Response of a Semi-permanent Prairie Wetland

to Climate Change: A Spatial Simulation Model.

by

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(ABSTRACT)

The objective of this research was to assess the potential effects of global warming on the hydrology and vegetation in semi-permanent wetlands located in the glaciated prairie region of North Dakota. As a means to that objective, a spatially-defined simulation model of the vegetation dynamics in these wetlands was contructed.

A hydrologic component of the model estimated water levels based on precipitation, runoff, potential evaporation and transpiration. Amount and distribution of emergent cover and open water were modeled using a geographical information system. Vegetation response to changes in water level was based on seed bank composition, seedling recruitment, establishment and plant survivorship. Simulation results were compared to actual distributions from aerial photographs (1979-89).

Results showed that the model was relatively good at calculating changes in water level for average years. Late-summer water levels were overestimated during dry years due to limitations in the Thornthwaite method of calculating potential evapotranspiration.

In general, changes in the ratio of emergent cover to open water

were accurately simulated. Tests of the model elucidated two areas that needed improvement. First, seedlings germinated too quickly on exposed mudflats in the model when drawdown occurred late in the season. The actual wetland had a thick mat of dried, submergent vegetation on top of the mudflats which impeded germination, which the model did not consider. Second, model conversions between open water and deep marsh vegetation were not always timed correctly. If water depth crossed a threshold value for a given period of time a cell would change its type. In reality, tolerance of emergents to deep water is more complex. A probability function with respect to time and water depth rather than a threshold value would better represent this relationship.

The model was used to assess the potential effects of global warming on the cover cycle in one wetland. An 11-year simulation was run using a normal versus greenhouse climate. Although water level fluctuations still occurred, peak values were significantly lower in the warming scenario and the wetland dried in most years. Simulations also revealed a significant change in the vegetation, from a nearly balanced cover ratio to a completely closed basin with no open water areas.

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This dissertation is dedicated to

Rebecca P. Wight.

(1959-1988)

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Introduction

The Prairie Pothole Region of North America (Fig. 1) covers about 780,000 square kilometers of the north-central United States and south-central Canada (Tiner 1984). Millions of glacially-formed small lakes and marshes which vary in size, water permanence and water quality occur throughout this region. This extensive network of wetlands provides the continent's most important habitat for breeding waterfowl, producing between 50 to 80 percent of the North American annual duck production (Kantrud, Krapu and Swanson 1989, Batt et al. 1989). In addition, these wetlands support numerous non-game bird species and other wildlife and are intricately linked to regional hydrology, land use and economics (Weller 1981, van der Valk 1989).

Water levels fluctuate widely both seasonally and annually in prairie wetlands due to well-known climatic variability in the Great Plains (Borchert 1950, Kantrud, Millar and van der Valk 1989). In spring wetlands usually refill from precipitation and runoff from melting snow on frozen or saturated soils while in summer water levels usually decline since evapotranspiration exceeds precipitation. A range of water permanence classes exists due to a variety of wetland basin characteristics (e.g., size, steepness of slope, topographic position, permeability of underlying substrates). The semi-permanent class is especially important to breeding birds (Duebbert and Frank 1984, Kantrud and Stewart 1984). Semi-permanent wetlands typically hold water throughout the growing season during most years and are dominated by deep marsh emergent plants (e.g., Typha spp.) in the central part of the basin (Stewart and Kantrud 1971).

Water level fluctuations in semi-permanent wetlands produce cyclic changes in marsh vegetation (Weller and Spatcher 1965, Weller and Fredrickson 1974). The proportion of emergent vegetation to open water (i.e., the cover ratio) changes during a cycle corresponding with wet/dry periods. Drought initiates the cover cycle by lowering water level and exposing the marsh bottom. A diverse marsh seed bank allows rapid re-colonization of mudflats by annual and emergent species (van der Valk and Davis 1978, Poiani and Johnson 1989). A return to wet conditions refloods the wetland. Mudflat annuals are eliminated. Vegetative growth of the emergents which germinated during exposure is stimulated unless their water depth tolerance is exceeded. Years of normal precipitation maintain a relatively balanced cover to open water ratio. Percent cover for semi-permanent ponds typically ranges from 25 to 75 percent (Weller and Spatcher 1965).

A cycle can be reset in years of high spring runoff (van der Valk and Davis 1978). The marsh is consequently characterized by a high proportion of open water to emergent cover, the latter of which is usually restricted to a narrow, landward band around the perimeter of the wetland. Emergents in the deeper part of the basin are eliminated because of prolonged flooding. Submerged and floating aquatic plants revegetate areas of deep water (van der Valk and Davis 1978).

The cycles are irregular due to the extreme variability of the prairie climate, and range in length from 5 to 30 or more years. The length of the cycle also varies geographically. In Iowa, muskrat 'eat-outs' expedite the loss of emergent cover during high water periods while outside the muskrat's range the cycle is driven only by hydrologic changes (Kantrud, Miller and van der Valk 1989). Erratic changes and reversals in the cycle can occur due to partial exposures or several dry periods over a short time. The cover ratio in semi-permanent wetlands has been shown to affect production of some breeding birds, both in natural and experimentally manipulated marshes and is, therefore, of interest to wildlife and marsh managers (Weller and Spatcher 1965, Weller and Fredrickson 1974, Kaminski and Prince 1981, 1984, Murkin _et al_. 1982).

A qualitative model predicting vegetation composition in freshwater wetlands was proposed by van der Valk (1981). Composition depends on: 1) the potential flora of the wetland, including the actual flora plus all additional species represented only by propagules in the seed bank, 2) the life history characteristics of the primary species, including life-span, propagule longevity and establishment requirements and 3) the primary environmental determinant, water level (van der Valk 1981). The amount and distribution of vegetation in a specific wetland can be predicted by adding a spatial component to the model (i.e., topographical and elevational characteristics of its basin).

The primary objective of this research was to develop and construct a spatial simulation model of the vegetation dynamics in a semi-permanent prairie wetland. The model included a hydrologic component which estimated seasonal and yearly water elevation based on potential evaporation, transpiration, runoff and rainfall. Vegetation response to changes in water level was based on seed bank composition, seedling recruitment, establishment and plant survivorship. The spatial distributions of emergent cover and open water were modeled using a geographical information system (GIS).

Hydrologic and vegetation data for parameterization of the model were from the Cottonwood Lake Waterfowl Production Area, North Dakota (Fig. 1), where wetlands have been monitored since 1975 (Winter and Carr 1980, LaBaugh et al. 1987, Swanson 1987a,b, Poiani and Johnson 1989). A decadal simulation series (1979-89) of cover/water distribution was produced in one semi-permanent marsh, wetland P1 (Fig. 1). Simulations were compared to actual distributions from aerial photographs, and several model parameters were adjusted to maximize fit.

The model was tested using a second semi-permanent marsh on the Cottonwood Lake study site, wetland P4 (Fig. 1). P4 was similar to P1 in water quality, species composition and hydrologic processes (e.g., runoff, refill, evapotranspiration) such that application of the similation model was appropriate. However, basin characteristics between the two marshes differed enough to cause differences in depth, duration and areal extent of standing water and, consequently, the cover ratio. This made P4 a good test wetland. Simulations of hydrology and vegetation in P4 were based on climate data over the same test period (1979-89); results were compared to measured changes from aerial photographs. Model performance was evaluated based on simulations of emergent cover and open water area and distribution.

Since hydrology and vegetation in the model were driven by climate, a second objective was to use the model to evaluate potential changes in the cover ratio due to global warming. Increasing atmospheric carbon dioxide and other 'greenhouse' gases are expected to significantly warm the earth's climate at an unprecedented rate (Schneider 1989, Cohen 1990). Regionally, global climate models project warmer, drier conditions for the North American prairies (Mitchell 1983, Rind and Lebedeff 1984, Manabe and Wetherald 1986, Takle and Zhong 1990). The impact of such changes on breeding habitat for waterfowl may be significant (Poiani and Johnson submitted ms). Potential changes in the cover ratio due to global warming were assessed in wetland P1 using projected temperature and precipitation values expected with a doubling of atmospheric carbon dioxide (Takle and Zhong 1990).

Study Site

The Cottonwood Lake Waterfowl Production Area includes a complex of various sized wetlands located in Stutsman County, south-central North Dakota (Fig. 1). The complex is situated on the eastern edge of the Missouri Coteau, a large glacial drift complex consisting of end and stagnation moraine, ice contact and outwash deposits (LaBaugh et al. 1987). Local relief of the site is about 30 meters and is typical of the Coteau in general (LaBaugh et al. 1987). Hydrologic and vegetation data (including a seed bank study) have been collected on the site since 1979 and 1975, respectively (Winter and Carr 1980, LaBaugh et al. 1987, Swanson 1987a,b, Poiani and Johnson 1988, 1989, G. Swanson unpublished data, T. Winter unpublished data). The simulation model was developed and tested using data from two semi-permanent marshes within the wetland complex, P1 and P4 (Fig. 1)

The climate of North Dakota is continental, characterized by warm summers and cold winters with wide variation in annual and seasonal temperature and precipitation. The mean annual temperature for the study site is approximately 4 °C. The extreme mean monthly temperatures for January and July are -14 and 21 °C, respectively (Winter and Carr 1980). Precipitation for the study site averages 45 cm, with most (35 cm) occurring between April and September. Snowfall averages 87 cm per year (Winter and Carr 1980). Long-term data indicate that annual potential evaporation at the study site is about twice annual precipitation (Rosenberry 1987).

Site Data

Rainfall data were collected adjacent to wetland P1 using a recording tipping-bucket gage with a non-recording backup gage (Winter and Carr 1980). Precipitation data from Woodworth, North Dakota, approximately 19 km north-west of the site, were used for periods when site data were missing and during much of the non-growing season when site data were not collected.

Water level (i.e., stage) data for P1 have been collected during the growing season since 1980 using a recording gage (LaBaugh *et al*. 1987). Data for 1979, spring 1980 and short, infrequent periods of recorder malfunction were from biweekly staff gage readings. All water level data for wetland P4 were from biweekly staff gage readings.

Two years of staff gage data for P4 contained only a single reading per year (7/25/85 and 4/10/86). The remainder of the data for these two years was estimated using staff gage and recorder data from wetland P1 since the magnitude of changes in water level for both wetlands was very similar during all other years (Fig. 2). Water level when P4 was nearly dry in 1981, 1985, 1988 and 1989 (Fig. 2) was estimated from basin topography since the staff gage was not placed in the deepest part of the basin. Standing water sometimes existed in a small portion of the wetland even though the staff gage read 'dry'.

Snow depth and air temperature data were acquired from the nearest weather stations since 11 complete years of site data for these variables were not available. Snow depth data were used from Jamestown, North Dakota, 45 km south-east of the site. Air temperatures were from Pettibone, North Dakota, 35 km north-west of the site. Pettibone station was selected since it is also located on the Missouri Coteau at a similar elevation to the study site. Temperatures at Pettibone and the study site were not significantly different (paired t-test; $p > 0.01$) for years during which a comparison could be made (1982-88, excluding 1986).

Data used to calibrate and evaluate the model were from aerial photographs of P1 and P4 taken annually since 1975 (G. Swanson unpublished data). Photos were digitally scanned for computer input. Deep marsh emergent vegetation and open water (or any other vegetation type located in the central area of the basin) were manually digitized and areal percent coverage was estimated. The upland and the next two

Study site

wetland zones (i.e., wet meadow and shallow marsh emergent types) were not clearly discernable and therefore were not evaluated in the model. Since the principal points in the aerial photographs were not always located in the exact center of the wetland, cover maps were somewhat distorted. Thus, actual values of cover and water were only approximate.

Wetlands P1 and P4

Wetland P1 was chosen for modeling since it was a semi-permanent pond with a relatively balanced cover ratio, which had been in various stages of the cover cycle since 1975. In addition, detailed hydrologic data were collected directly on this wetland as described above. P1 was classified as slightly brackish (i.e., specific conductance = 500-2000 micromhos/cm^3) (Stewart and Kantrud 1971). It was approximately 2 hectares, contained water throughout most years and had no surface water outlet. Because it was located at an intermediate elevation in the local topography it primarily received ground water (Lissey 1971); however, reversals sometimes occurred where water from P1 leaked into underground aquifers (LaBaugh et al. 1987).

Basin topography of P1 greatly influenced wetland hydrology and vegetation. The basin was steep-sided with a nearly flat central area (Fig. 3A) and as a result, even shallow water covered a relatively large area (Fig. 4). When water depth was 50 cm at the deepest point, standing water covered about 12,880 square meters of the basin (≈61%; Fig. 4). When water depth was half that depth, 25 cm, standing water covered about 10,060 square meters of the wetland (≈48%). Even a water depth of 10 cm covered 6,315 square meters or nearly 30% of the basin (Fig. 4).

The vegetation in P1 was characteristic of a slightly brackish, semi-permanent pond. The deepest part of the basin usually contained a fairly stable, extensive open water zone dominated by submerged and free-floating aquatic vegetation such as *Potamogeton pectinatus*, *Lemna* spp. and *Utricularia vulgaris* (Table 1, Fig. 5). The open water area also contained secondary species such as *Zannichellia palustris* and *Chara* spp.

The next three landward zones were the deep marsh emergent, shallow marsh emergent and wet meadow zones. The deep marsh emergent zone was dominated by a single genus, *Typha* spp. (Table 1, Fig. 5). A small area of *Scirpus acutus* was located where high salinity had occurred during previous drawdowns (G. Swanson personal communication, Stewart and Kantrud 1971). The shallow marsh emergent and wet meadow zones contained emergent grasses, sedges and forbs, which were progressively shorter and finer in texture landward. For example, *Scolochloa festucacea* and *Carex atherodes* dominated the shallow marsh zone while *Calamagrostis* spp., *Juncus balticus* and *Agropyron repens* commonly occurred in the wet meadow zone (Table 1, Fig. 5).

Wetland P4, located approximately 200 meters northeast of P1 (Fig. 1), was used to test the model. P4 was similar to P1 in water quality, zonation pattern and species composition (Table 1), and the same basic hydrologic processes operated in both wetlands. Water level changes over the past decade in P4 and P1 followed a nearly identical pattern (Fig. 2).

Basin topography, however, was different in wetland P4. In contrast to the steeper-sided, flat-bottomed basin of P1, the basin in P4 sloped much more uniformly and gradually toward the center (Fig. 3B). As a result, standing water in P4 was usually shallower and covered less area compared to P1, especially when water depth at the deepest point was less than 50 cm (Fig. 4). For example, when water depth was 25 cm at the deepest point in P4, standing water covered only 2,950 square meters of the wetland, compared to 10,060 square meters in P1 (Fig. 4).

These differences in basin topography and hydrology produced differences in the cover cycle and cover ratio between the marshes. Wetland P4 with shallow, less extensive standing water dried up more often than P1 (Poiani and Johnson 1989). In the last decade P1 was dry for a short period only in 1989, while P4 dried up in 1985, 1988 and 1989 (Fig. 2). Because of shallower water and more frequent drying P4 was dominated by deep marsh emergent vegetation with only small patches of open water or exposed soil (less than about 5% of the wetland area) in contrast to the larger, more extensive open water area in P1.

Model Structure

Cover dynamics in wetlands P1 and P4 were simulated using a spatial, deterministic, process-based model (Fig. 6), i.e., the model attempted to represent the primary underlying physical and ecological processes in the system, in contrast to a statistical or probabilistic model which is based on observed correlations in the data, usually without specifying mechanisms (Costanza et al. 1990).

A hydrologic sub-model, written in BASIC, calculated seasonal and yearly water elevations primarily from climatic variables. Amount and distribution of emergent cover and open water were simulated using a geographical information system (MAP) written in FORTRAN (Tomlin 1986). The geographical information system provided the capability to spatially process, analyze and display hydrologic and vegetation data (Burrough 1986). Simulation results were compared to actual cover distributions from historic aerial photographs.

Hydrology Model

The hydrologic sub-model included three primary processes: 1) calculation of initial spring water elevation, 2) increase in stage from precipitation and runoff from heavy rains during the open-water season and 3) decrease in stage due to evaporation and transpiration during the open-water season. In general, initial spring water elevation was calculated for each year from previous fall elevation and spring precipitation. Water elevation was updated daily during the open-water season (Fig. 7).

Although ground water processes were important in the overall hydrology of wetland P1 they were not directly considered in the model. It was beyond the scope of this project to attempt to measure and simulate seepage losses and gains, particularly since ground water/surface water interactions in P1 were complex (LaBaugh et al. 1987). Runoff calculations, in part, included inputs from subsurface aquifers. Estimates of water loss due to evapotranspiration included outputs to ground water.

In model simulations, May 1st and October 31st were chosen as the beginning and ending dates, respectively, of the open-water season (Eisenlohr and Sloan 1968, Shjeflo 1968, LaBaugh et al. 1987). Water elevation on October 31st was assumed to remain constant over the winter since water inputs and outputs to a frozen pond are relatively small (Ficke 1972).

Model structure

Initial Spring Water Elevation

Refilling of a prairie wetland in spring is primarily from direct precipitation and runoff on frozen or saturated soils (Shjeflo 1968). The actual rise in water elevation from the previous fall is affected by the amount of spring precipitation, spring snow depth, timing of snow melt and soil conditions (Willis et al. 1961, Eisenlohr and Sloan 1968, Shjeflo 1968, LaBaugh et al. 1987).

A stepwise regression analysis was performed on data from P1 to determine the statistical relationship between a number of easily obtainable climatic variables and change in stage (Δstage) from the previous fall (last date stage was measured) to May 1st (Table 2). Data were limited to those years during which detailed hydrologic measurements were available for P1 (79/80 through 88/89).

Spring precipitation (sprpre; March + April) was the only significant variable in the regression analysis [Δ stage (cm) = 1.685 + 4.59 * sprpre (cm); $p < 0.001$] (Fig. 8). This parameter accounted for 87.7% (R^2) of the variability in stage changes. Two outliers were omitted from the analysis (81/82 and 86/87) after initial examination of the data (Fig. 8, asterisks). An additional factor or factors clearly caused the large rise in stage in 81/82 and 86/87 since total spring precipitation was low. Snow depth in these two years was greater than 30 cm in March. When all years of snow depth data in March were considered in the regression analysis this variable was not significant (Table 2). Thus, only relatively heavy snowfall in March affected spring stage.

It was necessary to include additional factors when estimating spring stage in 81/82 and 86/87. The standard water equivalent (2.54 cm snow = 0.254 cm water) of the maximum March snow depth multiplied by 1.5 to account for drifting into the basin (Shjeflo 1968) was added to spring precipitation for both years; these adjusted values of spring precipitation were then used in the regression equation derived above. Besides March snow depth, however, an additional source of water increased stage in 86/87. During the previous fall (1986), November was an exceptionally wet month and hence, 4.2 cm was also added to spring precipitation to calculate spring rise in stage for this year.

Precipitation and Runoff

Water gains over the remainder of the open-water season consisted of direct precipitation plus runoff during heavy rainfall events (Fig. 7). Daily gains in stage were calculated by simply adding recorded precipitation and an estimate of runoff to stage elevation.

The occurrence of runoff (rise in stage after a rainfall event minus the amount of precipitation) from summer rain is dependent on antecedent soil conditions and the intensity of the event. Most rainfall events (87%) that were less than 2.4 cm produced no runoff in wetland P1 from 1980 through 1988 (Fig. 9). In contrast, almost 58% of the rainfall events greater than 2.4 cm produced some runoff (Fig. 9). Hence, in the simulation model, runoff was only calculated for rainfall events greater than this value.

