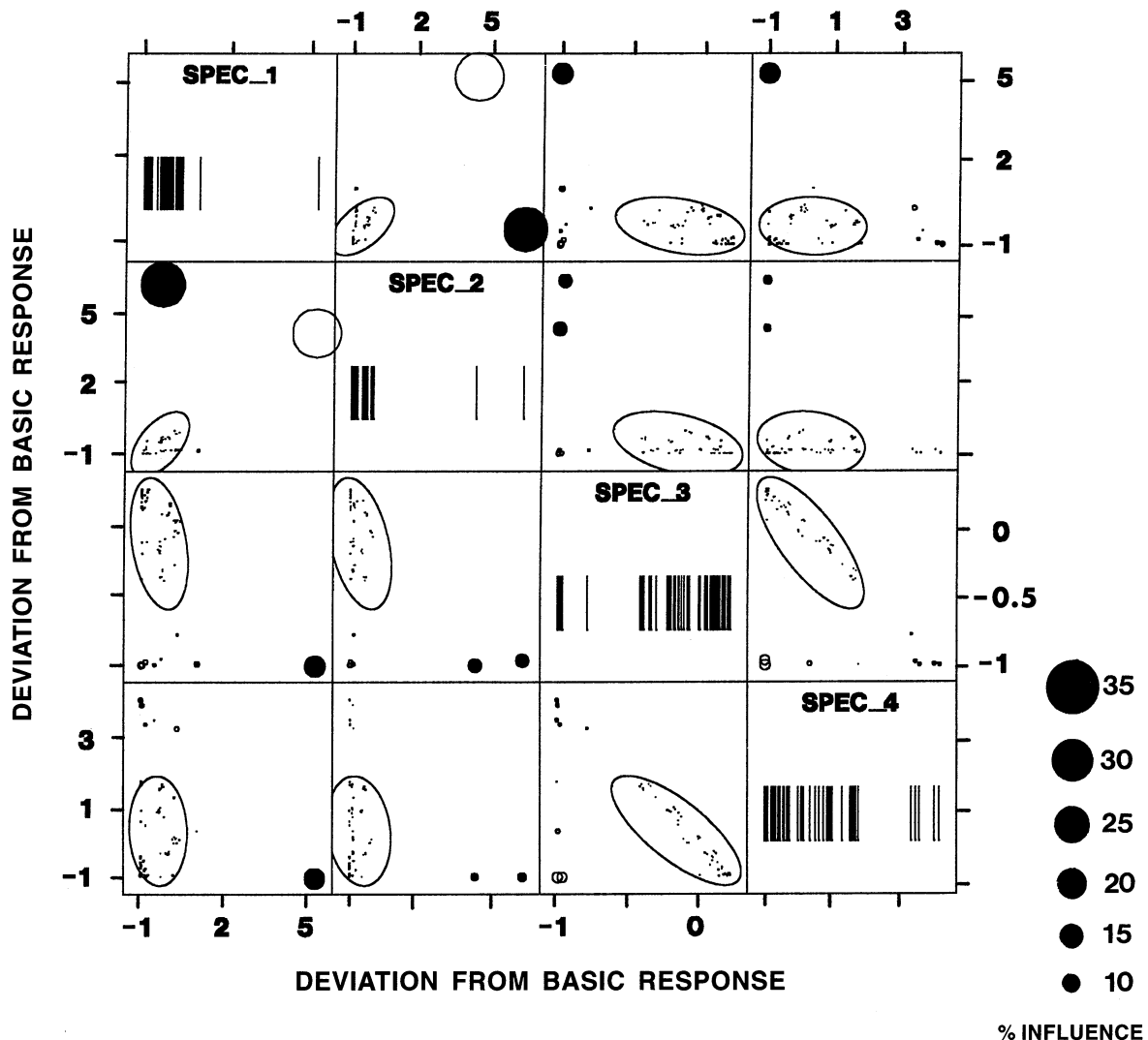
FIG. 8. Symmetrical scatterplot matrix of correlated responses between species under "dry" conditions. The elements on the diagonal of the matrix illustrate density "stripes" (Wilkinson 1990) of the distribution of the deviations from basic values for each of the four functional species in the sensitivity analyses. Each deviation is represented as a single line at a location along the x-axis equal to its value. Extreme "stripes" point to potential outliers along the x-axis. Points on each scatterplot with disproportionate influence on the correlation coefficient for that species pair are sized relative to their influence; a larger size indicates a greater influence. The influence scale (lower right) indicates the approximate percent change in the correlation coefficient if a point of that size were removed (corresponding correlation coefficients in Table 3 were calculated using *all* points). Solid points represent points with severe positive influence on the correlation coefficient, while open points indicate points with severe negative influence. The variable name in the boxes along the diagonal corresponds to x-axis variables of plots below the diagonal, and y-axis variables above the diagonal. Scatterplots above the diagonal are mirror images (axes transposed) of scatterplots below the diagonal. Bivariate 50% confidence ellipses are superimposed on the scatterplots.

