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A Quantitative Reconstruction of WAUBESA MARSH

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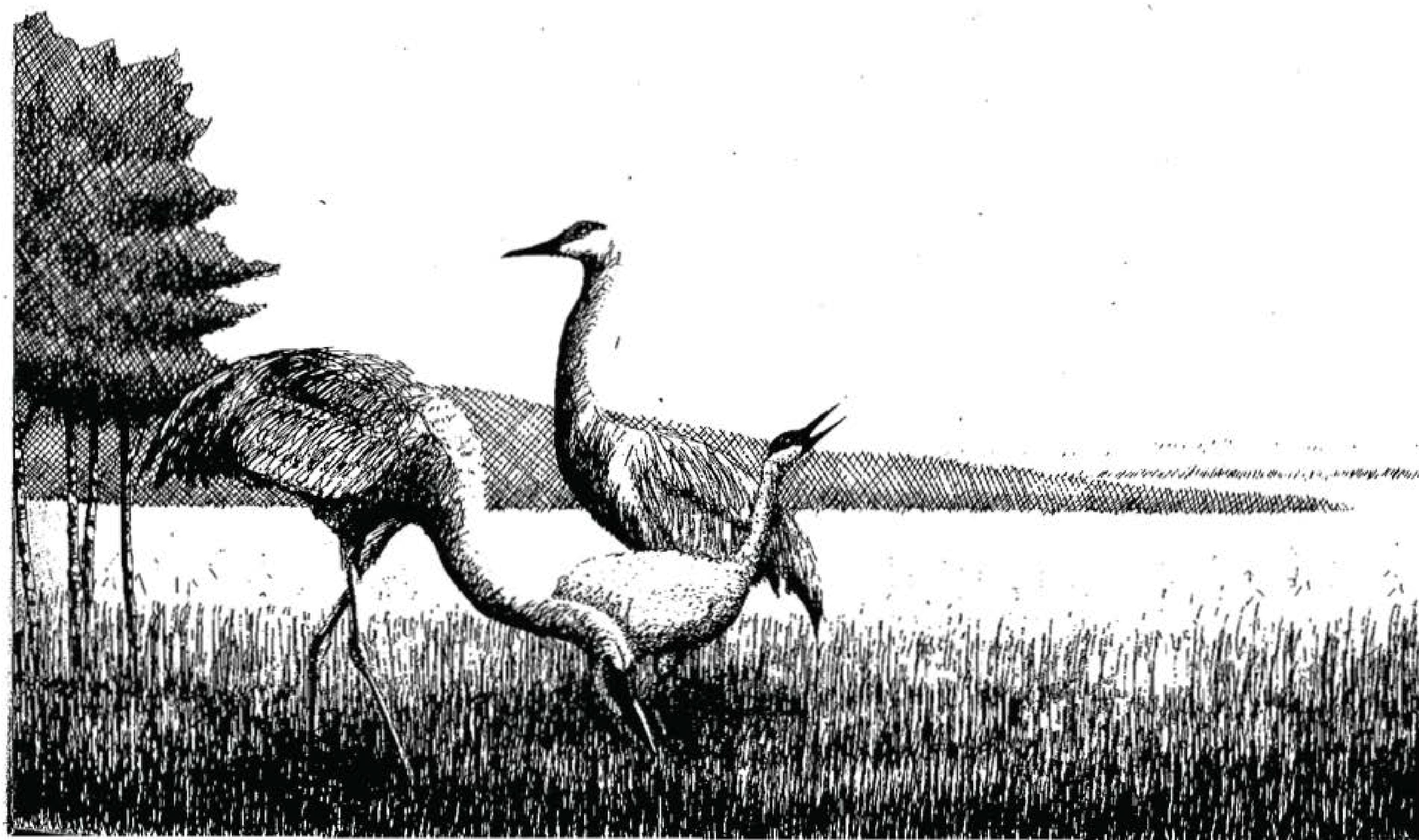

SIMULATING POSTGLACIAL WETLAND FORMATION: A QUANTITATIVE RECONSTRUCTION OF WAUBESA MARSH

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# # # #

Robert M. Friedman currently is a Congressional Fellow with the Office of Technology Assessment, U.S. Congress, worked on the Waubesa Marsh development study from its inception in 1972 through to its completion as his doctoral thesis in Ecosystems Analysis at Wisconsin in 1978.

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Cover illustration depicting Sandhill Cranes on Waubesa Marsh is by Kent Anderson and is reprinted from the Town of Dunn Open Space Preservation Handbook with permission from the Environmental Awareness Center, University of Wisconsin-Madison and the Town of Dunn Open Space Committee, Dane County, Wisconsin.

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ABSTRACT

The developmental history of a wetland ecosystem is quantitatively reconstructed: (a) at the level of resolution of the ecosystem itself, (b) dynamically, throughout the postglacial period, and (c) spatially, considering the wetland as a 3-dimensional entity. The goal of the research effort was to gain an understanding of the ecological and physical processes controlling lake-edge wetlands formation, particularly the landscape or spatial factors involved. A secondary, supportive goal was to develop quantitative methods appropriate for analyzing ecosystems spatially.

A conceptual model describes the formation of lake-edge wetlands as a dynamic process involving vegetation growth, decay and transport of dead vegetation into the lake, and eventual deposition of organic matter, providing more substrate suitable for the establishment of vegetation. The morphometry of the wetland and the lake basin in which it forms is postulated to be a primary controlling factor. Surface transport characteristics, sediment slopes, basin configuration, and location with respect to lake circulation patterns are examples of important morphometric characteristics. The formation of a wetland is considered to be a total system response to the landscape in which it forms and to the history of past responses.

To test the hypothesis of the importance of spatial determinants in the wetland formation process, the conceptual model was formalized into a computer model that simulates the size and shape of a wetland in southern Wisconsin throughout its developmental history of 6,500 years. A spatial modeling strategy was developed that incorporates the general ecological principles proposed and the morphological specifics unique to each wetland. The model was constructed to predict the extent of the wetland at known points in time for subsequent comparison to radiocarbon dates. The model predicts the data within experimental error of the radiocarbon analysis. Several alternative hypotheses to the conceptual model were simulated and found to yield less satisfactory predictions of the data. A discussion of ecosystem energy relationships during the formational period of the wetland studied is included.

Key words: ecosystem development, holocene, lake-edge wetlands, model, peat formation, simulation, spatial model, wetland formation, wetlands, Wisconsin.

CONTENTS

TABLES

FIGURES

INTRODUCTION

Wetland Ecosystems

Wetlands is a broad term used to describe many types of ecosystem with one common characteristic: they all include, literally, wet land (Quigley 1977). Ecosystems too wet to be considered terrestrial, yet not quite aquatic, wetlands exhibit ecological processes distinctly different from the two major ecosystem categories, water and land. Of the many ways one might classify wetlands, one is especially appropriate to this paper, a landscape view. By this we mean the location of the wetland in, and the subsequent interaction with, the landscape.