Positive values of runoff were plotted against rainfall for events greater than 2.4 cm and a non-linear exponential curve was fitted to the data [runoff (cm) = 0.164 (-0.377, 0.709; asymptotic 95% confidence interval) * precip (cm)$^{1.25}$ (-0.725, 3.22)] (Fig. 10). This equation was used in all hydrologic simulations to calculate runoff for any rainfall event greater than 2.4 cm. Some of the increase in stage after a heavy rain attributed to runoff may actually have been due to an input of ground water. As mentioned previously, these factors are difficult to separate.

An elevation of 559.3 m above sea level was set as the upper limit for increases in stage in P1 (i.e., IF WATEL > 559.3 THEN WATEL = 559.3). Water level has not exceeded this elevation at least since 1967 (G. Swanson unpublished data) which included numerous wet years (1967, 1970, 1975). Overflow into adjacent seasonal ponds and seepage to groundwater from more permeable substrates higher in the basin may prevent water level from exceeding this limit.

Potential Evaporation and Transpiration

Potential evaporation[1] (PE), the major water loss from the wetland

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[1]Thornthwaite calls this term *potential evapotranspiration* since it estimates the total water loss from a moist closed cover of vegetation (Mather 1978). In this study it was necessary to estimate an additional loss due to transpiration, thus, this term will be referred to as *potential evaporation* even though it includes a transpirational component.

during the open-water season, was calculated daily using the climatic water budget method (Thornthwaite and Mather 1957) (Fig. 7). Potential evaporation in the climatic water budget method was based on day length and air temperature. This relatively simple method of calculating PE has some significant limitations compared to more sophisticated techniques (e.g., mass transfer, eddy correlation, energy budget), yet has very wide applicability and is based on routine measurements made at weather stations (Crowe and Schwartz 1981b).

Use of the Thornthwaite method to calculate PE was also favorable for this study since it is based on air temperature. Changes in air temperature with a doubling of atmospheric carbon dioxide as estimated by global climate models were easily substituted into the model for climate change simulations. Calculation of PE and other aspects of the water budget using more sophisticated methods are part of the ongoing research by the U.S. Geological Survey team monitoring the site (T. Winter personal communication).

Unadjusted PE (cm/day) was calculated in the following manner (Mather 1978):

$$\text{unadj. PE} = 1.6\ (10t/I)^{a}$$

where t = average daily temperature (°C), I is an annual heat index and a is a nonlinear function of the heat index equal to:

$$a = 6.75 \times 10^{-7}\ I^{3} - 7.71 \times 10^{-5}\ I^{2} + 1.79 \times 10^{-2}\ I + 0.49$$

The annual heat index, I, is determined by summing the 12 monthly heat index values [$I = \Sigma i$ where $i = (t/5)^{1.514}$, and t = mean monthly temperature]. A long-term average annual heat index (I = 36.88) was determined for the region using 21 years of data (1966-1986). This value was used in all calculations of PE, including climate change scenarios.

Unadjusted PE from the climatic water budget method was the estimated water loss for a day with 12 hours of sunlight. To calculate daily potential evaporation, this estimate was adjusted by day length. Actual evaporation was equal to potential evaporation whenever there was standing water in the wetland (Kadlec et al. 1989) and was subtracted from stage for daily water loss (Fig. 7).

Actual water loss in P1 was significantly greater than estimates from the climatic water budget method (Fig. 11A). Two additional ctors may have accounted for this difference, increased transpiration from emergent vegetation and/or seepage to ground water. Although wetland P1 had occasional flow reversals, it primarily received ground water (LaBaugh et al. 1987). Water loss due to seepage outflow, therefore, would not have accounted for the difference in observed versus calculated values (T. Winter personal communication).

Transpiration from emergent vegetation was most likely the additional source of water loss in P1. To maintain the simplicity of the hydrologic sub-model and because the same meteorological factors influence transpiration, adjusted PE values were increased by a constant percentage for transpirational losses. This percentage is referred to as the vegetation or transpiration coefficient. Three values (0.15, 0.25, 0.30) were tested to determine the closest approximation (Fig. 11B,C,D). A coefficient of 0.25 was chosen and used in all simulations including climate change scenarios.

An elevation of 557.7 meters above sea level was set as the lower limit for decreases in stage in P1 (i.e., IF WATEL < 557.7 THEN WATEL = 557.7) at which point the entire wetland basin was dry. Ground water elevation below the wetland basin was assumed to stay constant because underlying substrates are low in permeability and porosity (T. Winter personal communication).

Vegetation Model

Changes in vegetation were modeled in time and space using a pre-existing geographical information system (Burrough 1986), Map Analysis Package (MAP) (Tomlin 1986). Basin topography of P1 and P4 was digitized from surveyed point elevations, and a computer readable matrix for use in MAP was generated from these points using an interpolation routine, SURFER (1987, Golden Software Inc., Golden, CO). Each cell of the matrix represented approximately 9.3 square meters on the ground. The spatial component of the model was based on this elevational matrix (matrix = overlay in MAP).

In general, the composition of the vegetation at each grid cell at any time, t, was a function of:

Model structure

$$VEG_t = f\ (WDC_t,\ WDC_{t-1},\ LENWDC_t,\ VEG_{t-1},\ t)$$

where VEG = vegetation type, WDC = water depth category and LENWDC = time period in that water depth category. The model simulated cover changes over a growing season (May through October) and produced monthly cover/water distribution maps.

Water Depth

Water elevations (day 1 of each month) generated from hydrologic calculations as previously described were input to MAP. Monthly water depth was calculated for each grid cell and the resulting value was placed in one of seven water depth categories (WDC): (1) < -55 cm, (2) -55 to -10 cm, (3) -9 to 3 cm, (4) 4 to 49 cm, (5) 50 to 55 cm, (6) 56 to 61 cm and (7) > 61 cm. Changes in water depth categories between succeeding months were calculated (i.e., OCT/MAY, MAY/JUN,..., SEP/OCT) and another overlay in MAP counted the number of months that a cell remained in the same depth category.

Vegetation Types

Six functional vegetation types which included species with similar life histories and an open water designation were used in the model (van der Valk 1981, Poiani and Johnson 1989, Ellison and Bedford in prep) (Table 1). Four of the groups represented the relatively permanent wetland zones present in P1: upland (UPL), meadow/shallow marsh emergent

(MSM), deep marsh emergent (DM) and open water (OW). These four types corresponded to specific water depth categories (e.g., OW => WDC 6 & 7). The other three vegetation types represented the more temporary plant communities present during the dry phase of the cover cycle and which usually occupy the central portion of the basin: seedlings (SEEDL), mixed young plants (MIXPLT) and mixed species of shallow and deep marsh emergents (MIXEM) (Table 1).

An initial vegetation type was assigned to each cell and was thereafter updated monthly. Specific conditions under which vegetation types changed are illustrated in Figure 12 and described below.

Process 1: *Germination of seedlings*. An in-depth seed bank study of several semi-permanent wetlands on the Cottonwood Lake site revealed that most of the dominant wetland species had ubiquitous seeds in all zones (Poiani and Johnson 1988, 1989). Therefore, in the model it was assumed that 'unlimited' seeds of the primary plant groups were available in every cell. Composition of seedlings included several species of mudflat annuals and emergent species from all the wetland zones (Table 1).

A cell in the model changed to the SEEDL type under the following three conditions: (1) the cell had no emergent vegetation (i.e., it had previously been OW), (2) the cell was currently dry (WDC 1-2) or was very shallowly flooded (WDC 3) and (3) drying occurred from June through the end of August (Meeks 1969, van der Valk 1981, Welling _et_ _al_.

1988a,b, Poiani and Johnson 1989, Merendino <u>et al</u>. 1990).

Process 2: *Fate of seedlings*. Seedlings which germinated on exposed mudflats during a drawdown had two possible fates. First, if a wetland remained dry or very shallowly reflooded, seedlings persisted and grew. In this case, the maturing plants included both emergents and mudflat annuals. Conversely, if a wetland was reflooded to a greater depth, seedlings died and open water was reestablished.

Cells in the model with SEEDL changed the month following germination. A cell with the SEEDL type converted to MIXPLT if water depth remained in categories 1-3, or the cell changed to OW if water depth was in categories 4-7.

Process 3: *Fate of mixed plants*. If a marsh was dry for the remainder of a growing season after an early- to mid-summer drawdown, a mixture of emergent and annual species occupied the central portion of the basin. Various emergent types or open water were selected the following spring based on new water conditions (Harris and Marshall 1963, Millar 1973). For example, an early-summer drawdown in wetland P1 in 1977 produced a dense plant cover (consisting of emergent and annual species) by late summer. When the wetland was shallowly reflooded in spring of 1978 a zone of mixed emergent species (i.e., primarily <u>Scirpus</u> and <u>Scolochloa</u>) established in the center of the basin (Swanson 1987b).

In the model, a cell occupied by MIXPLT changed to MSM if May water depth was in category 1, to MIXEM if May water depth was in categories 2-5 or to OW if May water depth was in categories 6-7.

Process 4: *Flooding of mixed emergents.* Following a dry period and shallow reflooding, the center of a wetland became inhabited by several species of emergents. When standing water returned to more normal depths for a significant length of time, mixed emergents in the deep part of the basin died, converting these areas to open water (McDonald 1955, Harris and Marshall 1963, Millar 1973, Weller and Voights 1983). In the example of P1 described above, this conversion occurred in early 1981, three years after the emergents established and normal water levels returned.

Cells with the MIXEM type in the model were converted to OW when standing water of any depth (WDC 4-7) persisted for greater than 17 months (i.e., almost 3 growing seasons).

Process 5: *Spread of deep marsh.* Deep marsh emergent species, such as Typha and Scirpus, established from the seed bank during exposure of the substrate (Harris and Marshall 1963, van der Valk and Davis 1978). This zone also spread vegetatively from its existing edges into either shallow marsh or open water areas when water depth was shallow for an extended period of time. A single cultured plant of Typha, for example produced rhizomes with a spread of 3 meters in a single growing season and formed 98 aerial shoots that were from 5-122 cm tall (Yeo 1964).

Model structure

The advancing edges of the deep marsh type competed with established vegetation on the upland side (i.e., meadow/shallow marsh vegetation) but had uncolonized emergent habitat toward the open water side of the zone (Fig. 5).

In the model, a cell converted to DM if water depth was in categories 3-5 for greater than four months and the cell was located directly adjacent to an existing DM cell. This vegetation type was only permitted to spread 3.05 meters (1 cell neighborhood) from the existing edge per growing season.

Process 6: *Spread of meadow/shallow marsh.* Similarly to the deep marsh, the meadow/shallow marsh type either established during a drawdown from seed or spread vegetatively under the appropriate water depth conditions. Vegetative spread of this type was assumed to take longer than the deep marsh type since the advancing edges must compete with established vegetation (i.e., deep marsh and upland) on both sides of the zone (Fig. 5).

In the model, a cell converted to MSM if water depth was in category 2 for greater than 12 months, and the cell was located directly adjacent to an existing MSM cell. This vegetation type was only permitted to spread 3.05 meters (1 cell neighborhood) from the existing edge per growing season.

Process 7: *Establishment of open water.* When water in a marsh was relatively deep and persistent, emergent vegetation died and open water areas were established (Harris and Marshall 1963, Millar 1973, van der Valk and Davis 1978, van der Valk 1981). Different emergent species had slightly different water depth tolerances yet most of the dominant species did not survive in water depths greater than 50 cm after several years of flooding (Harris and Marshall 1963, Millar 1973, Shay and Shay 1986, Welling et. al 1988a).

Any cell in the model changed to the OW designation if water depth was in categories 6-7 for greater than 12 months. This transformation occurred regardless of the previous vegetation type.

Process 8: *Establishment of upland.* Upland vegetation was relatively permanent adjacent to a wetland. However, during the second year of a continuous drawdown some plant communities progressed relatively quickly toward upland communities (Harris and Marshall 1963). Upland vegetation also encroached into the meadow zone if conditions were very dry for a long period.

A cell in the model changed to the UPL type if it was very dry (WDC 1) for greater than 12 months. This transformation occurred regardless of the previous vegetation type.

Vegetation parameters such as water depth category boundaries, number of months for changing a vegetation type and distance an emergent zone spread during a growing season were initially determined based on available literature and personal observations (Harris and Marshall 1963, Yeo 1964, Millar 1973, Kadlec and Wentz 1974, Shay and Shay 1986, Welling et al. 1988a,b, Poiani and Johnson 1988, 1989). For example, the elevational range of the DM type was similar to the distribution of Typha spp. and Scirpus lacustris in the Delta Marsh, Manitoba, Canada (Welling et al. 1988a).

Initial conditions of the emergent cover/open water ratio (proportion and spatial distribution) for the first year, 1979, were determined from aerial photographs of P1. Simulations were initially run using vegetation parameters estimated from the literature and from personal observations. These results were compared to actual distributions of DM and OW (or any other vegetation type located in the central area of the basin) for 1980-89. Two of the main parameters (water depth category boundary between DM and OW and number of months for changing a vegetation type) were critical in determining the cover ratio. These two parameters were both increased and decreased within a narrow range and simulations were rerun (Costanza et al. 1990). Final values were chosen when model results best matched actual conditions.

Model Validation

The simulation model was tested using wetland P4. Hydrologic parameters identical to those in P1 (i.e., temperature, precipitation, initial water level regression, runoff equation, PE calculations, heat index and transpiration coefficient) were used to calculate water level changes in P4 from 1979-89. An elevation of 558.2 meters above sea level was set as the lower limit for decreases in stage at which point the entire basin in P4 was dry. No upper limit in stage was set for P4 since none was known to occur.

Calculated water levels were compared to observed values using a paired t-test for individual and all years combined. An early (May-July) and late (Aug-Oct) period were also analyzed for years with low water levels. Results from these and other statistical tests described below should be interpreted with caution. Water level and cover ratio data violated an important assumption of the parametric tests used. For example, daily stage values were not independent observations since water level at time t was partly determined by water level at time t-1. Statistical tests were used to give a general indication of whether or not differences were significant.

Parameters in the vegetation sub-model (i.e., WDCs, vegetation types, WDC boundaries, length of time for changing a type and distance an emergent type can spread during a growing season) were as described for P1. Initial conditions of the cover ratio (proportion and spatial distribution) in P4 were determined for 1979 from aerial photographs.

To evaluate the performance of the model two simulations were run. First, cover changes in P4 were modeled from 1979-89 using actual water levels. Thus, only the vegetation sub-model was evaluated without confounding error from hydrologic calculations. Second, cover changes in P4 were modeled from 1979-89 using water levels calculated from the hydrologic sub-model. This simulation evaluated the performance of the overall model.

Accuracy was assessed from the percent, spatial distribution and time behavior of changes in the cover ratio. Percent of the wetland occupied by open water and deep marsh emergent cover from: (1) the simulation using actual water levels, (2) the simulation using calculated water levels and (3) the actual wetland were compared using analysis of variance (ANOVA). Data from 1979-89 were combined for the ANOVA.

Individual years had only a single value of percent water and cover since one aerial photograph was taken per year. This precluded a statistical test on these data. A simple comparison was used to highlight individual years with *extreme* differences between simulated and observed values. An individual year was shown to be different if:

$$(\%OW_{sim} - \%OW_{obs}) > \sqrt{MS_{error}} * z_{\alpha=0.05} \quad \text{or}$$

$$(\%OW_{sim} - \%OW_{obs}) < \sqrt{MS_{error}} * -z_{\alpha=0.05}$$

where $\%OW_{sim}$=percent open water from simulations (using actual and calculated water levels), $\%OW_{obs}$=percent open water in the actual wetland, MS_{error}=mean square error from ANOVA and $z_{\alpha=0.05}$=1.96. The same calulations were performed using percent non-vegetated area (i.e., open water and/or exposed soil).

Climate Scenarios

Atmospheric carbon dioxide is projected to double by the year 2100, primarily from the burning of fossil fuels (Harrington 1987, Post et al. 1990). Increasing concentrations of this and other greenhouse gases are expected to result in a significant increase in mean global temperature over the next century (Post et al. 1990).

Our need to understand the potential impacts of global warming on natural ecosystems, agriculture and water resources, to name a few examples, has initiated a relatively new research effort, climate-impact assessment (Cohen 1990). Although many climate-impact studies provide quantitative estimates of the potential effects of climate change, their main contribution is to disclose uncertainties in our current knowledge (Cohen and Allsopp 1988, Adams et al. 1990). More specifically, climate-impact studies can identify linkages and sensitivities between climate and ecosystems, identify data gaps and research needs and raise awareness of possible impacts on regional resources (Cohen 1990).

As a first step in assessing the potential effects of global warming on the hydrology and vegetation of prairie marshes, simulations in wetland P1 using two climate scenarios were compared. First, an 11 year simulation was run using actual temperature and precipitation data from 1979-89 ($1xCO_2$). Initial conditions consisted of nearly equal emergent cover and open water (ratio=49:51). Model parameters were as previously described. A second simulation was run using 1979-89 temperature and precipitation data adjusted for a doubling of atmospheric carbon dioxide ($2xCO_2$). All other parameters and initial conditions were as in the $1xCO_2$ run.

Water levels from the two simulations were compared using a paired t-test for individual and all years combined. Vegetation types (i.e., total area) were also compared between scenarios for combined years using a paired t-test. Statistical tests could not be performed on individual years since cover was often constant for a period as short as a year and thus, variability was equal to zero.

Vegetation changes within each climate scenario were evaluated by calculating a Spearman's rank order correlation coefficient (r_s) with respect to time. Values for this coefficient lie between -1 and +1. An $r_s > 0$ indicated that a vegetation type increased linearly over the 11 year simulation and $r_s < 0$ indicated a linear decrease. An $r_s=0$ indicated no linear relationship. The same cautions as stated above apply to the interpretation of statistical results comparing climate scenarios.

Climatic adjustments

Numerous general circulation models have been developed to evaluate the effects of increasing atmospheric carbon dioxide on climate (Manabe and Wetherald 1975, Mitchell 1983, Hansen et al. 1987, Harrington 1987). The models agreed that temperatures in the Great Plains will increase; however, the magnitude of that increase and changes in precipitation for this region were much more uncertain (Rind and Lebedeff 1984, Bradley et al. 1987, Cushman and Spring 1989, Adams et al. 1990).

Climate data used in simulations of wetland P1 were adjusted using output from the global climate model of the Goddard Institute for Space Studies (GISS) (Hansen et al. 1987). Model output was supplied by E. Takle of Iowa State University (Takle and Zhong 1990). The GISS model was not thought to give the 'best' projections of climate change, but rather, time and resource constraints restricted this study to the use of output from one model.

In the GISS model the global atmosphere was represented by grid boxes 8° latitude by 10° longitude with nine levels in the vertical. Control runs performed by climatologists at the Goddard Institute (Hansen et al. 1987) used an atmospheric carbon dioxide level of 315 ppm, the measured average value in 1958. To simulate both the control and the greenhouse climates, they ran the model with a constant concentration of carbon dioxide for 35 years. The average of the last 10 years of these simulations represented the mean climate (Takle and Zhong 1990).

Temperature and precipitation output from the larger grid boxes were interpolated by Takle and Zhong (1990) to specific weather stations in North and South Dakota, including Jamestown, North Dakota, located

Model structure

near the study site. According to Takle and Zhong (1990), increases in temperature at Jamestown ranged from 3-6° C with a doubling of carbon dioxide (Table 3). Increases during the fall, winter and early spring were greatest (≈5° C), while summer temperatures increased somewhat less (≈3° C). Daily temperatures for the Cottonwood Lake site from May through October were increased according to these projections.