DISCUSSION

The results of the simulation model run with the basic parameter set (Fig. 4A; Tables 1 and 2) were in general rank-order agreement with observed patterns of vegetation change at the Columbia site (Fig. 5). In particular, the model simulates well the apparent effects of the power plant in the area of the wetland subject to the most severe increase in water depth (impact zone III; Bedford 1980). The simulated results are in better

agreement with data for long-lived species whose populations showed less within-year variability than for annual, fugitive species. As such, the model appears to be verified (sensu Horn et al. 1989), but validation (sensu Horn et al. 1989) requires use of the model to examine other data sets for which the model explicitly was not constructed. We know of only one other long-term data set for a wetland that has undergone substantial hydrologic disturbance that could be used in
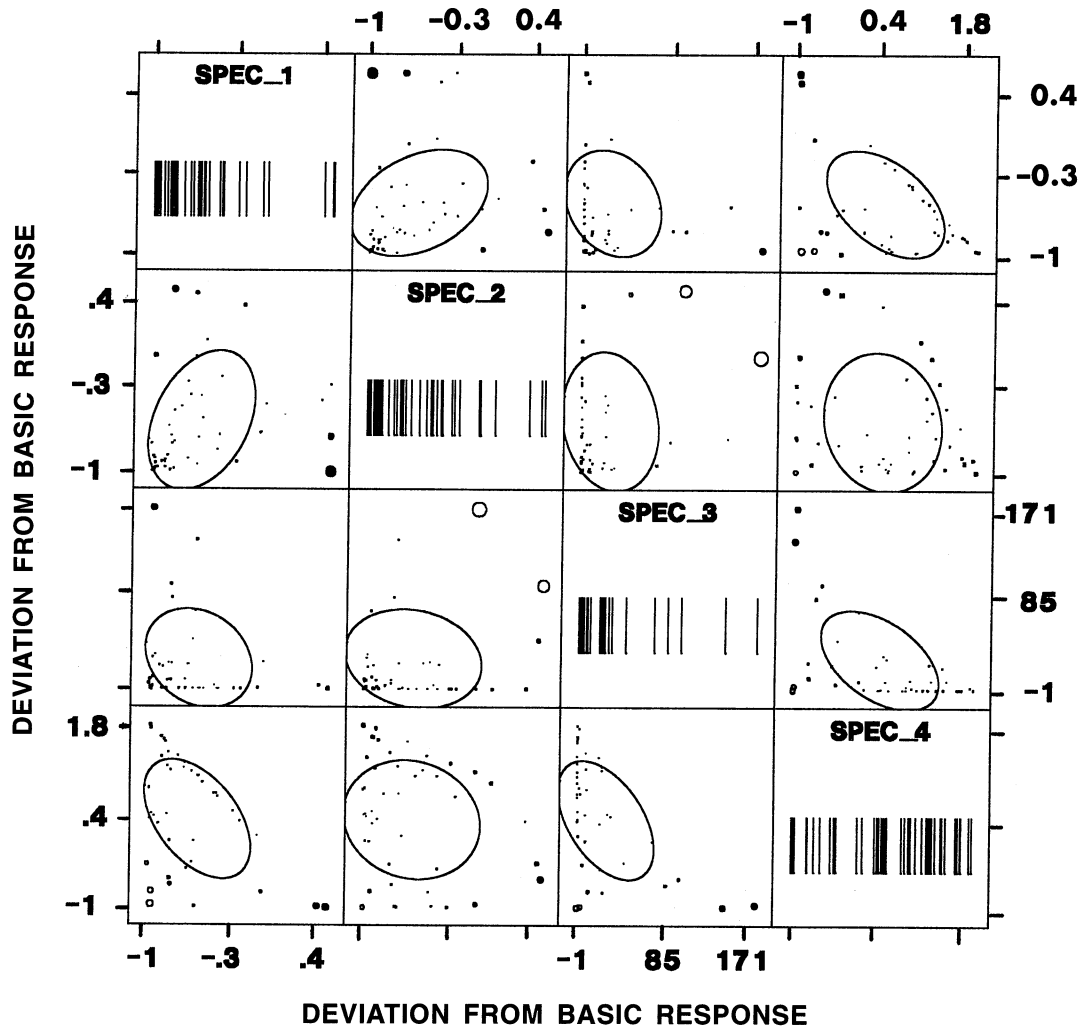
FIG. 9. Symmetrical scatterplot matrix of correlated responses between species under flooded conditions. Notation as in Fig. 8 (corresponding correlation coefficients in Table 4 were calculated using *all* points).

validating this model (van der Valk et al. 1994). Although our model could be used as a predictive tool in assessing potential environmental impact of projects involving wetland alteration, we do not suggest its use in this way without further refinements, validation, and sensitivity analyses. To refine and validate the model, we encourage those with long-term databases to use our model in working with their data.