Recent years have seen a resurgence of interest in wetland ecosystems, due primarily to the role these ecosystems play in the protection of environmental quality. Lake-edge and river-edge wetlands have been the subject of much scientific investigation, recognizing that the location of these ecosystems in the landscape may help maintain adjacent surface water quality by acting as buffer areas for flood waters and nonpoint source pollution. Most of this research has concentrated on ecosystem processes that occur within the time span of one, or possibly several, growing seasons.

In this paper, we will discuss ecosystem dynamics occurring over a much longer time scale: the development of lake-edge wetlands from their origins in bays of postglacial lakes to the present. We present a dynamic computer model that reconstructs the formation of a wetland ecosystem as a 3-dimensional entity changing through time. The purpose of our computer model is to test and formalize a conceptual model of the ecosystem dynamics controlling the formation of this wetland type.

Lake-edge wetlands form when the rate of productivity of the associated vegetation exceeds the decomposition rate, the excess organic matter resulting in peat. Indeed, one of the major differences between wetlands and other ecosystems is the extent to which wetlands form their own habitat, the peat substrate on which the wetland plants thrive. For the formation of wetlands to occur, several factors must fall within a range that allows the productivity of the ecosystem to exceed decomposition. Controlling factors commonly identified include the hydrologic regime, nutrient inputs, and climate. Yet given that these conditions are met, for example, within a chain of lakes, why and how do wetlands form in some regions of these lakes and not in others?

We have tried to answer this question by taking a landscape view of the formation process. By taking such a view, the absence of spatial characteristics from the above usual list of requirements for wetland formation becomes apparent. In this paper, we test the hypothesis that spatial factors are important determinants of the wetlands formation process. Spatial characteristics that we hypothesize are important to the functioning of the system include:

- The morphometry of the water body in which the wetland forms.
- The shape and structure of the wetland edge and the proximity to prevailing lake circulation patterns.
- The paths of materials transported across the wetland surface due to water flow. The patterns of such spatial characteristics change through time. The present state of a wetland is a result of all past states, including both the histories of past spatial characteristics and the response to external factors such as climatic and nutrient regimes.

Goals of the Research

The goal of our research effort was to gain an understanding of the ecological and physical processes controlling lake-edge wetlands formation, particularly the landscape or spatial factors involved. A secondary, supportive goal was to develop quantitative methods appropriate for analyzing ecosystems spatially.

To test our hypothesis of the importance of landscape determinants in the wetland formation process, we have formalized a conceptual model of the process into a computer model that simulates the size and shape of a specific study site throughout the postglacial period. To enable us to construct the model, we have developed a spatial modeling strategy that incorporates both the general ecological principles proposed and the morphological specifics unique to each particular wetland.

In our research we address this 3-pronged question:

Can the developmental history of a wetland ecosystem be quantitatively reconstructed:

- *at the level of resolution of the ecosystem itself?*
- *dynamically, throughout the postglacial period?*
- *spatially, considering the wetland as a 3-dimensional entity?*

Our reporting procedure will be organized according to an outline presented by Mirham (1972). This organizational scheme helps to clearly and logically present the results of a modeling based research study.