In general, precipitation at Jamestown increased with a doubling of carbon dioxide, however, in most months changes were relatively small (Takle and Zhong 1990). Slight increases occurred during most months (3-29%; Table 4). Precipitation decreased in two months, September and October, by 17% and 4%, respectively (Table 4). Daily precipitation data for the Cottonwood Lake site were adjusted from March through October according to these projections.

Adjusting daily temperature and rainfall values with monthly projections was not ideal since it assumed a uniform change over the entire month which may or may not actually occur. At this time, however, output from climate models is limited, particularly regional projections (Rind 1987, Schneider 1989, Cushman and Spring 1989). Climate models are relatively crude and inadequately treat the effects of deep oceanic circulation and global cloud cover (Rind 1987, Schneider 1989, Post et al. 1990). It is important, however, to initiate ecological research on climate-impacts using available projections but keeping their limitations in mind (Cohen and Allsopp 1988, Cushman and Spring 1989, Adams et al. 1990).

Model structure

Results

Base Model

Hydrology

Annual and seasonal patterns of water level fluctuations over the past decade in P1 were simulated by the hydrologic sub-model (Fig. 11C). Both model calculations and the actual wetland had relatively high water in 1979, 1982, 1983, 1984 and 1987, intermediate levels in 1980, 1981 and 1986 and relatively low water in 1985, 1988 and 1989 (Fig. 11C). Seasonal changes in hydrology were also portrayed by the model, with refilling in spring and a significant decline in stage over the remainder of the growing season.

Simulated changes in water level were within 15 cm of actual stage values in P1. In most years calculated values were slightly lower than measured ones. Calculated water levels in 1980 during the later part of the growing season were almost 14 cm lower than actual values (Fig. 11C). In 1982, 1983, 1984 and 1987 calculated water levels were also lower throughout the growing season by between 0-15 cm. Model water levels in 1979, 1981, early 1985, 1986 and early 1989 were very similar to actual levels (Fig. 11C).

In contrast, calculated values in many of the dry years were higher than actual water levels, especially late in the season (i.e., 1985, 1988, 1989) (Fig. 11C). Water elevation on October 1st, 1985, was 558.0 and 557.9 meters above sea level (masl) in the simulated and actual wetland, respectively. A greater difference existed at the end of 1988 (557.9 and 557.7 masl for calculated and actual values, respectively, on October 15) (Fig. 11C). Differences between calculated and actual water level were also in this range for 1989 (12 cm on October 15).

Vegetation

Changes in the cover ratio (percent, spatial distribution and time behavior) in P1 were simulated during the last decade (Fig. 13 & 14). P1 was dry in early summer 1977, and a zone of mixed emergents established in the center of the basin when the wetland shallowly reflooded in 1978. Beginning with these initial conditions in 1979, the model accurately simulated the change of this mixed emergent type to open water in 1981 (Fig. 13). A few small scattered patches opened up in P1 during 1980. These small patches, which amounted to less than 2% in area, were not present in the simulation results (Fig. 14).

The slight decline in percent open water from early July 1981 (41%) to late July 1989 (30%) in P1 also occurred in the simulation (36% to

27%; values on August 1) (Fig. 13). This decline primarily occurred from 1985 to 1987 in the actual wetland, while in model simulations open water declined in 1985 and 1989 (Fig. 13). Among-year variability in percent open water and emergent cover was greater in the actual wetland than in model simulations (Fig. 13), i.e., changes in vegetation were more conservative in the model compared to the actual wetland.

The spatial distribution of cover and water estimated by the model was similar to that of the actual wetland (Fig. 14). Smaller patches of open water which were scattered toward the edge of the wetland, however, were not present in the simulations (Fig. 14).

Model Validation

The simulation model was tested using wetland P4. Recall that two simulations were run from 1979-89 using: (1) actual water levels (to evaluate the vegetation sub-model without confounding error from hydrologic calculations) and (2) calculated water levels from the hydrologic sub-model (to evaluate the overall model). Accuracy was assessed from the percent, spatial distribution and time behavior of changes in the cover ratio.

Hydrology

There was no difference between calculated and observed water level in wetland P4 when all years over the past decade were combined ($p=0.78$). High and low water levels occurred in the correct years (Fig. 15). Both model calculations and the actual wetland had relatively high water in 1979, 1982, 1983, 1984 and 1987, intermediate levels in 1980 and 1986 and relatively low water in 1981, 1985, 1988 and 1989 (Fig. 15).

Seasonal changes in hydrology were also correctly simulated by the model, with refilling in spring and a significant decline in stage over the remainder of the growing season. Water level changes calculated by the model, however, were less sensitive in magnitude than actual changes in P4. Calculated water levels often did not reach spring highs, especially after a previously dry fall, nor did they drop low enough in late summer and early fall (Fig. 15). Rainfall events that caused a significant rise in stage during the growing season also increased stage in hydrologic calculations, but again, calculated increases were usually more moderate than actual increases.

More specifically, the hydrologic sub-model underestimated stage in P4 in three years: 1980 ($p=0.016$), 1982 ($p=0.031$) and 1986 ($p=0.024$). The greatest difference during these years occurred in 1980 late in the growing season when calculated water level was about 11 cm lower than the actual value (Fig. 15). Calculated water levels in 1979, early 1981, 1983, 1984, early 1985, 1987 and early 1988 were not different ($p > 0.05$) from observed levels (Fig. 15).

Calculated water levels in dry years were higher than observed water levels, especially late in the season (Aug-Oct 1981, p=0.041; Aug-Oct 1985, 1988 and May-Oct 1989, $p < 0.0001$) (Fig. 15). Calculated water level in P4 was 558.77 masl and only 557.5 masl in the actual wetland on October 1, 1981. Differences of approximately 25 and 18 cm existed on October 1, 1985 and 1988, respectively. Differences between calculated and actual water levels were in this range for 1989 (10 cm on October 1st).

Vegetation

Model simulations of vegetation dynamics in P4 using actual water levels were evaluated for percent, distribution and time behavior of the emergent cover/open water ratio (Fig. 16 & 17, Table 5). Over the entire decade the amounts of emergent cover and open water from simulations (actual water levels) were not different (p=0.28 and 0.59, respectively, for all years combined) from observed values (Fig. 16, Table 5).

For individual years the greatest difference occurred in 1980 when P4 had almost 4% open water in mid-July while the model showed none (Fig. 16, Table 5). Comparisons of percent non-vegetated area (i.e., open water and/or exposed soil) differed by no more than about 2% for all other years (Table 5). In 1989 vegetation occupied the former central open water area in both the actual wetland and in model simulations. This area was smaller (2.7%) than simulated (6.3%) and was occupied by seedlings rather than by mixed emergents (Table 5).

Evaluation of these yearly differences using the z-statistic support these observations (Table 5). Annual variability of percent open water and emergent cover was much greater in the actual wetland than in model simulations (Table 5, Fig. 16).

The spatial distribution of open water, exposed soil and emergent cover in model simulations (using actual water levels) for P4 was similar to the actual wetland in some years and different in others (Fig. 17A,B). In 1980-83 the small areas of open water in P4 were distributed near the wetland edge, similar to initial conditions in 1979 (Fig. 17A). Although the model estimated a similar percentage of open water (excluding 1980; Table 5), it was located in the center, or deepest part of the basin rather than in scattered patches around the edge (Fig. 17B). A central area started to open in P4 in 1984 (Fig. 17B) and remained through 1989. Thus, from 1984-89 the distribution of open water, exposed soil or a vegetation type (as in 1989) in the simulation model and the actual wetland was similar (Fig. 17A,B).

Patches of open water, exposed soil or seedlings also occurred in small depressions scattered throughout wetland P4 in addition to a central open area (1984-89; Fig. 17A). As in simulations of P1, these small open areas were not present in model results (Fig. 17B).

Temporal changes which occurred in the cover cycle in simulations (actual water levels) of P4 were mostly in agreement with actual changes in the cover cycle. Percent open water decreased in simulations and in the wetland from 1979 to 1980, rose slightly in 1984-85 and decreased again in 1989 (Table 5). There were three notable exceptions when cover changes did not coincide. First, as mentioned previously, the central area in the deep part of the basin did not open up until 1984. The model simulated this event in 1981 (Table 5, Fig. 17A,B). Second, in 1985 the central area of the basin was exposed by the end of July; the model showed standing water in this area on August 1 even though actual water levels were used (Table 5, Fig. 17A,B). The simulated basin dried completely by late August, however, and seedlings germinated in September. Finally, during the last two dry years of the decade the model simulated the germination of seedlings (September 1988), change to mixed plants (October 1988) and selection of mixed emergents in the deep part of the basin (May 1989), whereas this area in the actual wetland was occupied by seedlings in late July 1989.

Overall Model

Model simulations of vegetation dynamics in P4 using calculated water levels were evaluated for percent, distribution and time behavior of the emergent cover/open water ratio (Fig. 16 & 17, Table 5). Overall, percent open water and emergent cover were not different ($p=0.59$ and 0.28, respectively, for combined years) in model simulations and the actual wetland.

More specifically, percent open water was slightly underestimated in model simulations from 1980-84 (Table 5, Fig. 16). Open water in P4 ranged from just over 2% to 5% for these years, while the model simulated 0-1.8%. After 1984, the size of the non-vegetated area in the model was very similar to actual conditions (Fig. 16). Evaluation of these yearly differences using the z-statistic support these observations (Table 5). Annual variability was much greater in the actual wetland than in model simulations using calculated water levels (Table 5, Fig. 16).

The spatial distribution of open water, exposed soil or emergent cover in simulations using calculated water levels was similar to distributions in simulations using actual water levels (Fig. 17A,B,C). The small open area simulated by the model for 1980-83 was located in the deepest, central part of the basin (Fig. 17C). In contrast, the small areas of open water in P4 for these years were distributed near the wetland edge (Fig. 17A). After 1983 open water (or vegetation as in 1989) was located in the same place in both the wetland and model simulations. Simulations after 1984 using calculated water levels revealed only one central open area and did not portray small areas scattered throughout the remainder of the wetland (Fig. 17A,C).

Many of the temporal changes in the cover cycle in P4 were correctly simulated in the model. Percent open water decreased from 1979 to 1980, rose slightly in 1984-85 and decreased again from 1988 to 1989 (Fig. 16, Table 5). There were three notable exceptions which were similar to results using actual water levels. First, the model simulated a central area opening up in 1981 versus 1984 in the actual wetland (Fig. 17A,C). Second, the central open water area by late July of 1985 and 1988 was partially or completely exposed by drawdown. Model results showed open water all season in this area for both years (Table 5). And third, in 1989 the model again simulated standing water in the central area all season. Although this area was similar in size and distribution to model simulations, it was occupied by seedlings in the actual wetland by late July (Fig. 17A,C, Table 5).

Climate Scenarios

Water surface elevation fluctuated about a meter in wetland P1 under the $1xCO_2$ climate scenario (Fig. 18). Four high water periods (558.6 masl) occurred during the 11 year run (years 1, 5, 6, 9). The three lowest water elevations occurred during years 7 (558.0 masl), 10 (557.9 masl) and 11 (557.8 masl) (Fig. 18).

Water level was lower in the $2xCO_2$ climate for combined ($p < 0.0001$) and individual years (1979, $p=0.03$; 1980-87, $p < 0.0001$; 1988, $p=0.0014$; 1989, $p=0.0075$). By the end of the third year of the simulation the entire wetland was dry (Fig. 18). Although water level rose again each spring, the wetland continued to dry up in almost every succeeding year of the simulation. Seasonal and annual hydrologic fluctuations still occurred under the simulated climate but over a much lower range than in the normal climate. Peak water levels were almost 0.5 meters lower in the $2xCO_2$ than in the $1xCO_2$ climate scenario (Fig.

18).

Overall, emergent cover and open water were significantly different between the normal and greenhouse climates ($p < 0.0001$, all years combined). Open water slowly declined during the 11 year simulation from the initial 51% to 27% in the $1xCO_2$ climate (r_s=-0.96). Decreases primarily occurred in the driest years (i.e., years 2, 7, 10, 11; Fig. 19A).

In contrast, open water decreased more quickly in the $2xCO_2$ climate from the initial 51% to 0% by year 4 (r_s=-0.75). Increased water loss from higher temperatures caused exposure of the substrate and germination of seedlings in August of year 2 (Fig. 19B). Most of these seedlings were inundated during the following spring but low water in August of year 3 again caused exposure and germination of seedlings over much of the central basin (Fig. 19B).

Since the wetland was only shallowly reflooded in year 4 in the $2xCO_2$ climate, a mixed emergent type developed in the central portion of the basin (Fig. 19B). Deep marsh vegetation slowly invaded this central mixed emergent type and gradually increased over the remainder of the simulation (r_s=0.996). Water level never rose to the depth and duration needed to cause mortality of the emergent types (Fig. 19B).

Although the meadow/shallow marsh zone (MSM) was not evaluated in the base model, it is interesting to note its behavior in climate simulations. Total area of this zone was significantly different between climate scenarios ($p < 0.0001$). In the $1xCO_2$ climate run this vegetation type expanded almost 20% (from 489 to 585 cells) over 11 years (r_s=0.84); in the $2xCO_2$ climate it declined almost 53%, from 489 cells in year 3 to 258 cells in year 4, to 230 cells in year 11 (r_s=-0.84) (Fig. 19A,B). Most of these cells converted to the upland type.

Finally, the overall size of the wetland (all types excluding upland) was significantly different between scenarios ($p < 0.0001$). Wetland area increased about 3% (from 2244 to 2309 grid cells) in the normal climate (r_s=0.86). A decrease of almost 12% (r_s=-0.84) occurred in the size of P1 in the greenhouse climate (2244 to 1978 cells) (Fig. 19A,B).

Discussion

Model Considerations

Hydrology

Hydrologic simulations in both wetlands revealed that the model satisfactorily calculated water level fluctuations during average years. One exception was in 1980 when model calculations underestimated water levels in both wetlands. This was due to the occurrence of unusually high runoff from a very heavy rainfall event in early-June. A total of 5.2 cm of rain fell on June 4 through 7 with 4.6 cm occurring in a single day. The model underestimated runoff from that event, therefore water levels remained low that year. Runoff estimates could be improved with more years of data. Data were few because heavy summer rains producing runoff were infrequent.

The major weakness of the hydrology sub-model was calculating water loss during years with low rainfall, especially late in the growing season when a wetland was nearly dry. This difference was most pronounced in P4, where standing water was shallower and dried up more quickly than in P1. As standing water gets very shallow it warms up. Warmer surface water evaporates more quickly (Ficke 1972, Viessman et al. 1977). The increased heating of the water from warmer bottom sediments, particulary when water was shallow, may have also increased evaporation rate. In Pretty Lake, Indiana, for example, fall evaporation was estimated to increase 0.03 cm/day (about a 14-17%/day increase in October) when sediment heat storage was considered in energy-budget calculations for two years (Ficke 1972).

Use of the Thornthwaite climatic water budget method for calculating potential evaporation did not directly consider specific changes in these and other important factors that occurred under certain circumstances such as low water levels. The climatic water budget technique is an empirical method primarily developed to estimate water loss from a moist closed cover of vegetation over an entire year or season (Mather 1978). A more exacting method of estimating PE which considers daily variations in wind and humidity, such as an energy budget or mass transfer technique, would greatly improve hydrologic calculations.

Similar problems occurred in at least one other study. In a sedge site at Houghton Lake, Michigan, evapotranspiration (ET) calculated by the Thornthwaite method also underestimated water loss compared to values measured in the field using several methods (Kadlec et al. 1989). Evapotranspiration curves for the two estimates diverged later in the season. Thornthwaite estimates of ET leveled off and decreased after July 19, while measured values increased slightly during the rest of the growing season (Kadlec et al. 1989).

Calculations of spring recharge in P4 were underestimated in two years (1982 and 1986) following a dry summer and fall. If water level simulations had accurately declined during the dry years, these differences would have been even more apparent (Fig. 15). Unaccounted runoff from snow melt was one possible factor contributing to a low estimate at least in 1982. Recall that 1982 was omitted from the spring water level regression analysis (Fig. 8). In addition to direct precipitation, runoff from snow melt contributed to spring rise in stage in this year. The input from snow melt was estimated and may have been too low.

Secondly, the condition of upland soils following a dry fall may have enhanced spring runoff, contributing to underestimations of recharge in 1982 and 1986. For example, in early-spring 1986, soil was extremely dry from the previous fall and a very dry February and March. In late April, two heavy rainfall events (i.e., nearly 3 cm each) occurred within four days of one another. The very dry upland soil may have been quite impermeable, causing a greater amount of runoff to occur than if soils were more moist (T. Winter personal communication). The increase in runoff due to extremely dry soil conditions could have also occurred in the spring of 1982.

Estimation of runoff due to snow melt and spring rain is a complex process. Few studies have evaluated this parameter in prairie wetlands (Willis _et_ _al_. 1961, Shjeflo 1968, Crowe and Schwartz 1981a,b), and errors associated with estimating overland runoff have not been described (Winter 1981). A more detailed model which incorporates soil moisture conditions, snow melt characteristics and watershed area would be necessary to refine this aspect of wetland hydrology.

Vegetation and Overall Model

Some of the differences between simulated and actual values of cover and water may be attributed to imprecisions in the data. Principal points of aerial photographs were not always at the exact center of a wetland. The resulting distortion may account for the greater among-year variability in percent open water observed in the actual wetlands. In addition, it was sometimes difficult when digitizing historic photos to choose between a cover or water designation if open areas had scattered emergents. Both these factors could account for some of the differences between simulated and observed values.

The lack of small, scattered patches of open water in model simulations compared to P1 and P4 was possibly due to two factors. First, subtle depressions in basin topography which could have caused these patches, may not have been detectable from the spatial resolution of the surveyed elevation data; these depressions could have also been lost in the interpolation process. Second, the small open water areas in P1 and P4 may have been caused by the patchy, stochastic distribution of specific emergent species that died under slightly different water depth conditions than the model dictated. In the model, conditions under which the deep marsh type converted to open water were generalized for a number of different species.

One difference between simulation results (using actual water levels) and observed data in P4 occurred in July, 1985. The simulated wetland had open water in the deepest part of the basin while the actual wetland had exposed soil. This difference occurred because water level was estimated in P4 in the deep part of the basin when the staff gage read dry.

Wetland cover changes in the model were driven by fluctuating water levels, and consequently, some of the discrepancies between simulated and actual values of cover and open water were due to inaccuracies in parameter estimates from the hydrologic sub-model. For example, water levels were overestimated in dry years and these errors were reflected in cover ratio simulations in P4. The model simulated open water in three dry years (August 1985, 1988, 1989) while the actual wetland had exposed soil or seedlings. Lower calculated water levels compared to observed values also caused lower estimates of percent open water from 1981-84.

Results from tests using P4 also elucidated two areas in which cover simulations did not agree with actual values due to a weakness in the vegetation sub-model. The first was in simulations of cover changes during the drawdown phase of the cover cycle, particularly seedling germination. Former open water areas in the actual wetland remained as exposed soil (1985 and 1988) when drawdown occurred in: 1) late-July and 2) following a previously wet year. When drawdown occurred in: 1) early-July and 2) following a previously dry year, seedlings were found on the exposed mudflats (1989). In contrast, seedlings germinated in the model on mudflats from May until the end of August as soon as they were exposed.

According to these results and other studies of prairie marsh seed banks, seedlings should not germinate if exposure occurs after early-July rather than through August (Harris and Marshall 1963, Welling et al. 1988b, Meredino et al. 1990), and consequently, an exposed soil type should be included in the model. Results from a seed bank study in Delta Marsh, Manitoba, Canada, showed relatively little germination in August and September even though the marsh was completely dry by June 1 (Welling et al. 1988b, Meredino et al. 1990). Soil moisture, moderate to high temperatures and low soil conductivity were thought to favor earlier germination (Harris and Marshall 1963, Meeks 1969, Galinato and van der Valk 1986, Welling et al. 1988b, van der Valk and Pederson 1989, Meredino et al. 1990). Lower temperatures and decreasing photoperiod were believed to reduce germination late in the season (Meredino et al. 1990).