The model presented here focused on the effects of flooding on wetland community structure. There is a substantial amount of information available on the responses of wetland plant species to waterlogging and flooding (e.g., Grace and Wetzel 1981*a, b,* Farmer and Spence 1987, Heathcote et al. 1987, Talbot and Etherington 1987, Talbot et al. 1987, Waldren et al. 1987*a, b,* Donovan et al. 1988, Grace 1989, Carter and Grace

TABLE 3. Pearson correlation matrix for scatterplots illustrated in Fig. 8 ("dry" conditions in 64 model runs). Bartlett chi-square (Bartlett 1947; tests whether overall matrix ≡ identity) = 134.73, df = 6, $P < 0.001$. Superscripts indicate significance level of correlation coefficient: [NS] $P > 0.05$; ** $0.01 > P > 0.005$; † $P < 0.005$.

Relative deviation	Species 1	Species 2	Species 3
Species 2	+0.548†		
Species 3	−0.326**	−0.383**	
Species 4	−0.051[NS]	−0.161[NS]	−0.757†

TABLE 4. Pearson correlation matrix for scatterplots illustrated in Fig. 9 (flooded conditions in 64 model runs). Bartlett chi-square = 66.95, df = 6, $P < 0.001$. Superscripts indicate significant level of correlation coefficient: [NS] $P > 0.05$; ** $0.01 > P > 0.005$; † $P < 0.005$.

Relative deviation in:	Species 1	Species 2	Species 3
Species 2	+0.346**		
Species 3	−0.220[NS]	−0.151[NS]	
Species 4	−0.482†	−0.111[NS]	−0.492†

1990, Squires and van der Valk 1992), and parameter choices reflect these data. We did not incorporate effects of increased water temperature in the model, but such additions would involve straight-forward modifications of model parameters known to be sensitive to temperature (Dunn and Scott 1987, Donovan et al. 1988). Further refinements of the hydrological portions, on the lines of the model developed by Poiani and Johnson (1993) and incorporating data from geographic information systems, would augment further the predictive power of the model. Although we conclude that our model results are in general agreement with the trends in vegetation change observed from 1974 through 1980 in impact zone III, the area of highest environmental impact due to flooding in the Columbia wetland (Bedford 1980), future versions of the model should be more accurately calibrated to reflect real time and to allow for multiple stems (and competitive interactions) within quadrats. For this model, as with any other, the use of the model, and translation of its results into quantitative, useful predictions of wetland responses to disturbance requires detailed knowledge of the biology, geology, and hydrology of the wetland itself.

Results of the sensitivity analyses that we conducted (Figs. 6–9; Tables 3 and 4) illustrate that seed dispersal and germination properties have the greatest effect on the relative abundance of each species in the model. Because flooding occurs from a point source in this model, species with long-distance dispersal can "escape" local flooding and persist in sections of the grid that have not yet been inundated. In real wetlands, small-seeded anemochorous species such as *Typha* and many annual composites (Asteraceae) readily colonize mudflats exposed during periods of drawdown, as well as areas that have been recently disturbed (e.g., van der Valk and Davis 1978, Poiani and Johnson 1989, Grillas et al. 1991).

The importance of the seed and seedling stages in wetland plant succession and vegetation structure shown by our results was suggested almost 15 yr ago by van der Valk (1981), based on a qualitative model of vegetation change in wetlands. Empirical data gathered in the interim (Keddy and Ellis 1985, Parker and Leck 1985, Leck and Simpson 1987, Welling et al. 1988*a, b,* Leck 1989, McIntyre et al. 1989*a, b,* Shipley et al. 1989) also have illustrated the critical role of establishment and germination strategies in affecting wetland plant community structure. Poiani and Johnson (1993), using a simulation approach, illustrated that changes in germination and establishment patterns in the face of global climate change can alter wetland vegetation significantly. There is a clear need to collect additional data on these life history attributes of wetland species, and to modify accordingly available models of wetland community structure. Wetlands are a primary focus of regulatory concern, and without accurate data to refine and verify existing models, pre-

dictions of changes in wetland community structure will remain in the realm of mysticism.

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