HISTORICAL OVERVIEW OF THE STUDY SITE

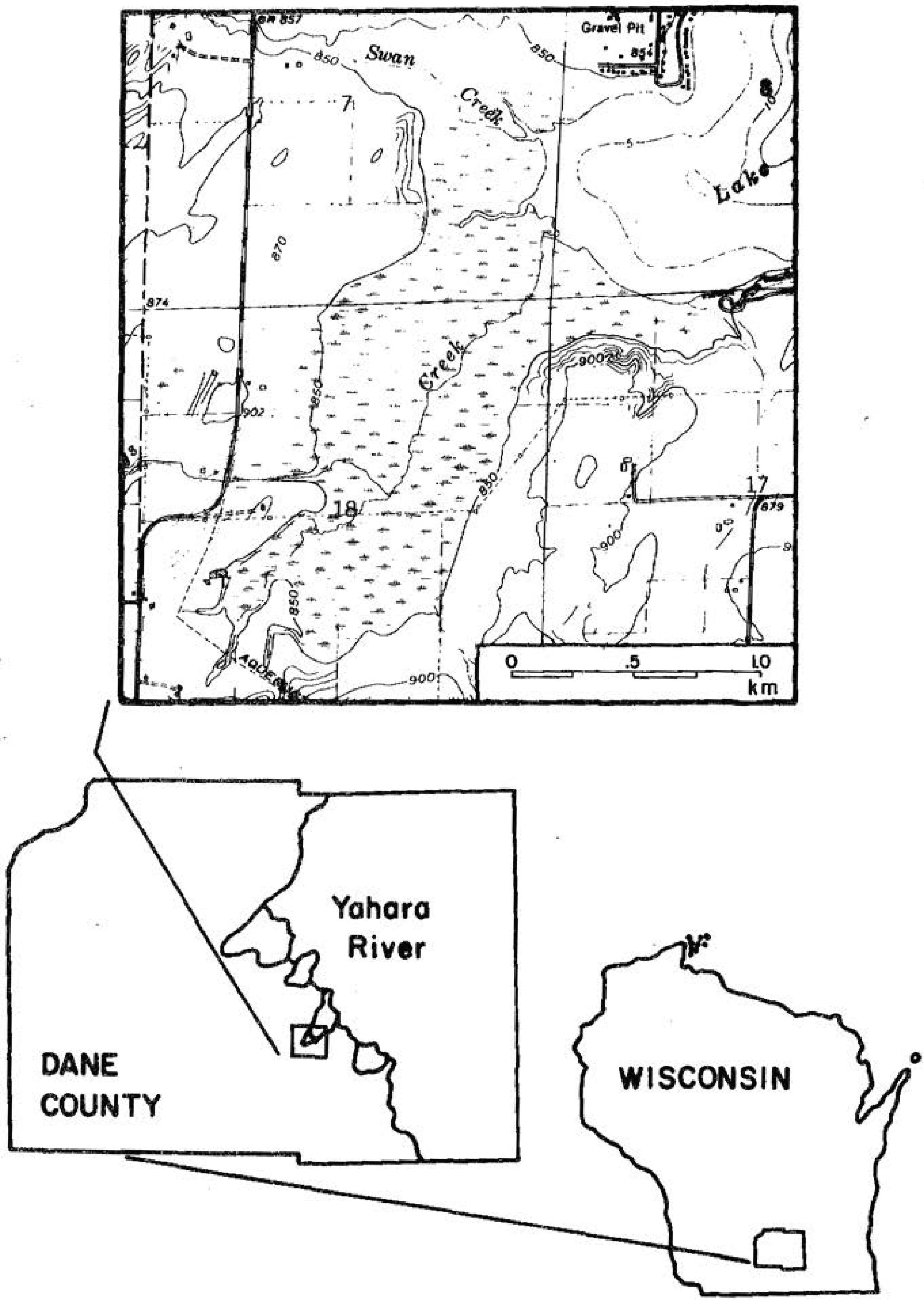
Glacial and Postglacial History

The study site, Waubesa Wetlands, is a 150 hectare lake-edge wetland located on the southwest shore of Lake Waubesa in Dane County, Wisconsin (Figure 1). It is a complex of sedge meadow, *Typha*, fen, and shrub carr communities and is bordered by agricultural and wooded uplands. From the available literature on the glacial history of the region (Bedford, Zimmerman, and Zimmerman 1974; Cline 1965), the Wisconsin Glaciation, the last glaciation of some 27,000 years ago, moved across Wisconsin scouring the landscape as it advanced. By about 18,000 to 20,000 years ago the Green Bay Lobe reached its maximum extent, covering the Yahara River Basin, location of the study site. As the glacier retreated 14,000 years ago, it left a deposit of glacial till that covered the old stream valleys in the Yahara River Basin. The same general pattern of drainage was reestablished but in a shallower basin, resulting in the current chain of lakes, connected by a slower-flowing Yahara River, of which Lake Waubesa is one (Figure 1).

From our observations of the stratigraphy of Waubesa Wetlands and with the aid of several radiocarbon analyses of the age of the wetland sediments (see the "Testing the Model" section for more details), we find the depth to glacial till at the middle of the lake edge of the present-day wetland to be approximately 30 meters. Above the glacial till are 27 meters of sediments from primarily lake origin. Overlaying the lake sediments are 2.5 meters of primarily wetland origin sediments (fibrous peat). The depths of fibrous peat within Waubesa Wetlands range from 1.5 to 2.5 meters and are found on top of a much thicker layer of lake sediments, in excess of 10 meters over most of the region. At a distance 300 meters from the present lake edge, the depth to glacial till is approximately 20 meters. Including a time perspective, at this location 15 meters of lake sediments had been deposited on top of the till from the time the glacier receded to 6,000 years ago. Ages of the wetland sediments from radiocarbon analysis range from 6,000 years old at a point near the present upland edge, to 1,000 years old near the present lake edge.

From these data, we infer that postglacial Lake Waubesa was once at least three times its present depth of 10 meters and the study site was a bay of the lake extending southwest for a distance of approximately 1,600 meters. Shortly after the retreat of the glacier, Lake Waubesa most likely became moderately eutrophic, filling the bay rapidly and, at some time prior to 6,000 years ago, the wetland began to form within the bay on top of the large accumulation of lake sediments. The wetland formation process took at least 5,000 years with the study site reaching its present extent within the last 1,000 years.

FIGURE 1. Map of Waubesa Wetlands and its location on the Yahara chain of lakes, Dane County, Wisconsin.



A HISTORICAL SYSTEM RESPONSE

In order to test our hypothesis of the importance of spatial relationships in the formation process, we identified an appropriate system response that we could measure in the field and simulate with a computer model. Our historical, landscape description suggests such a measure of system performance: the extent of the wetland, i.e., the 3-dimensional shape of the wetland, at any point in its formational history. The model we have developed has been constructed to simulate the age of wetland sediments dated with radiocarbon methods; the age of the sediments at a given location corresponds with the extent of the wetland at a point in time.

In addition to suggesting an appropriate system response, our historical description:

- provides the basis for defining the system's spatial and temporal boundaries
- establishes the need for a modeling methodology that allows the inclusion of the spatial component
- suggests appropriate delineation of entities that interact with one another, i.e., the choice of system variables.

SYSTEMS ANALYSIS

The identification of components, interactions, and dynamic behavior of the system is necessary for construction of a model of the wetland ecosystem development process (Mirham 1972). We must perform several tasks in specifying the conceptual model:

- Delineate the system boundary, a division that allows a meaningful separation of (a) system entities, the components that interact with each other, and (b) system environment, the components that affect the system but are not affected by the system's dynamics
- Identify the entity attributes (also called 'state variables'), the variables necessary to describe the changes that occur to the system entities
- Locate the intrinsic feedback mechanisms, the internal activities of the system that are responsible for much of the system's dynamics
- Specify the system's behavioral structure, the interactions of the entities and attributes, and the way the interrelationships vary through time.

In order to translate the conceptual model into a computer-implemented model, the conceptual model must be constructed to insure: (1) that the extent of the wetland at any point in time (the measurable system response) is one of the system state variables and can be explicitly modeled, and (2) that the system is delineated so that all other state variables are modeled at an appropriate level of resolution.

Modeling Strategy

To facilitate inclusion of spatial interrelationships into an ecosystem model, the system's structure must be conceptualized differently than in ecological mass and energy flow models. Figures 2 and 3 and the following text explain this difference and the advantages of a spatial modeling approach.

Let us proceed to construct a model of the following statement: *the formation of a wetland ecosystem may be considered a response of the total system interacting with its environment and itself.* Figure 2A illustrates this in a most general way: the inputs are the environment of the system, the outputs are any variables we wish to follow explicitly (e.g., the volume of peat stored), and the feedback loop represents the system interacting with itself.

The purpose of any modeling effort is not to describe the entire system, but only those aspects of a system necessary to meet one's objectives (e.g., testing hypotheses, organization of information, experimental design, etc.). A general procedure that one might follow has been listed earlier: delineation of the system boundary, environment, entities, entity attributes, feedback mechanisms, etc. The form of the result of this procedure is often illustrated as a flow chart (Figure 2B). The process of proceeding from Figure 2A to Figure 2B for a particular system and research goal is not a trivial operation: a multitude of representations may result, each with its own strengths, weaknesses, and inherent biases for further understanding of the real world system.

Figure 3 illustrates two possible alternatives for delineating system entities and feedback structure. The most common expression of ecological systems is illustrated in Figure 3A. This is a mass and energy flow point model that identifies as entities the physical components of the system (e.g., the biological organisms, the soil or lake bottom substrate, etc.). The attributes of these entities are the energy content and mass of nutrients contained within each component. The system boundary is implicitly drawn around the total of these entities with no reference to spatial location, hence the term *point model*. The arrows represent the feedback mechanisms, i.e., the nutrient and energy flows between the entities of primary producers, decomposers, and the organic substrate of peat and dead vegetation. The system's behavioral structure is defined by interactions that result in a transfer of nutrients and energy among components; this is usually expressed as a set of simultaneous differential equations with the attributes (mass and energy content) as state variables.

FIGURE 2. Modeling strategy: the system interacts with its environment and itself: (A) generally, and (B) with pertinent attributes.