Seedling germination during a late-season drawdown may also be reduced by a dense mat of dried submerged vegetation on top of the exposed soil (Meredino et al. 1990). This mat was common in all of the semi-permanent wetlands on the study site after they dried in 1988, and the mat was observed to impede germination (personal observation), similarly to emergent litter (van der Valk 1986). Harris and Marshall (1963) found only a few mudflat annuals penetrated a similar algal mat if exposure occurred in late summer. This mat may be significantly thicker after previously wet years with abundant submerged vegetation than in years following a dry period where exposure and decomposition have occurred.

The second problem in the vegetation sub-model evident from tests using P4 occurred in relation to the conversion of deep marsh emergents to open water and vice versa (i.e., emergent death and growth, respectively). The deepest part of the wetland opened in 1981 in the wetland versus 1984 in model simulations. The scattered, open areas near the wetland edge closed in 1980 in simulations versus 1984 in the actual wetland (Fig. 17).

Conversion from deep marsh to open water in the model occurred at a threshold water depth of 55 cm. If water level was below or above this value for a given period of time a cell changed to deep marsh or open water, respectively. In reality, emergent plant growth and death are much more complex. The upper limit for even a single species of Typha, for example, is variable (Kadlec and Wentz 1974, Welling et al. 1988a, Shay and Shay 1986, Grace 1987, 1989), and growth rate for two common species of Typha was shown to vary with depth (Grace 1987, 1989). A probability function including time and water depth rather than a threshold value would better represent changes in emergent vegetation caused by water depth (Grace 1987, 1989; Ellison and Bedford in prep). Incorporating a more complex relationship for this parameter would improve the model.

In addition, lumping species into vegetation types does not consider different requirements of individual species. Composition of the deep marsh type included at least two species of Typha and one species of Scirpus. Each of these species has a slightly different water depth tolerance (Shay and Shay 1986, Grace 1989) which was generalized in the model.

Overall, the results of this study support the use of the van der Valk (1981) conceptual model for predicting vegetation changes in freshwater wetlands. The conceptual model was also used to predict changes in wetland species in a freshwater lacustrine marsh after a drawdown (van der Valk and Pederson 1989) and in a Great Salt Lake marsh following a fire (Smith and Kadlec 1985). Predictions of species composition (and less so abundances) were successful in the freshwater wetland. The model applied poorly to the saline marsh since the impact of salinity on germination and establishment was not considered (Smith and Kadlec 1985). If species rather than vegetation groups were used in this study it is likely that spatial variation in salinity would need to be considered to accurately portray composition (LaBaugh et al. 1987, Swanson et al. 1988).

Implications of Climatic Change

The potential effects of global warming as evaluated by this model revealed much drier hydrologic conditions in semi-permanent wetland P1. Water levels were significantly lower, and drying occurred more frequently in the 2xCO_2 climate. The slight increase in precipitation projected by the GISS climate model in most months did not compensate for the dramatic increase in evapotranspiration due to higher air temperatures.

These results are consistent with projections of potential changes in drought and water supply (i.e., precipitation minus PE) due to climatic warming (Dracup and Kendall 1990, McCabe et al. 1990). One study which evaluated projections from three global climate models found that decreases in the annual water supply in most areas of the country, including North Dakota, resulted primarily from increases in temperature relative to changes in precipitation (McCabe et al. 1990).

Simulated global warming also affected the emergent cover/open water ratio in P1, which changed from a nearly balanced condition to a completely closed basin with no open water areas. These changes could result in a dramatic decline in habitat quality for breeding birds (Poiani and Johnson submitted ms). Habitat studies on semi-permanent wetlands have shown that the most productive condition for breeding waterfowl is when emergent cover and open water are nearly equal in proportion (Weller and Spatcher 1965, Weller and Fredrickson 1974).

In natural marshes, both breeding bird density and species richness were greatest when habitat was close to this ratio. In wetlands that were manipulated to have different cover:water ratios (i.e., 30:70, 50:50, 70:30), density and diversity were also greatest when cover and water were in equal proportions (Kaminski and Prince 1981, 1984, Murkin *et al*. 1982). The equal interspersion of water and cover appears to provide both the required water areas for feeding and brood rearing and the visual isolation that unbalanced ratios do not.

A significant decline in total wetland area also occurred with over half of the meadow/shallow marsh zone converting to upland by the final year of the simulation. The reduction of moist vegetation around the wetland edge and drier conditions in general may exacerbate the use of wetlands for agriculture, particularly shallow, seasonal types. Agricultural development has already caused the destruction of more than half the original wetland habitat in the glaciated prairie region and is thought to be a major cause of declining waterfowl populations (Johnson and Shaffer 1987, Krapu and Duebbert 1989).

Changes in vegetation and hydrology could be more extreme or the predicted changes could occur more quickly than indicated due to a number of possible factors. First, the simulation model developed here usually underestimated water loss during dry years in both P1 and P4. Thus, the model may also have underestimated water loss in climate scenarios for P1, particularly the 2xCO_2 climate.

Second, as mentioned above, precipitation estimates in a greenhouse versus normal climate from the GISS model increased for most months. Many of the other global climate models project decreases in precipitation during most months for the Great Plains (Mitchell 1983, Manabe and Wetherald 1986, Adams et al. 1990) which would result in more rapid water loss and greater colonization of exposed mudflats by plants.

Finally, hydrologic simulations did not include a winter snowfall component. Initial spring water elevation in the model was calculated using spring rainfall. Higher winter and early spring temperatures will likely affect the amount of snowfall and the amount and timing of runoff from snowmelt. Increased temperatures may decrease the ratio of snow to rain and reduce total snowpack volumes, leading to earlier and faster spring snowmelt (Cohen 1986, Gleick 1987, Croley 1990). It is likely that these potential changes in hydrology, which were not evaluated by this model, will also have a worsening effect on water loss in P1. The results presented here are probably a conservative estimate of the possible effects of global warming (as currently projected by climate models) on the hydrology and vegetation changes in wetland P1.

Much more research is needed in both climate modeling and wetland ecosystem modeling to improve predictability. In climate modeling, cloud cover and other feedbacks need to be incorporated into global circulation models, and regional predictions require considerable refinement (Rind 1987, Schneider 1989, Cushman and Spring 1989).

New research on wetlands is needed to address the relationship between hydrology and a changing climate (Waggoner 1990). Most hydrologic studies in prairie wetlands have focused on the water budget and groundwater flow in the existing climate (Meyboom 1963, Shjeflo 1968, Eisenholr and others 1972, Sloan 1972, Winter and Carr 1980, Crowe and Schwartz 1981a,b, 1985, LaBaugh _et al_. 1987). Warmer temperatures will likely affect all hydrologic processes in prairie wetlands and, as mentioned above, those such as transpiration from emergent vegetation and spring refill from runoff are inadequately understood. The biotic response to these physical changes is also unknown and may include major changes in composition and abundance or shifts in the geographic range of wetland species.

Further simulations of potential changes in wetland hydrology and vegetation associated with global warming are needed. A logical improvement in wetland modeling is to simulate changes in an entire wetland complex, including ponds of all sizes and water permanence types. A mix of wetland permanence types found in a wetland complex provides most habitat requirements for breeding birds (Swanson 1988, Swanson and Duebbert 1989, Krapu and Duebbert 1989). Our ability to mitigate the effects of climate change on this valuable resource will be enhanced by such research.

Manangement Applications

Ecological models and in particular, wetland models (Costanza and

Sklar 1985) aid resource managers in conservation and management decisions (Sklar _et al_. 1985, Cowardin _et al_. 1988, Neckles and Wetzel 1989, Brody _et al_. 1989, Costanza _et al_. 1990). In addition to evaluating the potential effects of global warming, the spatial model of vegetation dynamics developed here has numerous management applications for prairie marshes.

Management of prairie wetlands for wildlife includes manipulation of water levels to produce an optimum ratio of emergent cover to open water (Kadlec 1962, Harris and Marshall 1963, Ball and Nudds 1989). Since changes in vegetation are driven by hydrology, the model can be used to determine the duration of drawdowns and floods necessary to produce better quality habitat for breeding birds. For example, water levels needed to drown out the existing emergent cover in P4 and restore the wetland to a more balanced cover ratio could be determined from model simulations.

Managers could also simulate wetland cover dynamics under various land use practices, such as agriculture or grazing. Changes in cover from heavy and moderate grazing could be incorporated into the vegetation parameters. Agricultural practices might be evaluated by changing runoff coefficients and/or evapotranspiration values.

Finally, the model could be used to estimate regional wetland conditions such as the area and number of semi-permanent ponds with water. These kinds of data are important when evaluating the productivity of waterfowl (Johnson _et al_. 1987, Cowardin _et al_. 1988).

Conclusions

1. Hydrologic simulations in wetlands P1 and P4 revealed that the model satisfactorily calculated water level fluctuations during average years. Some of the differences between calculated and observed water levels may be due to inaccurate estimates of runoff. Runoff estimates could be improved with more years of data.

2. The major weakness of the hydrology sub-model was calculating water loss during years with low rainfall, especially late in the growing season. Water levels were overestimated by the model due to limitations in the Thornthwaite method of calculating potential evapotranspiration.

3. A second weakness in the hydrology sub-model occurred in spring following a previously dry summer and fall. Calculations of spring recharge in wetland P4 may have been underestimated for these years due to inaccuracies in estimating spring runoff from rain or melting snow. When upland soil is extremely dry and relatively impermeable after a dry

summer and fall, spring runoff may be greater than in normal years. A more detailed model incorporating soil moisture conditions, snow melt characteristics and watershed area would improve predictions of spring recharge.

4. In general, changes in the cover ratio were accurately simulated and the results of this study support the use of the van der Valk (1981) conceptual model for predicting vegetation changes in freshwater wetlands.

5. Seedlings germinated too quickly on exposed mudflats in the model when drawdown occurred late in the season. The model did not consider the thick mat of dried, submergent vegetation on top of the mudflats in the actual wetland which impeded germination.

6. Model conversions between open water and deep marsh vegetation were not always timed correctly. If water depth crossed a threshold value for a given period of time a cell would change its type. In reality, tolerance of emergents to deep water is more complex. A probability function with respect to time, water depth and species rather than a threshold value would better represent this relationship.

7. The potential effects of global warming as evaluated by the model showed dramatic changes in the hydrology of wetland P1. Although water

level fluctuations still occurred, peak values were significantly lower in the warming scenario producing a wetland which dried in most years.

8. Simulations also revealed a significant change in the vegetation of P1 with global warming, from a nearly balanced cover ratio to a completely closed basin with no open water areas. In addition, a significant portion of the meadow/shallow marsh zone converted to upland and the overall size of the wetland decreased by about 12%. These changes could result in a dramatic decline in habitat quality for breeding birds.

9. The model developed here has numerous management applications in addition to evaluating the potential effects of climate change. These include: 1) determining the duration of drawdowns and floods to produce a more productive cover ratio, 2) assessing the effects of land use practices on the cover ratio (e.g., grazing, agriculture) and 3) estimating regional wetland conditions of semi-permanent ponds (i.e., wetland area and number of ponds with water) for use in evaluating productivity of waterfowl.

Figures and Tables

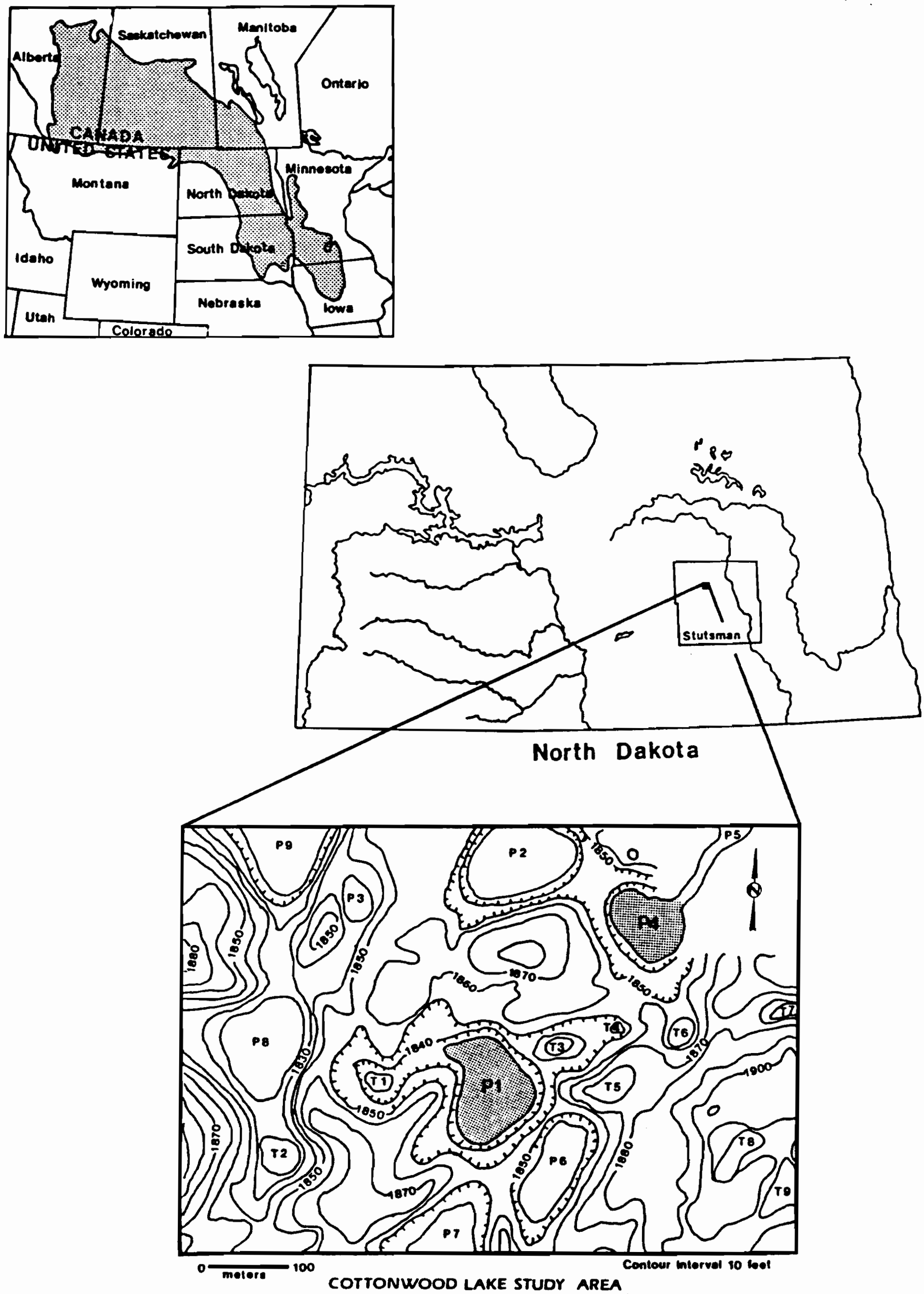


Figure 1. Location of prairie wetlands of glacial origin in North America and of semi-permanent wetlands P1 and P4 on the Cottonwood Lake study area in Stutsman County, North Dakota, USA.

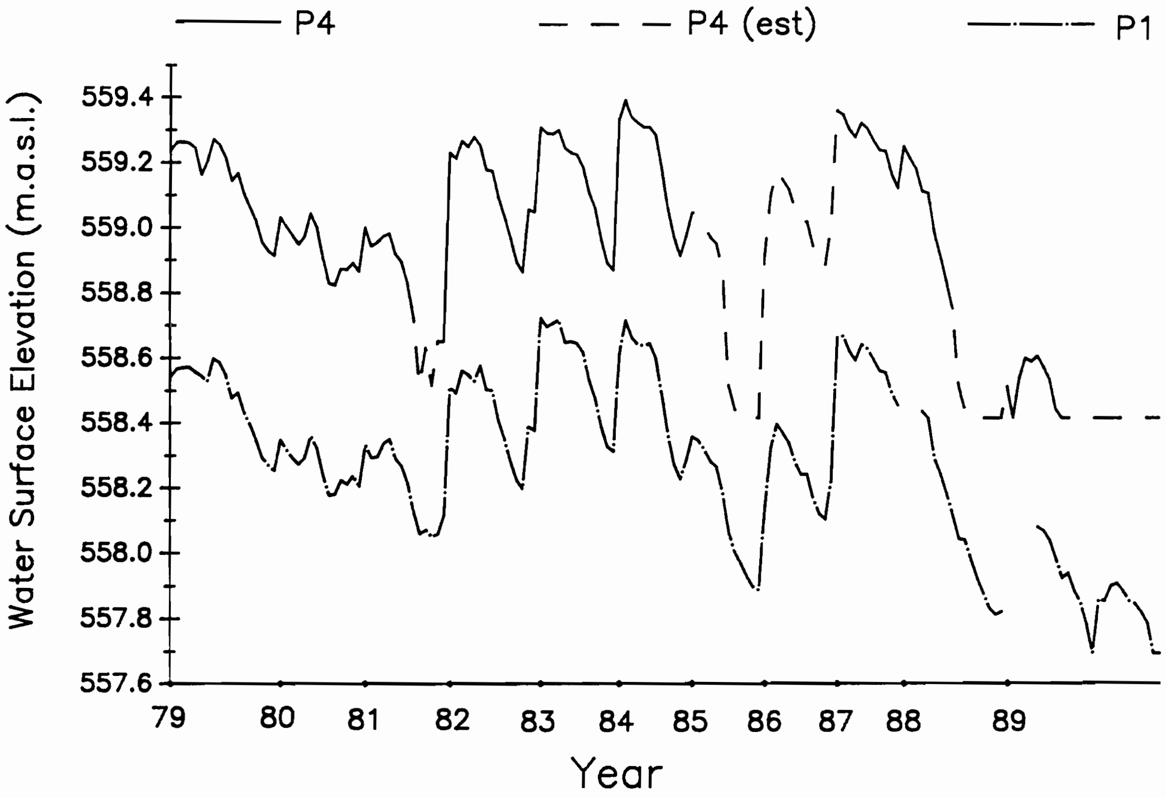


Figure 2. Water surface elevation (meters above sea level) in wetlands P1 and P4, 1979-89. Periods of missing data in P4 were estimated (broken line). P1 was dry at 557.7 m.a.s.l. P4 was dry at 558.4 m.a.s.l.

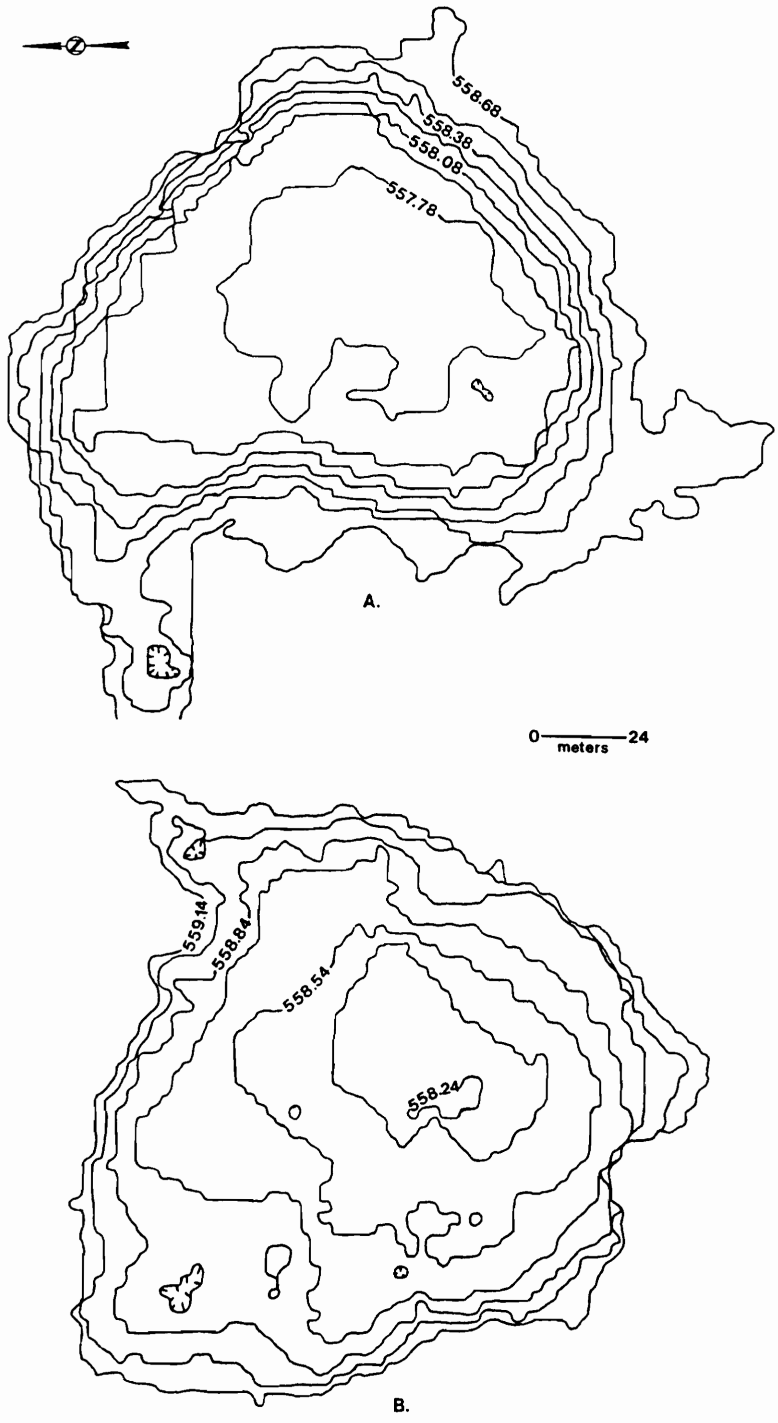


Figure 3. Basin contour elevation maps (meters above sea level): (A) wetland P1 and (B) wetland P4. Computer-generated maps were made using digitized point elevations and interpolation routine SURFER (1987, Golden Software Inc., Golden, CO). Contour interval = 0.15 meters. Hatched contour = depression.

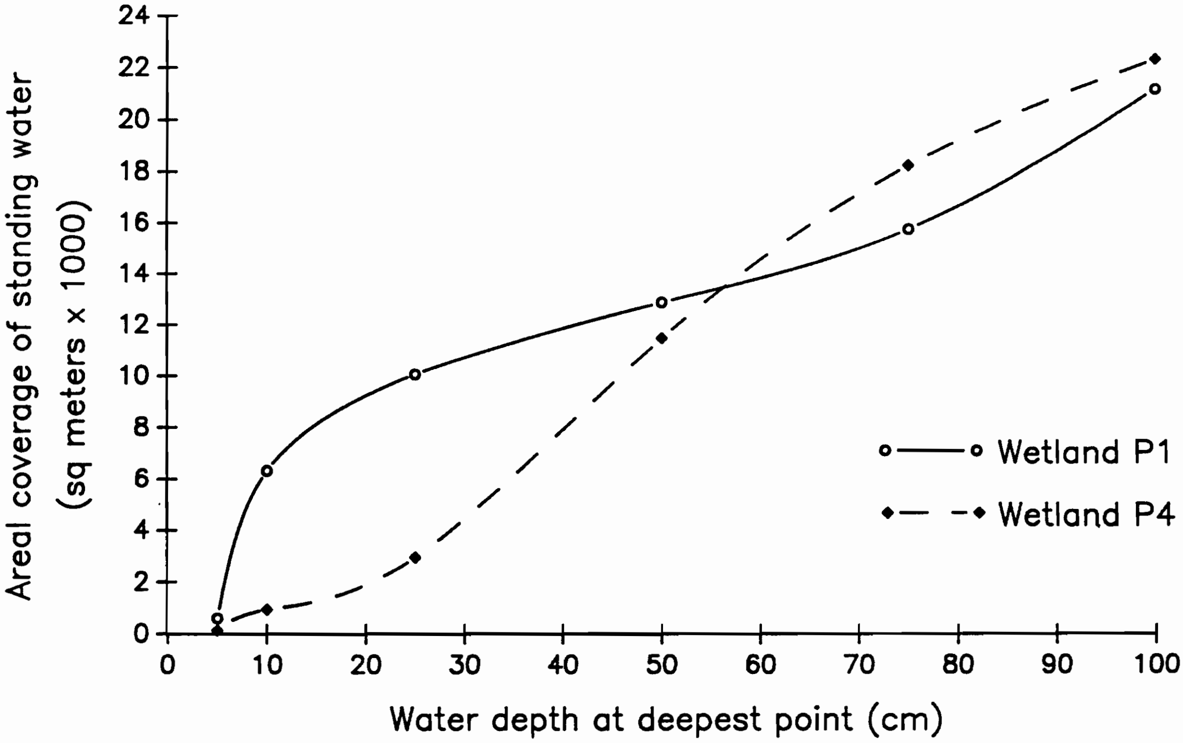


Figure 4. Areal coverage of standing water (sq meters x 1000) for various water depths (cm) in wetlands P1 and P4. Water depth is measured at the deepest point in the wetland. Standing water is of any depth.

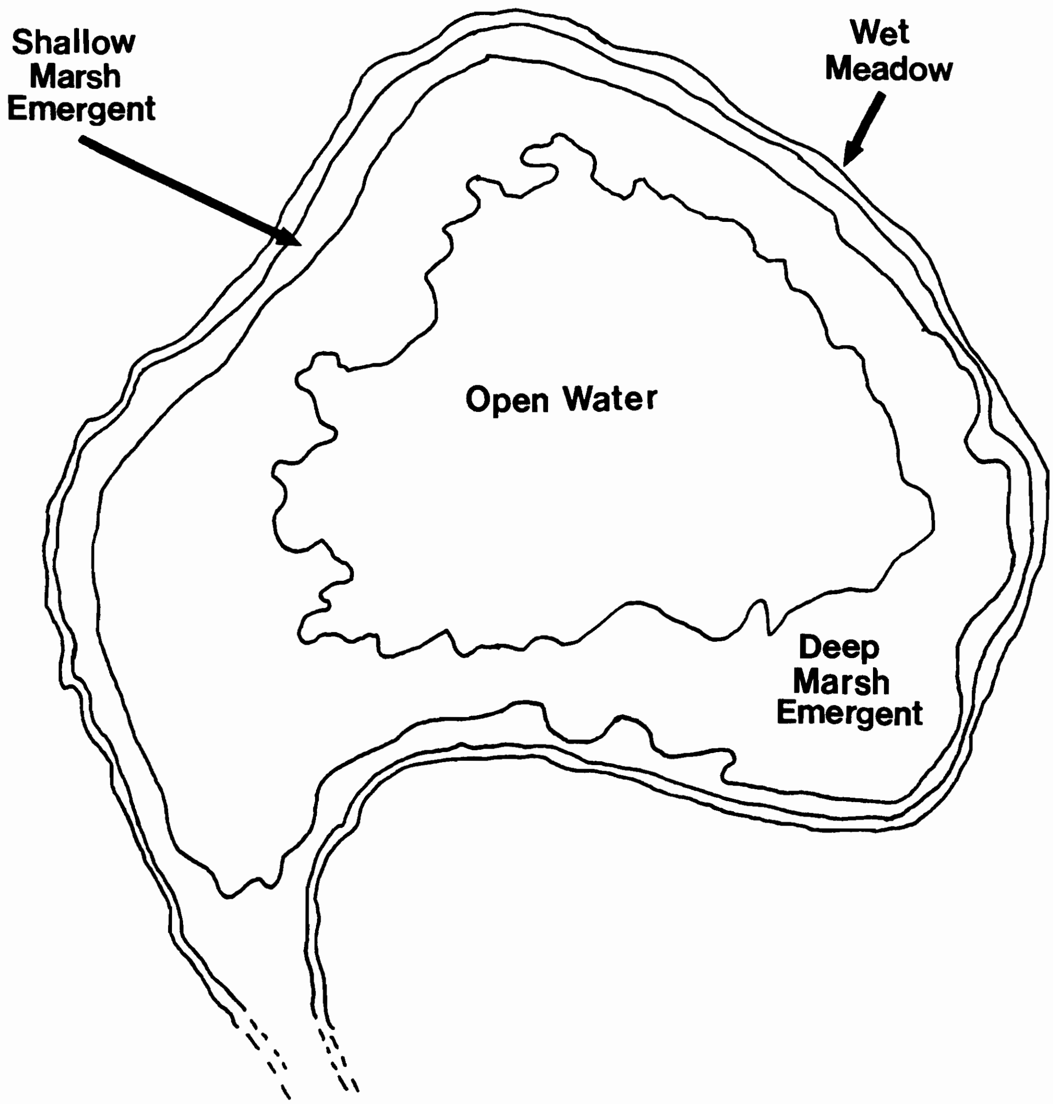


Figure 5. Location of concentric wetland zones as represented by semi-permanent wetland P1.

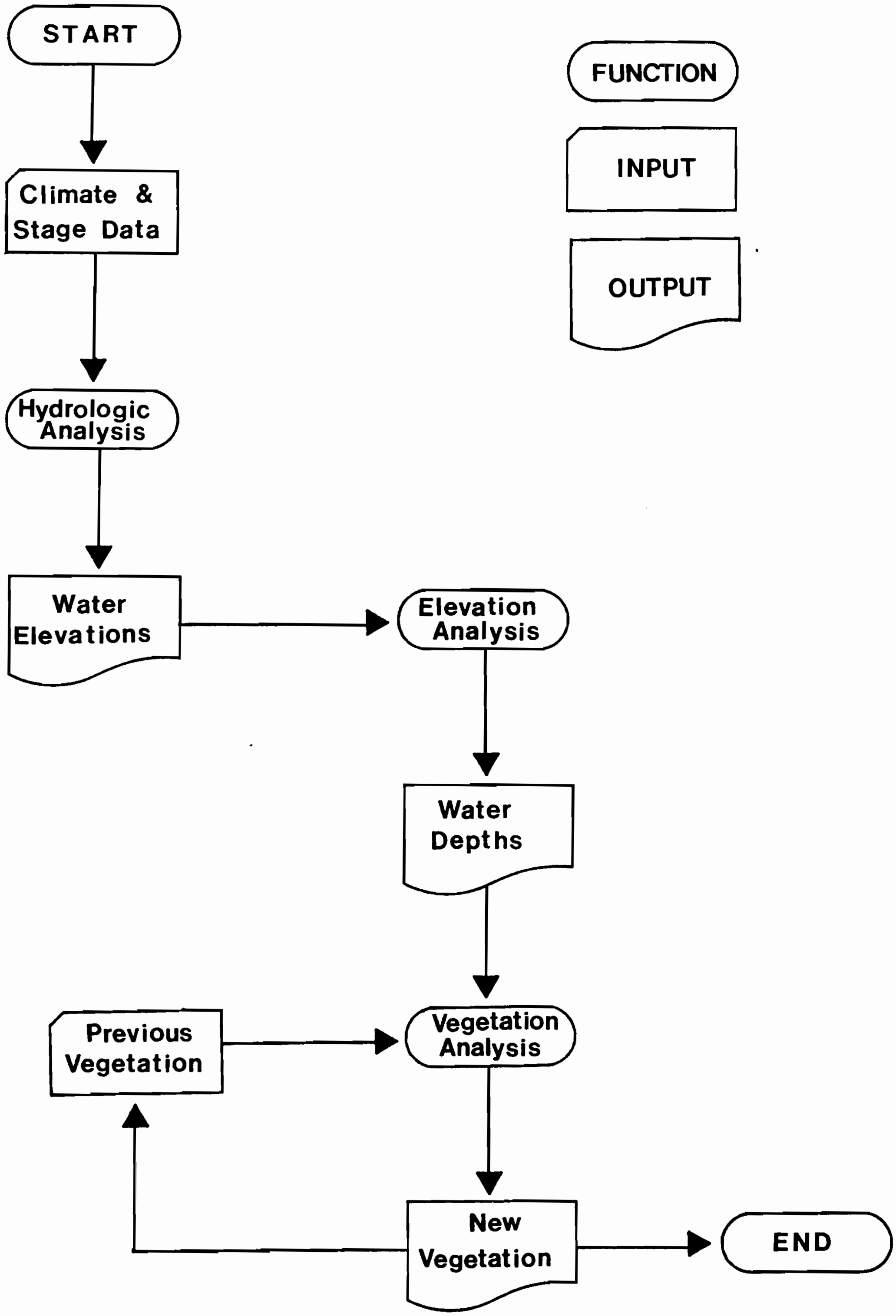


Figure 6. Flowchart of overall simulation model.

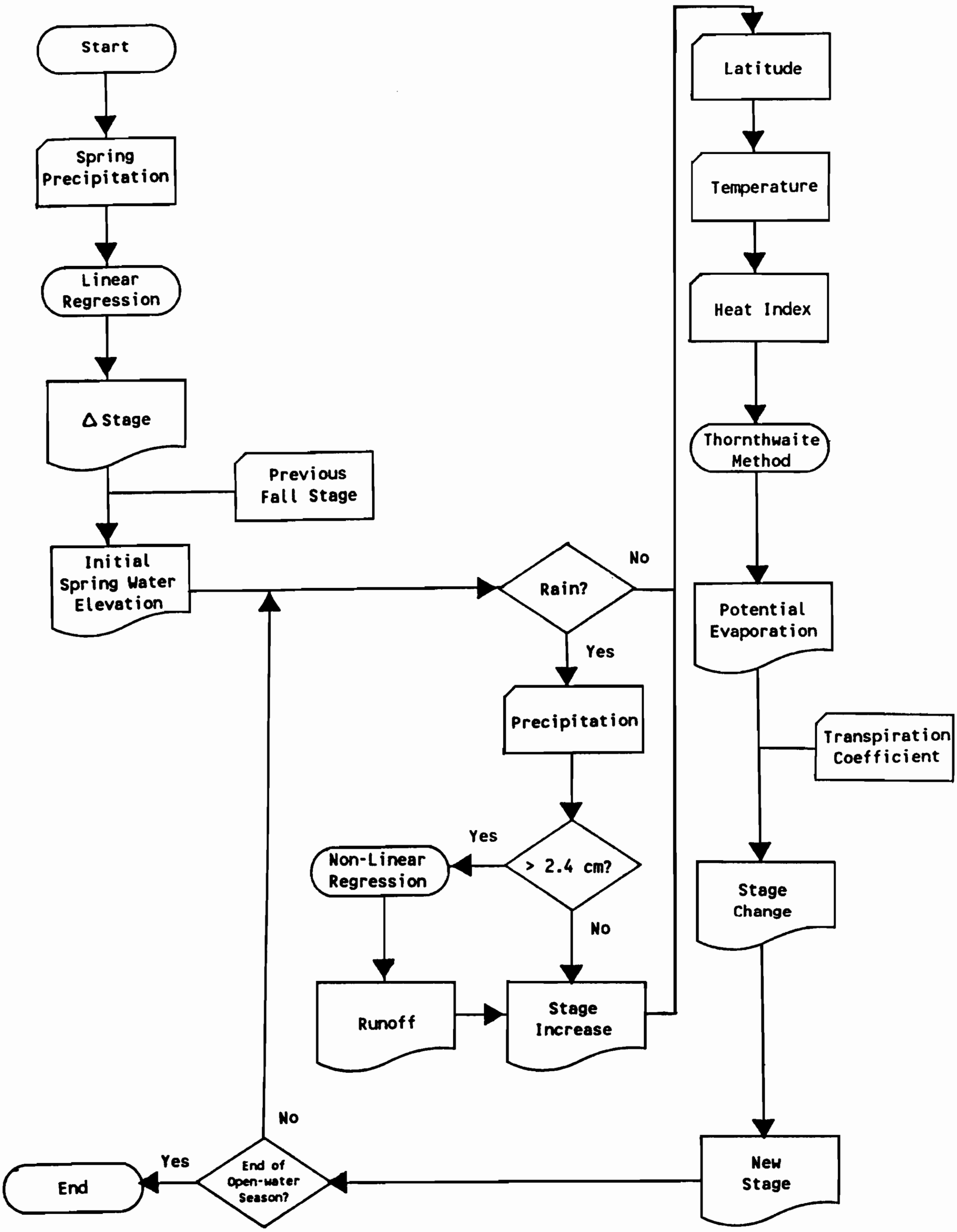


Figure 7. Flowchart of hydrologic sub-model.

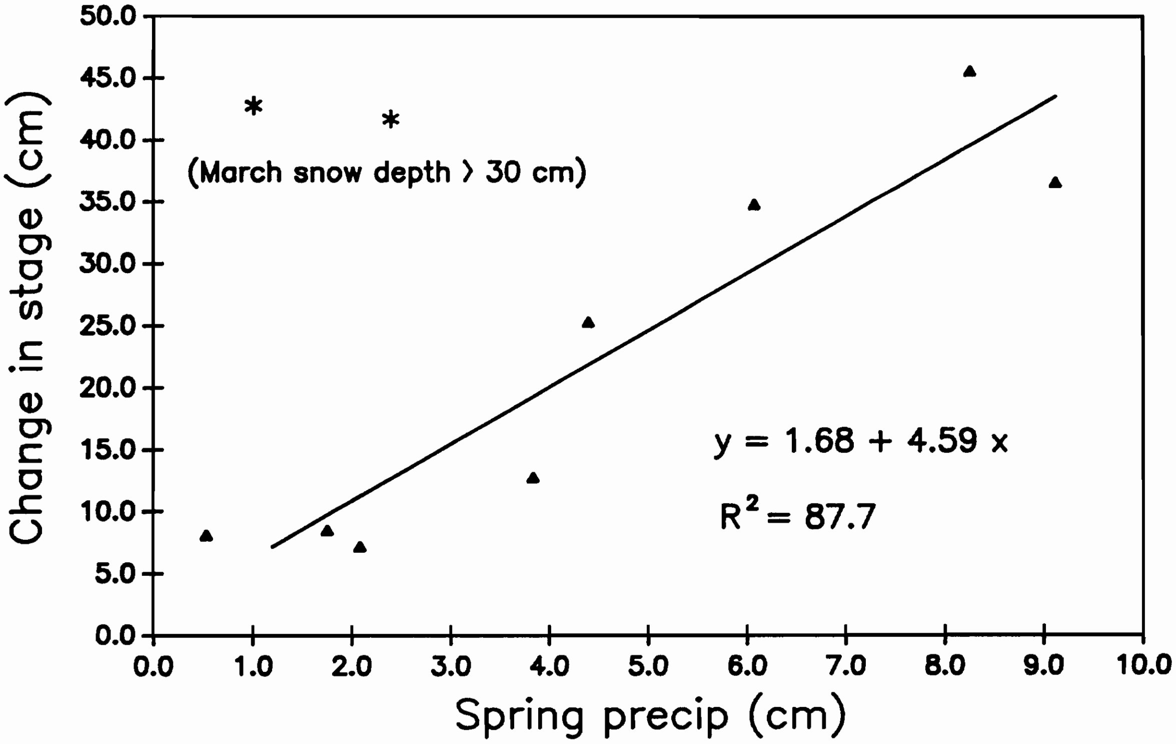


Figure 8. Relationship between spring precipitation (March + April) and change in stage (last date stage recorded in fall to May 1) in wetland P1. Data were from 79/80 through 88/89. Line is fitted regression line: $p < 0.001$, $R^2 = 87.7$. Two outliers (81/82 and 86/87) were omitted from the analysis (*). March maximum snow depth was > 30 cm in these two years.