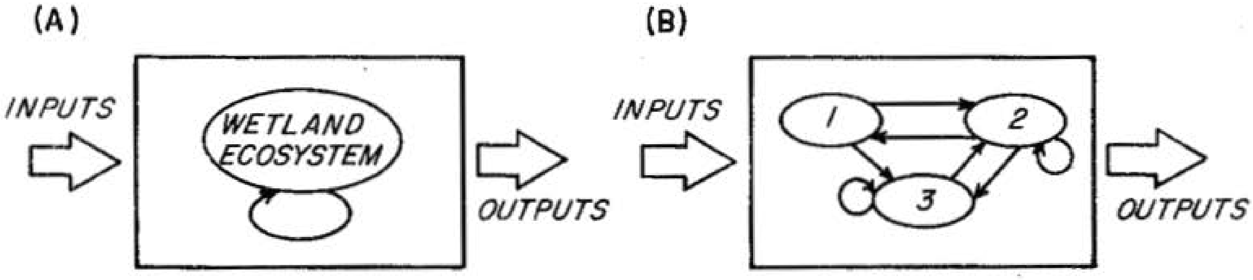


FIGURE 3. Modeling strategy: choices of attribute identification and system structure with mass and energy flows considered as (A) interactions between attributes, and (B) as attributes in their own right.

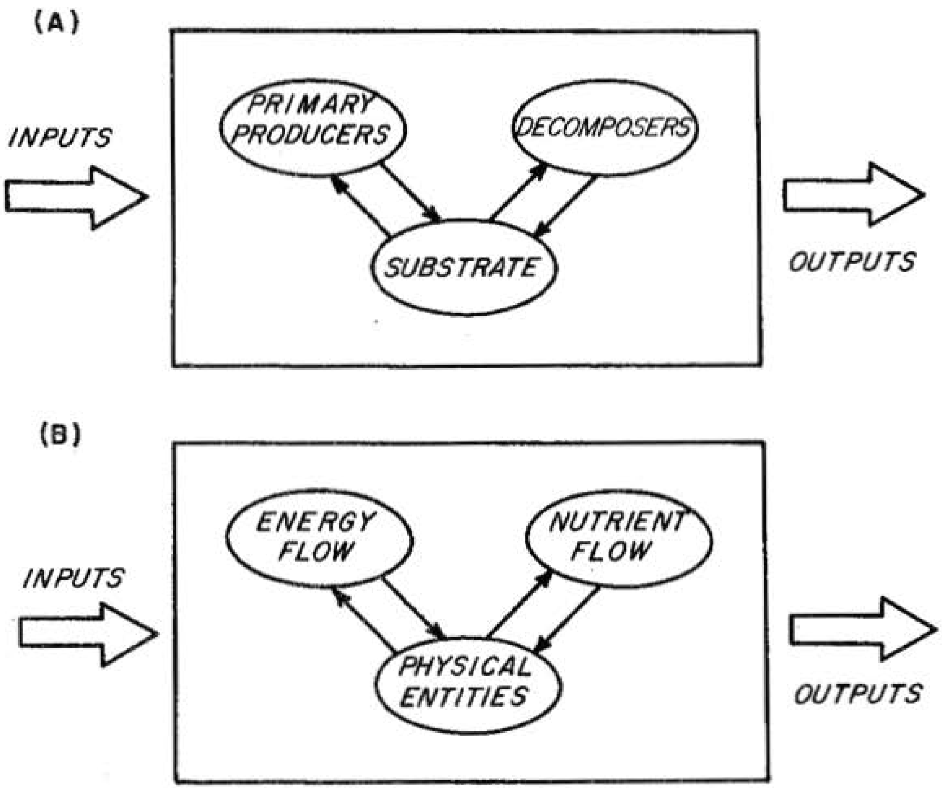
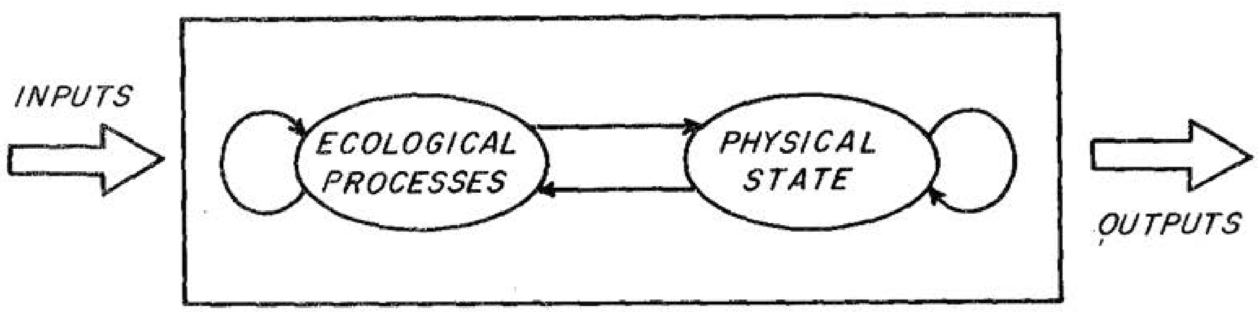


Figure 3B represents an alternative perspective of this same system. Energy and nutrient flow characteristics are identified as system entities in their own right, rather than as interactions between entities. Attributes of these entities might be, for example, net productivity per unit area per time or nutrient storage per unit volume per time in the peat. The physical entities (primary producers, decomposers, and substrate) or the previous formulation are also included. The arrows, instead of representing physical flows, indicate interactions in abstract terms, i.e., the paths of causation or the information necessary to describe the interrelationships among entities. The system boundary is no longer implicitly drawn; spatial boundaries can be explicitly included.

The advantages of considering a system by the latter approach should become apparent upon consulting Figure 4, a generalization of this last model and the method we are advocating. The two entities we have isolated are: (1) the physical state of the system, and (2) the ecological processes involved in the system's dynamics. This allows us to consider separately the ecological principles that are invariant from specific system to system, and the physical state of the system that varies from site to site. Each of these entities is then modeled separately by identifying the pertinent subentities and attributes. This results in a hierarchical model that maintains distinctions between site specific and general processes.

FIGURE 4. Modeling strategy: separation of ecological processes and the physical state. Generalization of Figure 3B; showing the physical state and ecological processes as the basic attributes of the wetland ecosystem.



The constraints imposed by the system's behavioral structure are considerably relaxed: (1) the system boundary can be explicitly drawn in 3-dimensional physical space, (2) the system environment is defined by what is outside the constantly changing physical system boundary, (3) system attributes need not all be of the same units, (4) the time scale of the model is not restricted to a range commensurate with physical flow rates, and (5) the model can directly address ecosystem level processes, rather than being constrained to the population or trophic levels.