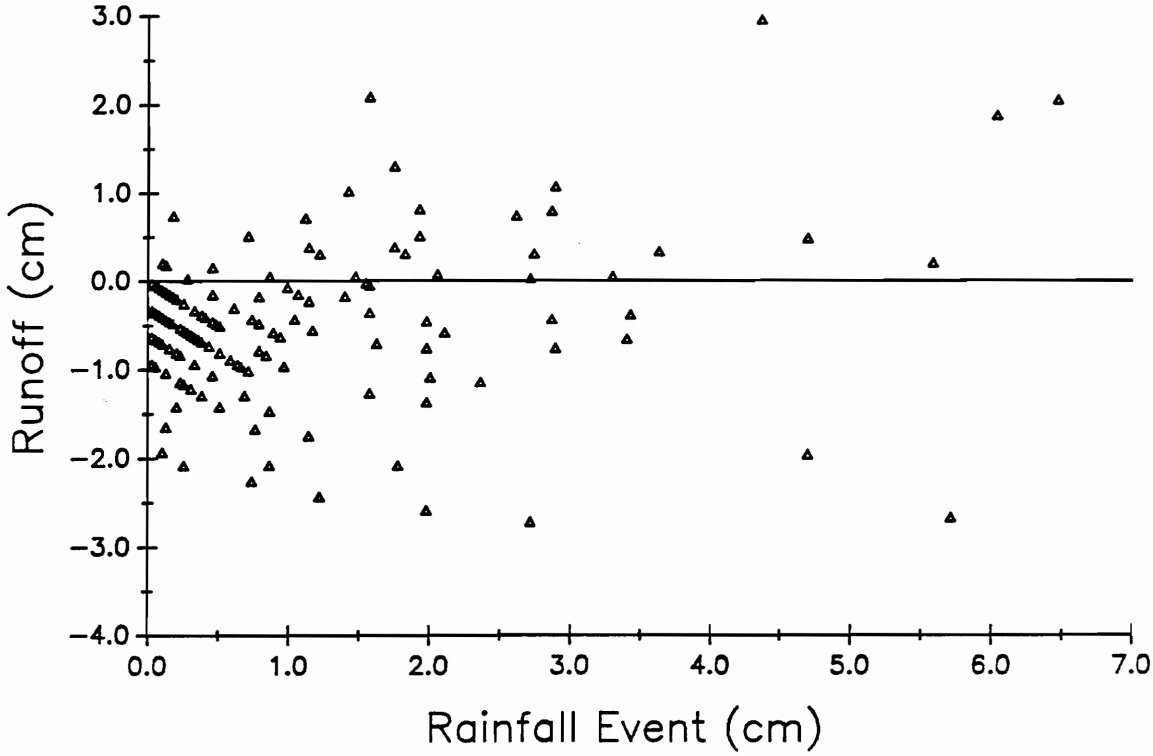


Figure 9. Amount of runoff in wetland P1 for various rainfall events (i.e., continuous days with some rain). Runoff = rise in stage after a rainfall event minus precipitation. Negative values of runoff occurred when stage decreased during a period with rainfall. For example, stage decline was measured for the entire day(s) and the actual rainfall event may have occurred in hours or minutes. Data were from 1980-88.

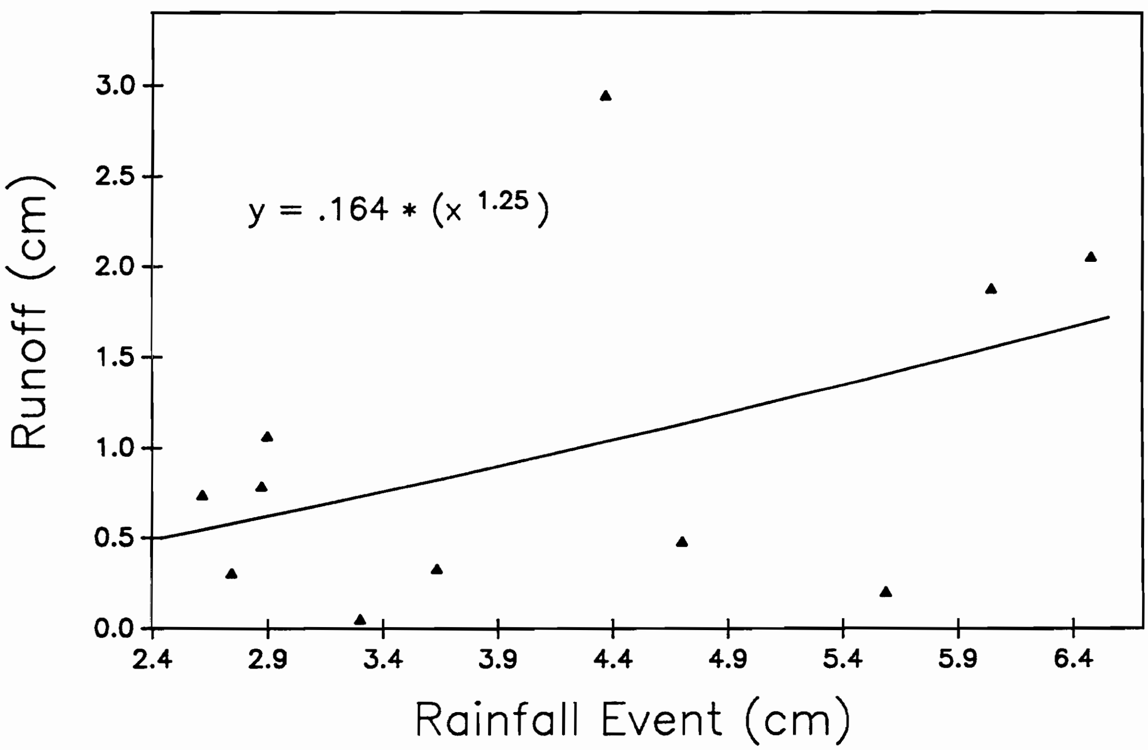


Figure 10. Positive values of runoff in wetland P1 for rainfall events (i.e., continuous days with some rain) greater than 2.4 cm. Runoff = rise in stage after a rainfall event minus precipitation. Line is fitted non-linear curve. (See text for asymptotic 95% confidence intervals of equation coefficients). Data were from 1980-88.

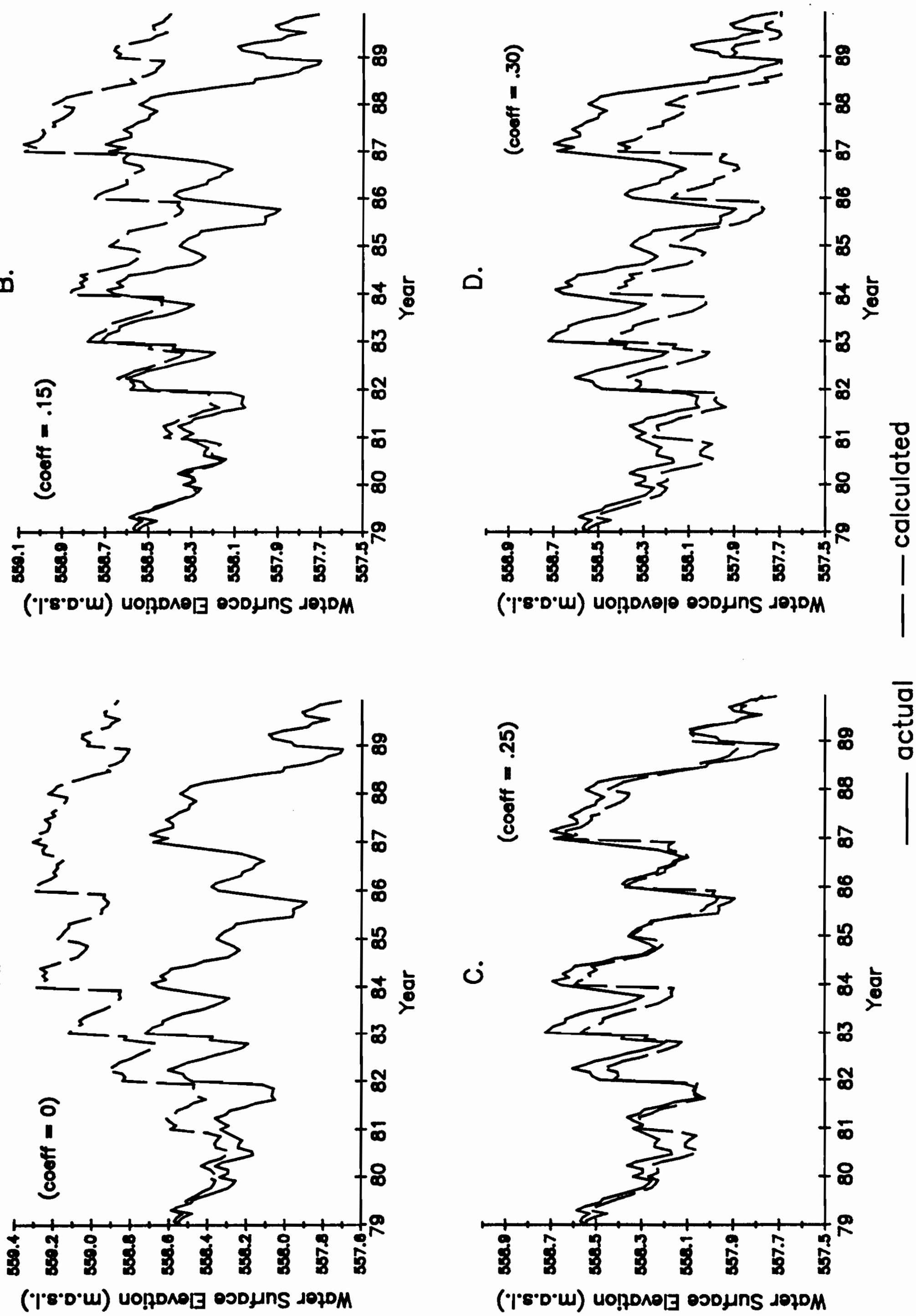


Figure 11. Water surface elevation (meters above sea level) in wetland P1 vs model calculations, 1979-89: (A) no transpiration coefficient, (B) coefficient = 0.15, (C) coefficient = 0.25, and (D) coefficient = 0.30. Entire wetland was dry at 557.7 m.a.s.l.

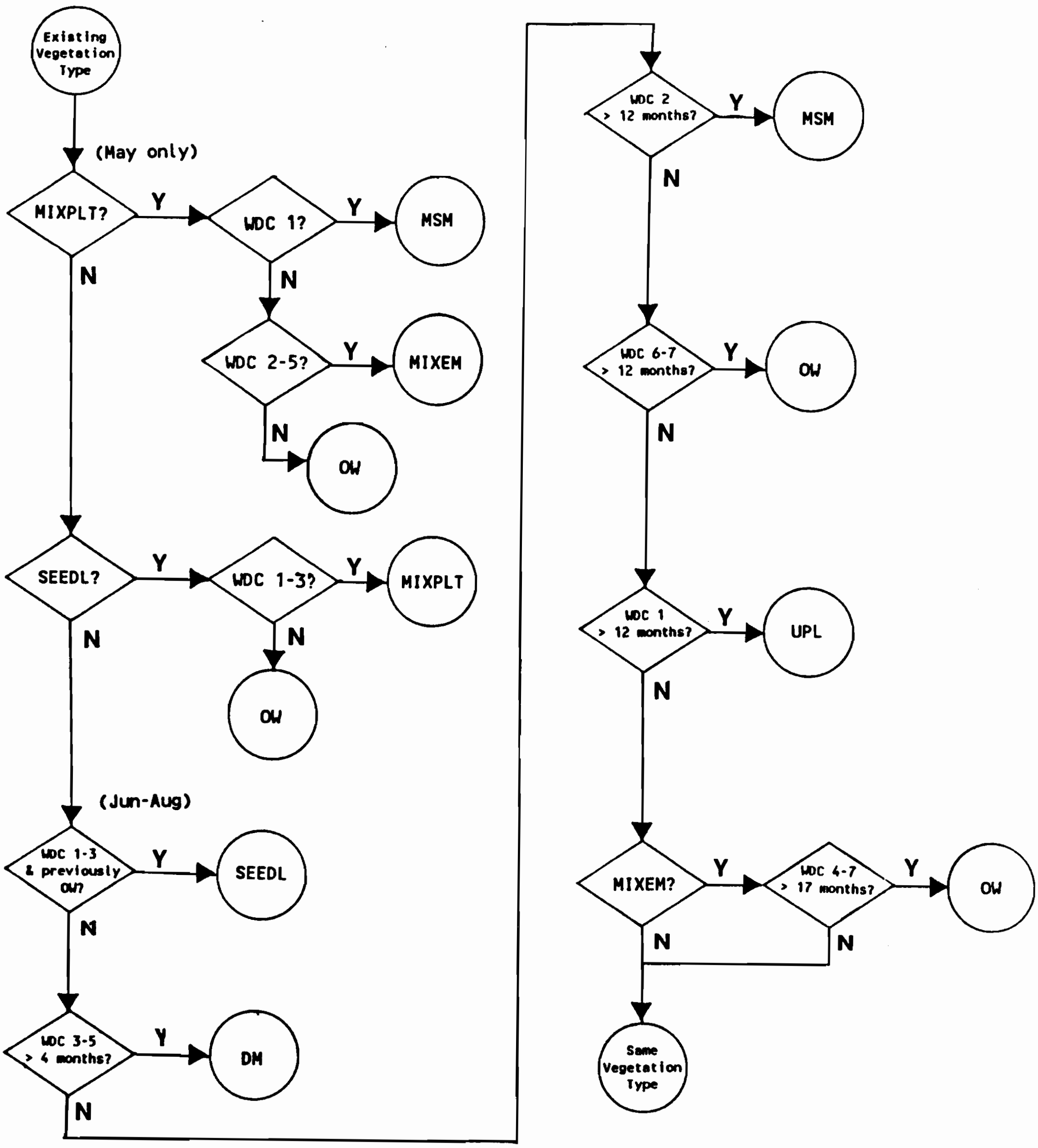


Figure 12. Flowchart of vegetation sub-model. UPL = upland, MSM = meadow/shallow marsh, DM = deep marsh, OW = open water, MIXEM = mixed emergents, MIXPLT = mixed plants, SEEDL = seedlings. Water depth category (WDC) (1) < -55 cm, (2) -55 to -10 cm, (3) -9 to 3 cm, (4) 4 to 49 cm, (5) 50 to 55 cm, (6) 56 to 61 cm and (7) > 61 cm.

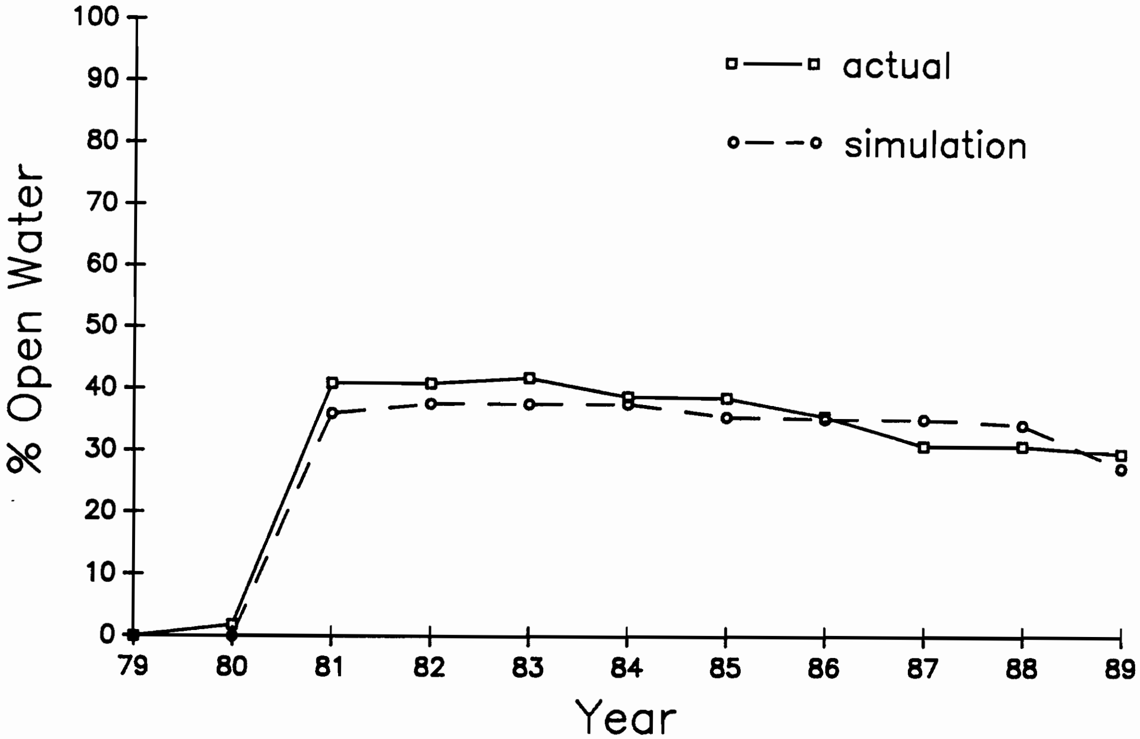


Figure 13. Percent open water in wetland P1 vs model simulations from 1979-89. Simulation values were on August 1; actual values were estimated from aerial photos taken in late-June, July or early-August.

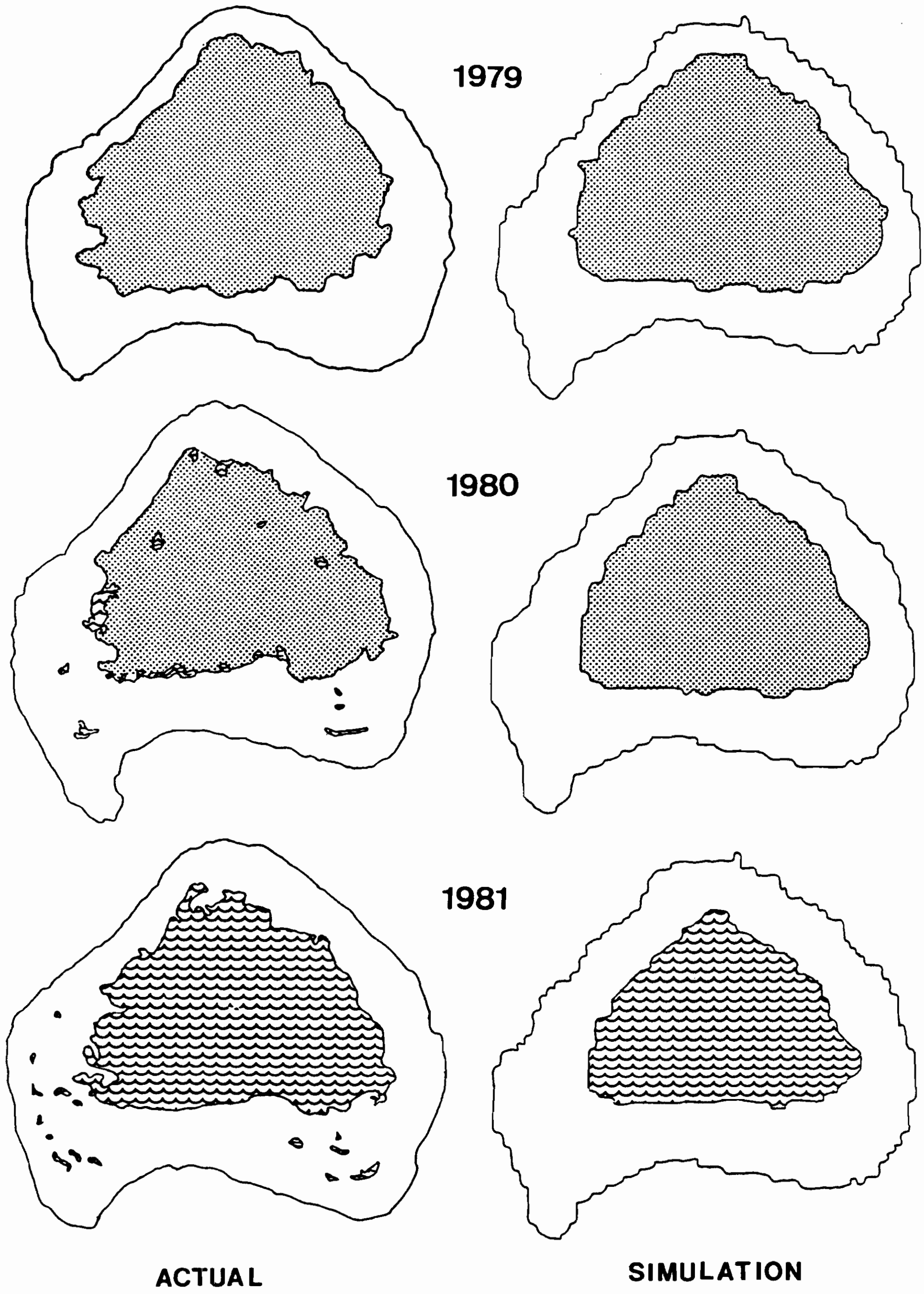


Figure 14. Cover/water distribution maps for wetland P1 vs model simulations, selected years, 1979-89. Simulations were on Aug 1; actual distributions were from aerial photos taken in late-June, July or early-Aug. Actual distributions were distorted since principal points in photos were not always at exact center of wetland. NOTE: Key on following page; OW=open water, DM=deep marsh, MIXEM=mixed emergents.

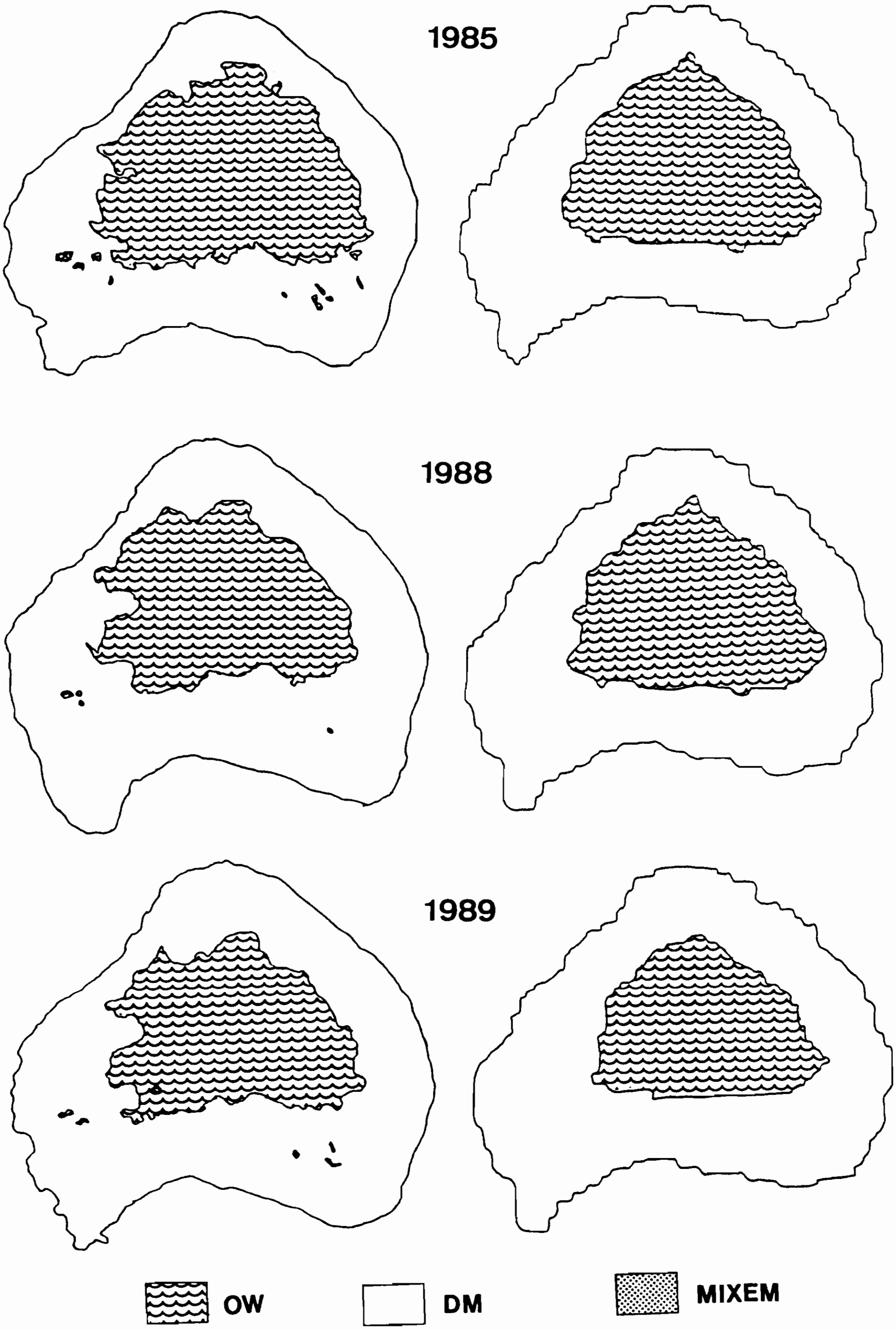


Figure 14 continued.

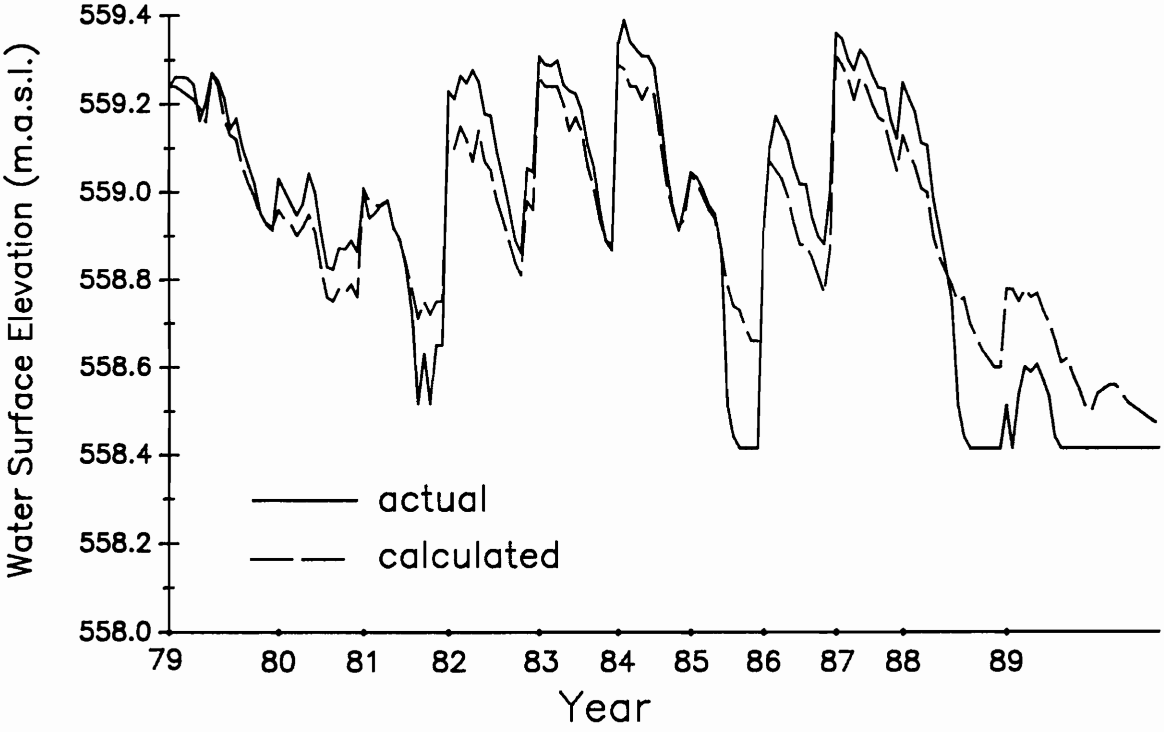


Figure 15. Water surface elevation (meters above sea level) in wetland P4 vs model calculations, 1979-89. Wetland was dry at 558.4 m.a.s.l.

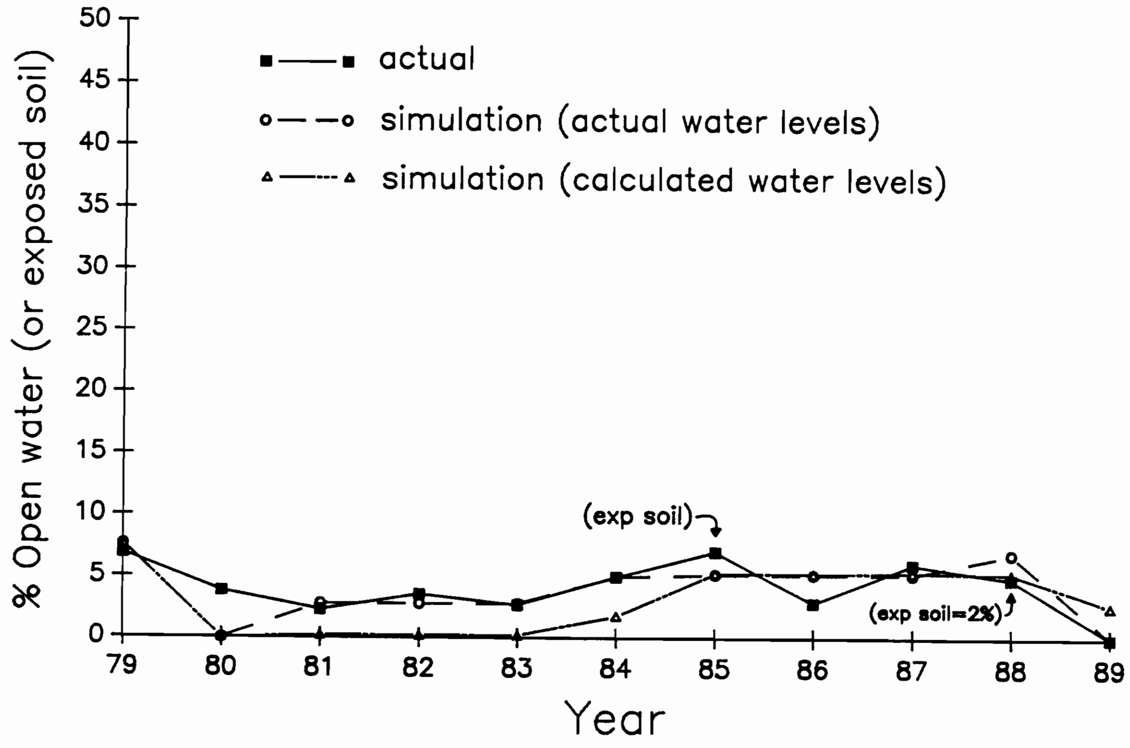


Figure 16. Percent unvegetated areas (i.e., open water or exposed soil) in wetland P4 vs model simulations (actual and calculated water levels) from 1979-89. Simulation values were on August 1; actual values were estimated from aerial photos taken in July or early-August, except for 1981 which was on November 3.

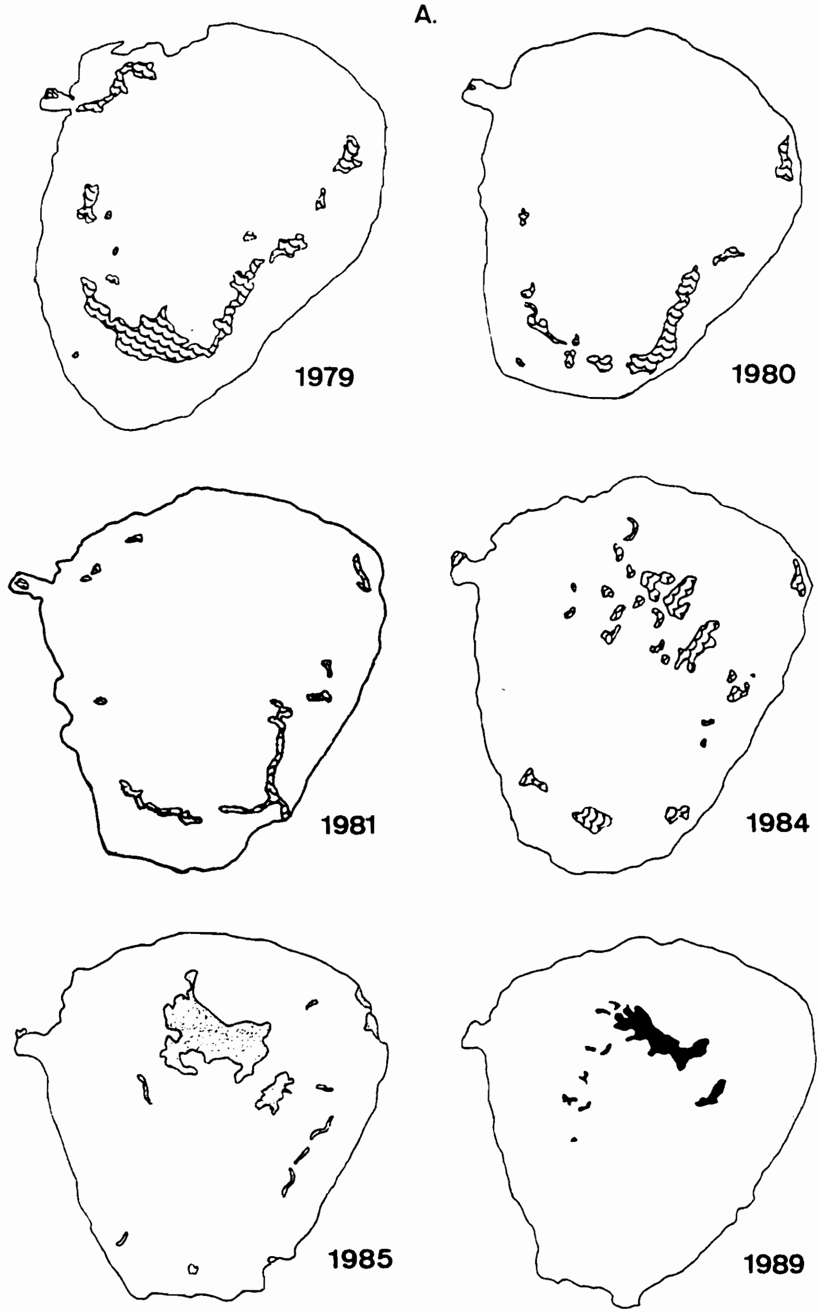
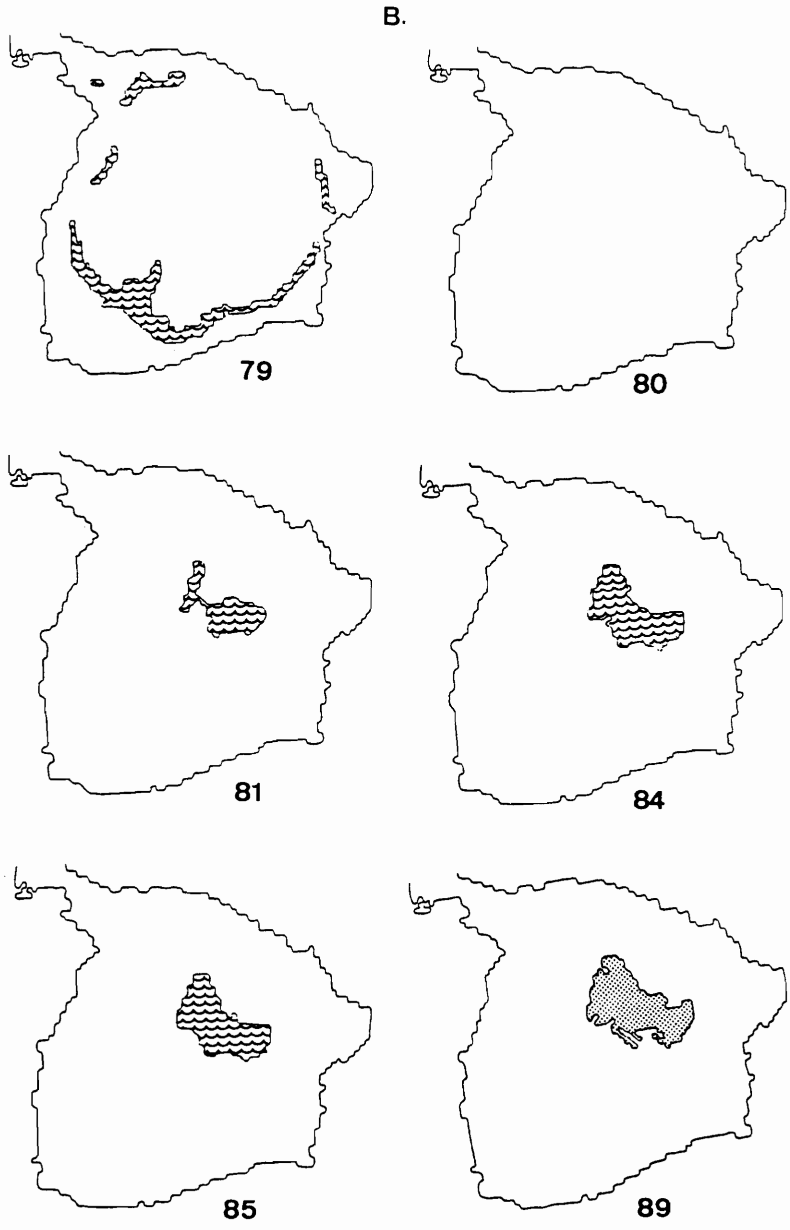


Figure 17. Cover/water distribution maps for wetland P4, selected years, 1979-89: (A) observed, (B) model simulations--actual water levels and (C) model simulations--calculated water levels. Simulations were on Aug 1; actual distributions were from aerial photos taken in July or early-Aug, except 1981 (Nov 3). Actual distributions were distorted since principal points in photos were not always at exact center of wetland. NOTE: Key on last page of figure; OW=open water, EXPS=exposed soil, DM=deep marsh, MIXEM=mixed emergents, SEEDL=seedlings.