The Importance of Considering Spatial Interrelationships

Ecological theory has to a large extent omitted the 3-dimensional world from its scope. The concept of the niche (Hutchinson 1957) refers to an N-dimensional hyperspace of important factors such as light, nutrients, etc.; the more familiar 3-dimensional world of distance, area, and volume has been only indirectly included. Models of population dynamics usually consider population interactions in a homogeneous environment or possibly a time-varying, yet spatially constant environment (May 1973). A few exceptions do exist, e.g., Huffaker's (1958) study of mites using oranges as a substrate and Levin's (1974) population studies that include migration between populations. These last studies make clear that incorrect conclusions can easily be drawn when the reality of physical space is omitted.

Ecosystem models have usually omitted the spatial component, concentrating on energy or nutrient flow governed by trophic level or population interactions. Examples include the aquatic CLEANER model (Park 1974), and the terrestrial models, ELM (Innis 1975) and TEEM (Shugart 1974). Each of these models is a member of the class of point models; one representative 'point' or location within the ecosystem that exhibits typical dynamics of the system is selected and interactions at this point are modeled and simulated through time. These models, because they disregard spatial interrelationships, can answer only a limited set of ecological questions.

Recognizing the limitations of the single point approach, de Caprarilis (1977) has modified the CLEANER model mentioned above to include several points, each representing a layer within a lake. Including spatial interrelationships in ecosystem models increases their realism and allows site specific differences to be considered. The Vollenweider (1976) eutrophication model provides possibly the best example of the generality inherent in models based on spatial concepts: this relatively simple, static model has widespread utility because its spatial component provides a framework that allows comparison of many lakes simultaneously.

Our modeling framework enables us to identify as separate entities, the physical state of the system and the site invariant processes. The framework specifies the spatial determinants of formation as part of the ecological processes entity; the spatial determinants interact on the basis of the physical state. Spatial determinants can be modeled as a "spatial metric," i.e., morphometric considerations that are important because they mediate ecological processes. The concept of a spatial metric may be considered in two parts: (1) most simply, as a procedure for normalizing factors such as nutrient concentrations and productivity estimates to allow comparisons within or between wetland systems or with results from aquatic and terrestrial systems, and (2) as a description of the system morphometry as a controlling factor of the dynamics of the ecosystem.

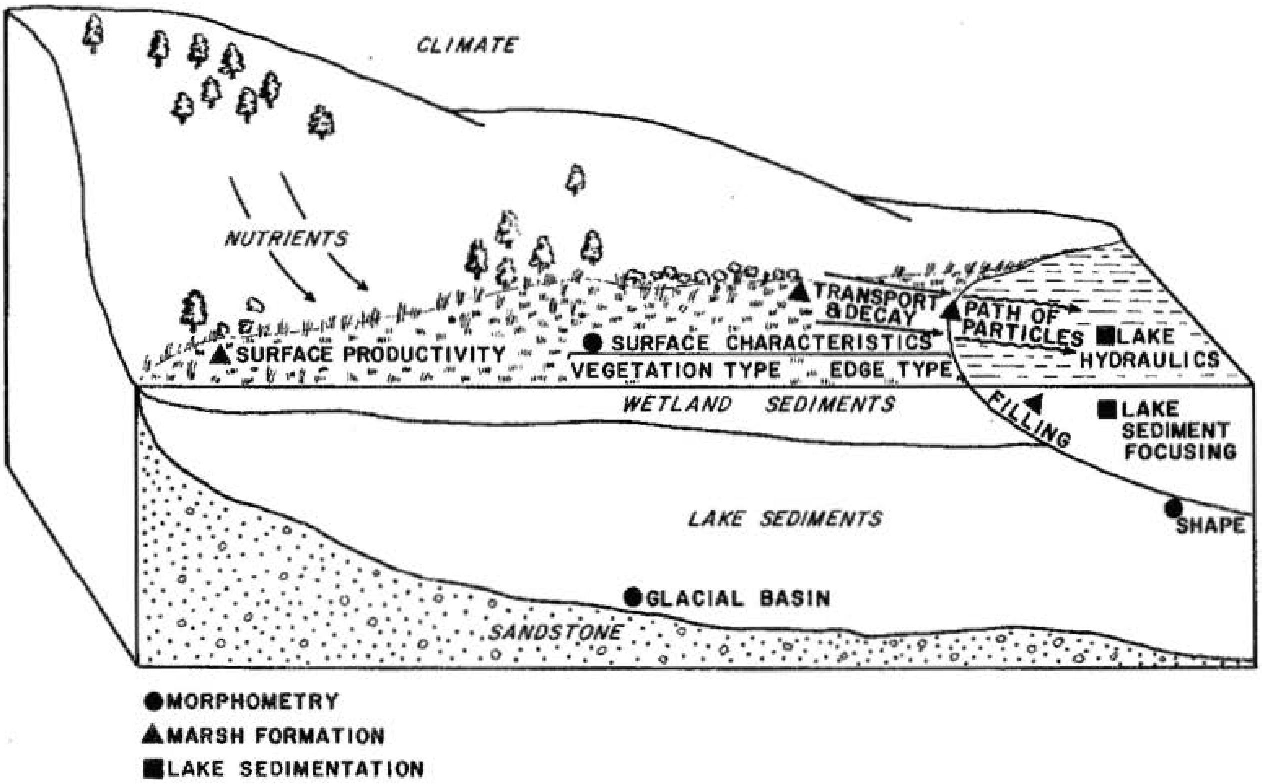
The Choice of System Boundary, Entities, and Attributes

Figure 5 is a pictorial diagram of the conceptual model we have used to simulate the formation of a lake-edge wetland. The system boundary, a physical surface, may be drawn in either of two places: (1) the interface between the glacial till and lake sediments, i.e., the old glacial lake bottom, or (2) the interface between the lake sediments and wetland sediments. We have chosen the second option for several reasons:

- The interface between lake and wetland sediments is a distinct transition at the study site.
- The first several thousand years of the bay filling process (before the wetland began to form) can be considered outside the realm of interest; i.e., outside the system boundary spatially and temporally. The lake sediments below the transition to wetland sediments are considered as part of the environment for the wetland formation process.
- From a practical standpoint, the lake sedimentation process is an extremely complex problem and is of secondary interest to the wetlands dynamics. The choice of the latter interface minimizes the errors introduced to the model from an incomplete description of lake sedimentation.

The system has been divided into three entities: (1) wetlands morphometry, (2) the marsh sediment formation process, and (3) aspects of the lake sedimentation process germane to the problem. The attributes of each entity are indicated in Figure 5 and listed below.

FIGURE 5. Conceptual model of the wetland formation process showing components.



These attributes of wetland morphometry include:

- The observed stratigraphy, i.e., the relative depths of wetland sediments, lake sediments, and open water
- The shape of the basin, e.g., basin slopes, the outline of the basin, and location in the landscape as it might appear on a topographic map
- Surface characteristics, including (a) the effect of the vegetation type on materials transport, and (b) the effect of the lake edge type on sedimentation in the bay.

Attributes of the marsh sediment formation entity include:

- Surface productivity of the vegetation, expressed as biomass per unit area per time as modified by the system environment (i.e., climate and nutrient supply)
- Transport and decay of dead vegetation across the wetland surface until the lake edge is reached
- The path that particles of decayed vegetation travel through the lake
- The filling process, resulting in changes in the lake edge morphometry as new wetland vegetation is established.

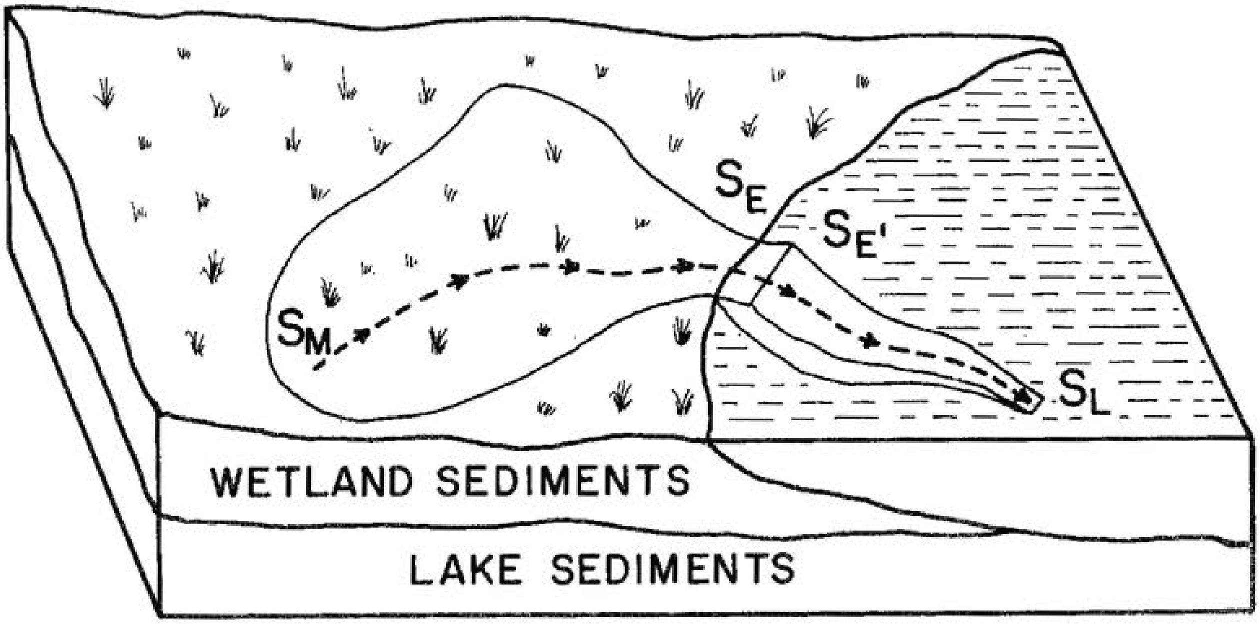
Attributes of the lake sedimentation entity include:

- Lake hydraulics, i.e., the circulation patterns within the lake as they affect the mixing of sediments and removal of wetland sediments
- Lake sediment focusing, the accumulation of sediments in part of the lake isolated from the major circulation patterns.

Feedback Mechanisms of the Conceptual Model

The dynamics of the model result from a linking of the attributes of the marsh formation entity into a feedback process. This process can be described as follows: (1) vegetation grows on the surface of the wetland, producing a volume of organic matter, (2) this organic matter is transported and partially decays until it reaches the lake edge, (3) the sediments enter the lake, flowing downhill, until (4) filling occurs at the lake edge, providing more substrate on which vegetation may grow, (5) year after year, the process repeats. Figure 6 and the equations below describe this process dynamically.

FIGURE 6. Primary feedback mechanism of the conceptual model. Shown for a section of the lake-edge wetland. See text for description.



Consider a point on the lake edge, noted as S_E in Figure 6. The decayed vegetation that eventually reaches the lake edge originates from within the wetland area enclosed by the solid line. This area can be considered as a function of the distance S behind the lake edge,

$$(\text{Area})_M = \int_{S_E}^{S_M} f(s)\, ds$$

where: S_M = the greatest distance in the marsh from which decayed vegetation reaches the lake edge, and

$f(s)$ = a function describing the area of the segment of wetlands a distance s from the lake edge.

We can denote the total sediment load from this area to reach S_E by:

$$(\text{Load}) = \int_{S_E}^{S_M} k \cdot f(s) \cdot g(s) \cdot ds$$

where: $g(s)$ = a dimensionless transport and decomposition relationship as a function of distance behind the lake edge, and

k = the productivity of the surface vegetation in units biomass/area per time.

Next we must describe the volume of lake filling that results from a lake-edge advancement from S_E to $S_{E'}$. This can be expressed by:

$$(\text{Volume}) = \int_{S_E}^{S_{E'}} (\text{Area})_L \, ds$$

where: $(\text{Area})_L$ = the area of the lake bottom covered by the sediments.

This area is the differential of the volume to be filled, expressed by:

$$d\,(\text{Volume}) = (\text{Area})_L = \int_{S_E}^{S_L} h(s)ds$$

where: S_L = greatest distance in the lake which the sediments can reach, and

$h(s)$ = a relationship which describes the segment of area (or volume differential) of the lake bottom as a function of distance from the lake edge.

The dynamics of the process can be expressed when one recognizes that the wetlands surface advances into the lake bay as a result of the vegetation produced on the surface traveling to the lake edge and filling part of the bay. This rate of advance can be expressed by:

$$\frac{ds}{dt} \propto \frac{(\text{Load})}{d\ (\text{Volume})}$$

where: ds/dt = the rate of advance (distance per unit time) of the lake edge into the bay.

Description of the System's Behavioral Structure

Figure 7 is a flow diagram for the wetland formation conceptual model, a representation of the system's behavioral structure. The heavy lines indicate the interactions most important for understanding the process, the broken lines indicate additional interactions that are necessary to specify the dynamics. The entities and attributes are the same as those shown in Figure 5.