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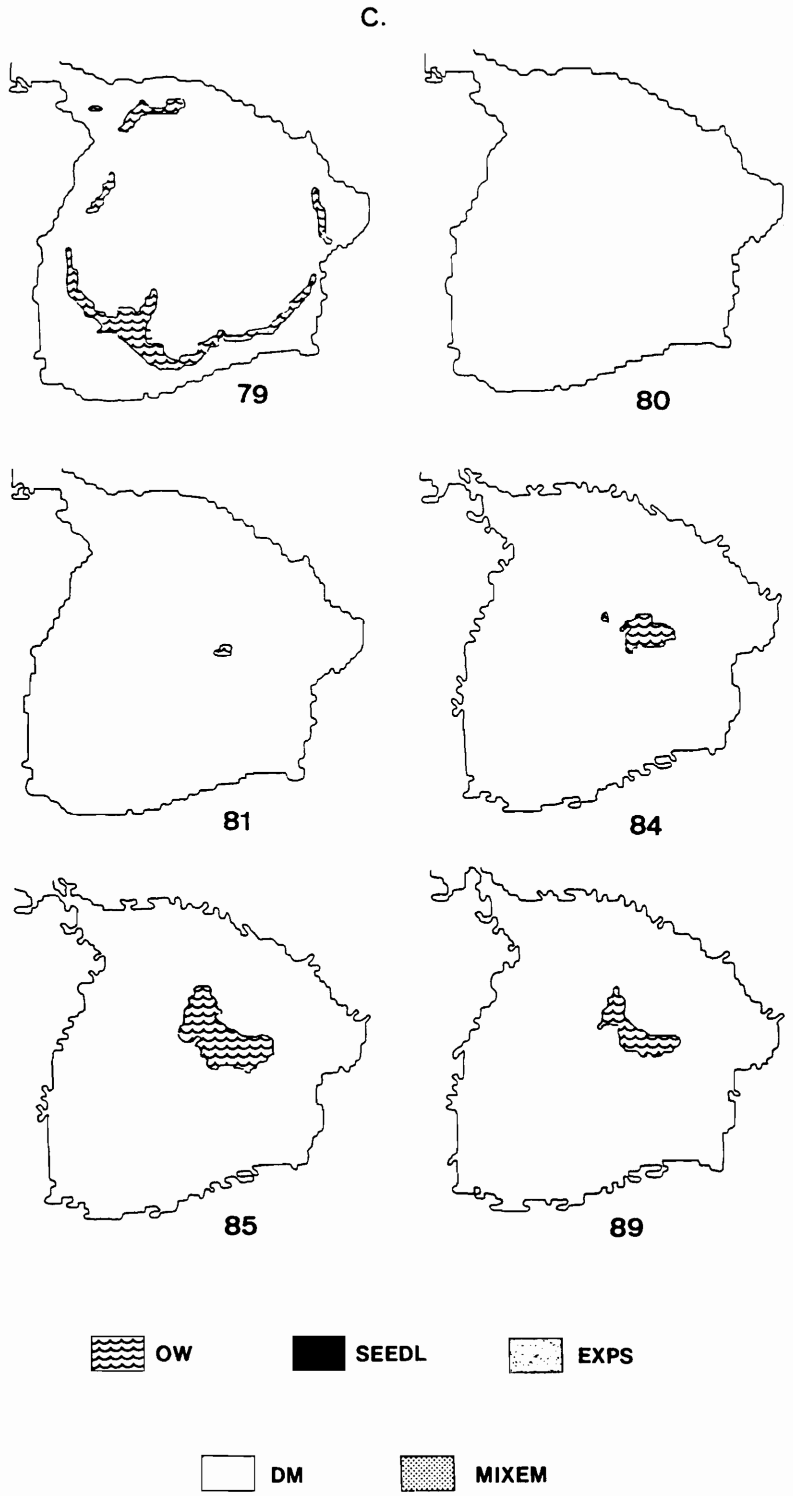

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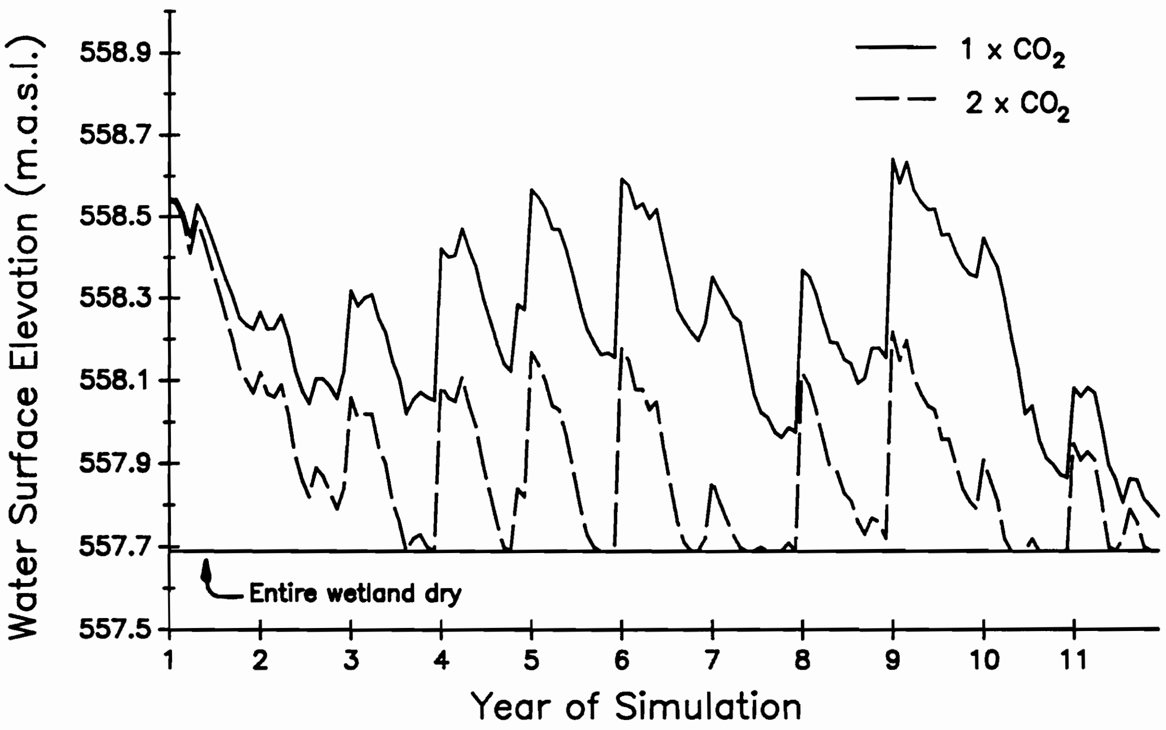

Figure 18. Model output of changes in water surface elevation (meters above sea level) for an 11 year simulation in wetland P1 under $1xCO_2$ and $2xCO_2$ climate scenarios. Entire wetland was dry at 557.7 meters above sea level.

A.

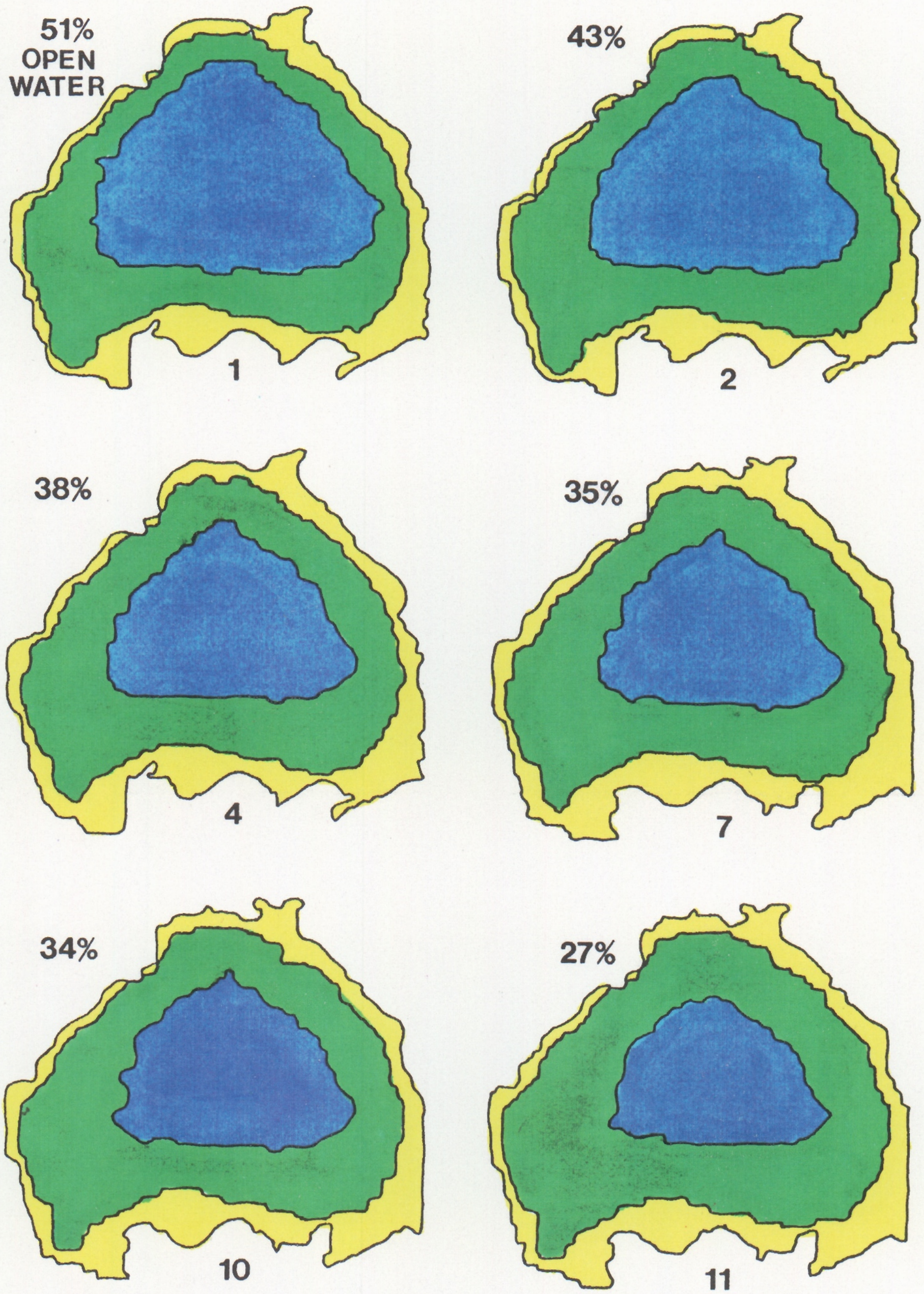

Figure 19. Model output of cover/water distributions on Aug 1, wetland P1, for selected years of an 11-year simulation: (A) $1xCO_2$ climate scenario and (B) $2xCO_2$ climate scenario. Percent open water shown in upper left corner. %OW = [No. OW cells ÷ (No. DM+OW+SEEDL)] x 100. NOTE: Key on following page; OW=open water, DM=deep marsh, SEEDL=seedlings, MIXEM=mixed emergents, MSM=meadow/shallow marsh.

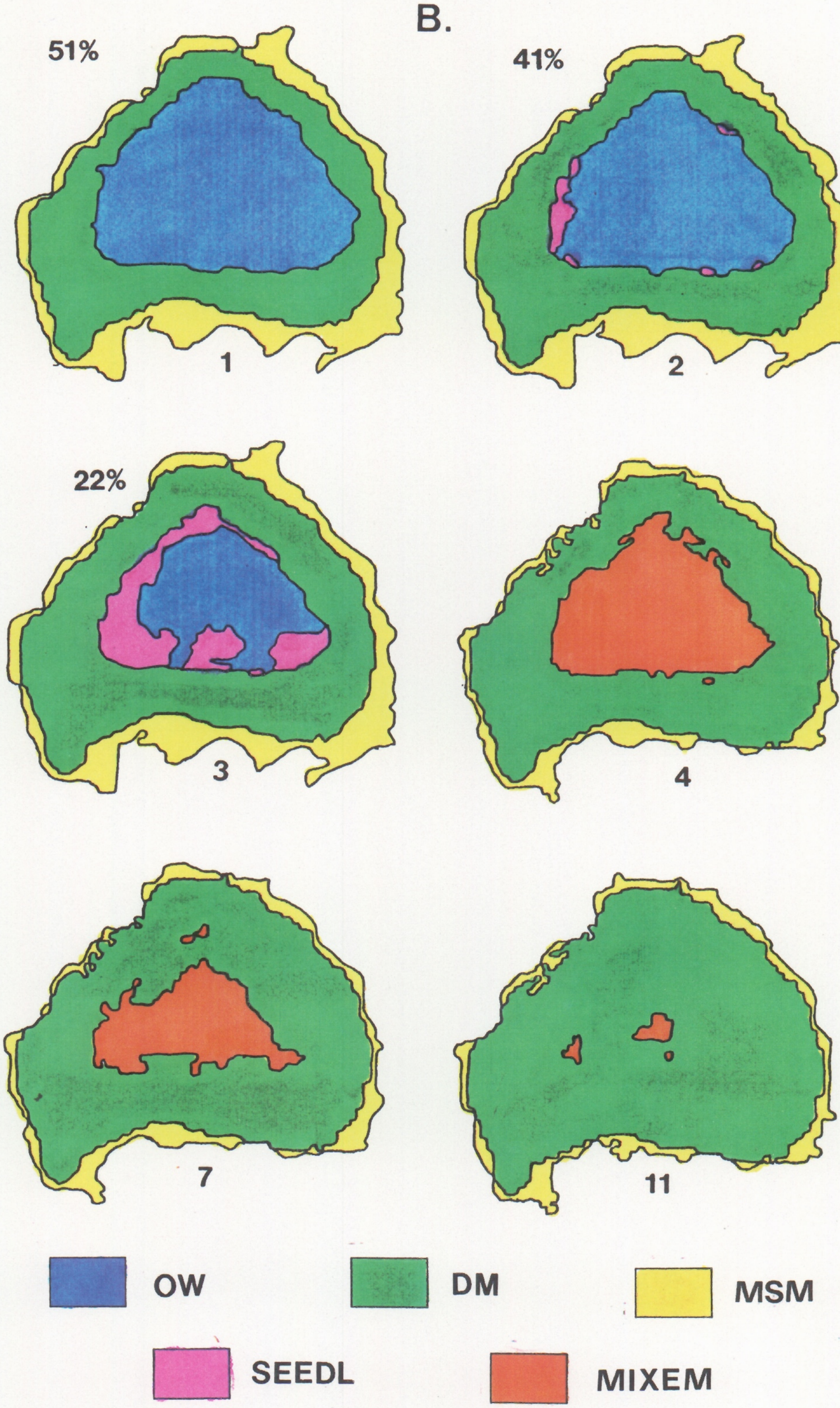

Figure 19 continued.

Table 1: Species composition of wetland vegetation and open water zones in P1 and P4 and vegetation types used in the simulation model. Nomenclature follows Great Plains Flora Association (1986).

VEGETATION TYPE (ABBRV.): species list[1]

MEADOW & SHALLOW MARSH (MSM): *Meadow:* Agropyron repens, Calamagrostis spp., Juncus balticus, Poa palustris, Rudbeckia hirta, Spartina pectinata, Teucrium canadense *Shallow marsh:* Carex atherodes, Cicuta maculata, Eleocharis spp., Hordeum jubatum, Scolochloa festucacea

DEEP MARSH (DM): Scirpus acutus, Typha angustifolia, T. latifolia, T. x glauca[2]

OPEN WATER (OW): Lemna minor, L. trisulca, Myriophyllum exalbescens[3], Potamogeton pectinatus[3], Utricularia vulgaris, Zannichellia palustris[3]

MIXED EMERGENTS (MIXEM): Carex atherodes, Eleocharis spp., Juncus spp., Scirpus acutus, S. maritimus var. paludosus[3], Scolochloa festucacea, Typha spp.

SEEDLINGS (SEEDL): *Emergents:* all species in **MIXEM** *Annuals:* Chenopodium rubrum, Ranunculus sceleratus, Rumex maritimus

MIXED PLANTS (MIXPLT): same as in **SEEDL**

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[1]Data from K. Poiani personal observations (1985-90), G. Swanson unpublished data (1980), and Poiani and Johnson (1988, 1989).

[2]Not known to occur in P1.

[3]Not known to occur in P4.

Table 2: Variables tested in stepwise regression for prediction of initial spring water elevation (May 1).

(1)
  a. Spring precip (March + April)
 or
  b. April precip

and

(2)
  a. Fall precip (last stage date through November)
 or
  b. Fall + winter precip (last stage date through February)

or

(3) Fall + spring precip

or

(4) Total precip (last stage date through April)

and

(5) March maximum temperature

(6) Spring snow (March through May)

(7) March maximum snow depth

(8) Actual fall elevation

(9) Maximum spring rain event

Table 3: Monthly normal surface air temperatures and GISS model predicted surface air temperatures (°C) for a doubled carbon dioxide climate, Jamestown, North Dakota. Data from Takle and Zhong (1990).

Month	Normal	$2xCO_2$	Diff[1]
Jan	-14.11	-8.14	5.97
Feb	-11.28	-5.40	5.88
Mar	-4.50	1.07	5.57
Apr	5.17	10.36	5.19
May	11.67	14.74	3.07
Jun	17.22	20.38	3.16
Jul	20.72	23.91	3.19
Aug	20.00	23.30	3.30
Sep	13.61	18.55	4.94
Oct	7.78	12.03	4.25
Nov	-2.33	3.70	6.03
Dec	-10.22	-4.80	5.42
Ann	4.48	9.14	4.66

[1]Diff = $2xCO_2$ - Normal

Table 4: Monthly normal precipitation and GISS model predicted precipitation (cm) for a doubled carbon dioxide climate, Jamestown, North Dakota. Data from Takle and Zhong (1990).

Month	Normal	$2xCO_2$	Ratio[1]
Jan	1.55	1.68	1.08
Feb	1.45	1.63	1.12
Mar	2.08	2.69	1.29
Apr	3.96	4.29	1.08
May	6.22	6.66	1.07
Jun	9.17	9.63	1.05
Jul	7.90	8.13	1.03
Aug	5.74	6.83	1.19
Sep	4.39	3.66	0.83
Oct	2.41	2.31	0.96
Nov	1.47	1.80	1.23
Dec	1.35	1.50	1.11
Ann	47.70	50.80	1.06

[1]Ratio = $2xCO_2$ / Normal

Table 5: Percent open water (OW), exposed soil (EXPS), seedlings (SEEDL) or mixed emergent vegetation (MIXEM) for wetland P4 and model simulations (actual and calculated water levels), 1979-89. All simulation values are on August 1; actual values are from aerial photos taken in July or August except 1981 which was on November 3.

Year	Actual	Simulation (actual wls)	Simulation (calculated wls)
79	6.9 (OW)	7.6 (OW)	7.6 (OW)
80	3.8 (OW)	0.0 (OW)[+]	0.0 (OW)[+]
81	2.3 (OW)	2.8 (OW)	0.2 (OW)
82	3.6 (OW)	2.8 (OW)	0.2 (OW)
83	2.7 (OW)	2.8 (OW)	0.2 (OW)
84	5.0 (OW)	5.0 (OW)	1.8 (OW)
85	7.0 (EXPS)	5.2 (OW)[1,++]	5.3 (OW)[++]
86	2.9 (OW)	5.2 (OW)	5.3 (OW)
87	6.0 (OW)	5.2 (OW)	5.4 (OW)
88	2.9 (OW) & 2.0 (EXPS)	6.9 (OW)[2,++]	5.3 (OW)
89	2.7 (SEEDL)	6.3 (MIXEM)[+]	2.6 (OW)

[1]5.2% SEEDL on September 1.

[2]6.9% SEEDL on September 1.

[+]Percent OW or vegetation type extremely different from observed value as evaluated by comparison using z-statistic (see text).

[++]Percent OW different from observed but not percent of non-vegetated area (i.e., open water plus exposed soil).

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