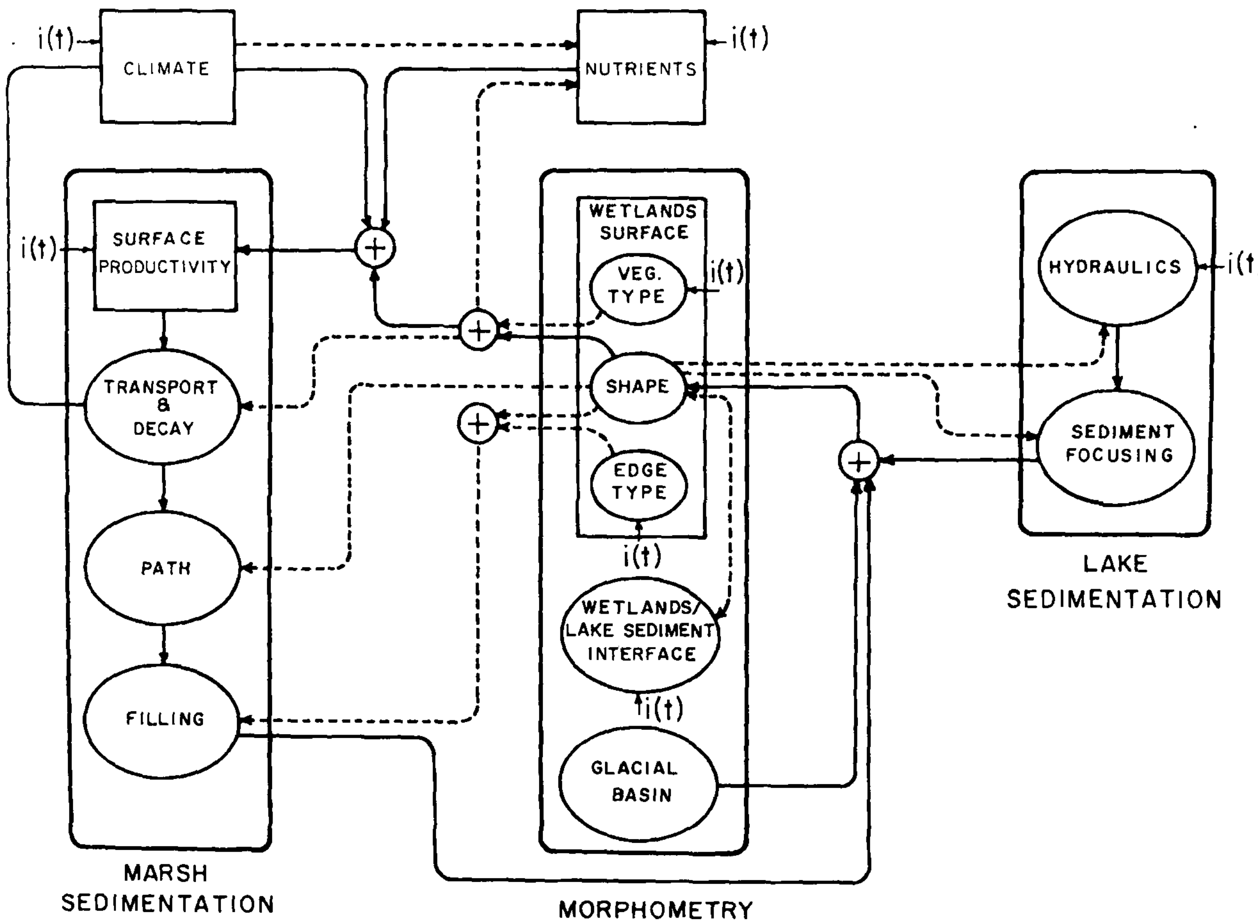
Notice, first of all, that contained within the behavioral structure is the feedback mechanism described in the last section: (1) 'surface productivity,' (i.e., the vegetation grows on the wetlands surface), (2) 'transport and decay,' (the decaying vegetation travels across the surface to the lake edge), (3) 'path,' (the decayed vegetation is distributed in the lake bay), (4) 'filling,' (the lake edge advances), and (5) 'shape,' (new substrate is formed that accommodates more wetland vegetation). Figure 5 completes the specification of interactions with arrows from the 'shape' attribute to each of the preceding four attributes. Each of these relationships was expressed in the last section as equations dependent upon s, the distance from the lake edge along a steepest descent line.

In addition, the shape attribute can affect other attributes not contained directly within the major feedback mechanism. Arrows are drawn from 'shape' to 'nutrients' and the two lake sedimentation attributes. Each arrow from the 'shape' attribute indicates a spatial interrelationship which we feel is important to the wetland formation process. The large number of arrows originating from the 'shape' attribute emphasize the need for a 3-dimensional implementation of the model.

The model allows a great deal of flexibility in defining the system boundary. The symbol i(t), (i.e., input as a function of time) denotes specification of the system environment. These are entered into the computer as either constants or functions of time. Examples include 'vegetation type' and 'edge type'; this information may be obtained from pollen profiles or may be assumed to be the same as present day. Some of the attributes may be considered as functions of the environment or may be determined by other attributes. For example, 'surface productivity' may be assumed as constant throughout the formation period or may be a function of the 'vegetation type' on the surface, 'climate,' and 'nutrients' attributes. The choice of specifying the physical boundary is similar. The 'wetlands/lake sediment interface' may be mapped and entered directly into the computer; or the 'glacial basin' may be entered and the 'wetlands/lake sediment' attribute calculated by the interactions of other attributes.

The computer model is an accurate representation of the conceptual model. However, several of the interactions are not included due to relatively constant conditions at the study site over its 6,500-year period of formation. Most notable among these are the effects of the climatic and nutrient regime. There is little to suggest changes in the nutrient regime at a scale that would show any appreciable effects on formation, and, pollen diagrams constructed from the sediments to determine climatic variations show that the surrounding vegetation has remained as oak-savannah throughout the formation period.

FIGURE 7. Detailed flow chart of the conceptual model of wetland formation. Solid lines indicate major interactions.



SYSTEMS SYNTHESIS: IMPLEMENTATION OF THE CONCEPTUAL MODEL

The SIMULA Language and Its Use for Ecological Simulations

Many computer languages exist that are suitable for implementing a simulation model with choices ranging from assembly language to FORTRAN to simulation languages, such as SIMULA or SIMSCRIPT. (For a comparison of these languages, see Fishman 1973). The majority of computer programs in the United States use FORTRAN, so why did we not choose this language for implementation of the model? The answer to this question is precisely the reason for the popularity of FORTRAN over assembly language: the higher level FORTRAN language already includes as system options many of the features one might have to program in assembly language. Simulation languages such as SIMULA include features that one would have to program in FORTRAN, for example, commands that organize lists of data, a large choice of statements that conditionally perform a calculation, etc.

Simulation languages may be divided into two types: continuous or discrete event languages. Continuous languages, such as DYNAMO, CSSL, and CSMP are useful for processes that can be described as systems of simultaneous differential equations. Discrete event languages, such as SIMULA, SIMSCRIPT, and GPSS are oriented towards processes that can be described using a mathematical or logical algorithm, but not necessarily with the differential calculus. Within the latter category, there is considerable variation in the features available and the general philosophy of the language. These languages were originally developed for scheduling and queuing problems, making some of the language structures inappropriate for ecological simulations.

Of the existing languages, we chose SIMULA (Norwegian Computing Center 1971) for the following reasons:

- We desired a discrete approach to increase the flexibility and generality of the model and for ease of assignment of initial conditions
- The philosophy of the language is consistent with the procedure of defining system entities, attributes, and structure. Attributes can be either physical quantities or process descriptions. Many of the details of the interactions can be specified with one or a small number of commands.
- The SIMULA language is designed to allow the model-building process to occur as an evolutionary sequence; new attributes and interactions can be included with a minimum of program changes.
- SIMULA allows hierarchical construction of entities, quite useful for ecosystem simulations
- The language includes features that handle data structures efficiently, reducing the cost of the simulation.

Entities and Attributes of the Computer Model

Many of the entities and attributes of the conceptual model are process oriented. These processes are calculated as sequences of statements (organized blocks of computer code) within the program, with logical or conditional commands determining which calculations are to be made and in what order. Because most of the interactions that occur in the model are based on spatial interrelationships, the entities of the computer model are a finite number of segments of the study site.

The surface of the wetland is divided into a hexagonal grid; the third dimension is the depth to the transition layer between lake and wetland sediments. The entities, a collection of hexagonal prisms or grid cells, can interact as either a segment of lake or a segment of wetlands. A second group of entities is actually a subset of the first: grid cells that correspond in location to the lake edge at a given point in time.

Each of the entities (segments of the study site) has associated attributes that may remain constant, continuously change in value, or be assigned a value only once during a simulation. These include:

- location of the grid cell on the surface of the study site
- depth of water above lake or wetland sediments
- location of the next cell along a sediment transport path
- biomass of decaying vegetation that leaves a cell within a specified time increment
- date a cell is considered 'wetlands' rather than lake
- average age of sediments at a specified depth below the surface to compare to ^{14}C analysis
- magnitude of sediment removal due to lake circulation patterns.

Cells that are located at the lake edge are considered as members of a second entity class, the membership of this class constantly changing. These entities have one additional attribute, the biomass on the surface that is to be distributed into the lake. This is defined separately for computational reasons.

The Event Structure of the Computer Program

The dynamics of the computer program result from the interaction of groups or blocks of computer code that correspond to the conceptual model attributes. The sequence of execution of the blocks is controlled by conditional statements that together comprise a timing algorithm. The structure of the computer program follows:

Input and initialization. The first part of the program assigns the model parameters, generates the entities (grid cells) with their appropriate initial conditions, determines the proper algorithm for a given scenario, and initiates execution. Model parameters that are assigned include:

- net productivity of vegetation per unit area per time
- decomposition constants
- slope of peat sediments under water
- area of each grid cell
- a lake circulation constant
- several simulation options.

The grid cells are generated with their appropriate initial conditions and formed into a list structure. The initial edge cells are entered and formed into a separate sublist. The desired timing sequence is specified and the simulation is started.

Execution sequence. The sequence of calculations performed by the model can be divided into two major portions. The first portion calculates the magnitude of spatial interactions given a particular wetland and lake morphometry. This portion is composed of blocks of code that calculate the cell-to-cell interactions specified by the attributes of the conceptual model. The second major portion takes the result of these calculations and distributes the biomass generated into the lake basin, changing the morphometry of the system.

The two major portions are executed sequentially for a desired time span, and are explained in detail as follows:

- Calculation of spatial interactions. Beginning at each edge cell, the path that wetland origin sediments follow along the lake bottom is calculated. The model uses a simple steepest descent algorithm, i.e., on the average, the path of materials will be downhill. The choice of hexagonal grid cells was based on the need for this algorithm; a hexagonal grid is 50% more efficient than a square grid in the search for the steepest descent directions. The results are stored for all cells on the lake edge and below (i.e., under water). For cells behind the lake edge (i.e., in the wetland proper) paths of transport of decaying vegetation are calculated using the same algorithm.

Each cell within the wetland has an associated net productivity of vegetation. A certain percentage of the biomass produced on each cell surface decomposes in situ and the remainder is washed to the neighboring cell. The model calculates the biomass of sediments that are transported cell to cell along the wetland surface to the lake edge. The cumulative result of biomass reaching the lake edge from all cells on the surface behind each respective edge cell is stored to be distributed in the second portion of the model.

Distributing the biomass. The biomass assigned in the last portion of the model is the total biomass that reaches each lake-edge cell in a specified time period. This time period can be varied to minimize computational errors; we find a time period of 30-50 years to be adequate. Calculations that determine the morphometry of the lake basin are more susceptible to computational error, requiring a shorter time resolution for this stage. The procedure for distributing the biomass and resultant changes in morphometry follows below.

The slope of wetland sediments below the water is observed to be constant along a steepest descent line. This characteristic angle of repose is a function of the physical properties of the sediments and the water in which it rests. The model calculates the volume of sediments necessary to completely fill the segment of the lake contained between the lake bottom and a surface defined by the characteristic angle of repose. This is computed separately for each lake-edge cell along the line of steepest descent from the edge cell into the lake. If the biomass stored at the edge cell is less than the calculated volume, the sediments are distributed and the lake edge at that point remains the same. If the biomass is greater than the volume, the sediments are distributed to the angle of repose line and the lake edge advances one cell. The old cell is removed from the lake-edge cell list, and the new cell is added. In both cases the basin morphometry is changed due to the influx of sediments.

The process is repeated around the lake edge in random order to minimize computational error until the entire biomass generated during one time period has been distributed. The dynamics at each lake-edge cell are a function of the system morphometry and therefore vary at each location and time. The model handles all the bookkeeping required: how many and which steepest descent lines a cell is located on, how much sediment originates behind a specific edge cell, etc.

If a new edge cell is formed during a time period, the date is stored for later reference. In addition, the prediction of a radiocarbon date taken at a known depth below the surface is computed when a new edge cell is formed. The date of the below surface sediments is computed as follows: at each point in time new sediments are added to the old sediments from previous time periods. As well, there is a deposition of lake origin sediments, some removal of older sediments, and mixing by lake currents. These factors are combined to calculate a new average age of sediments below the lake level.

After implementation of this portion of the model, the calculations of the spatial interactions are performed for the new basin morphometry. The model repeats the process until the present-day lake edge is reached.

Model output. Output from the program is quite flexible. The standard output consists of a map of isochrons (constant time lines) corresponding to the location of the lake edge at any point in time. As an option, a similar map may be printed with time lines that correspond to predicted radiocarbon dates of the below surface sediments. The simulation takes place with an arbitrarily assigned time step between calculations. Incorporated in the model is a procedure to statistically estimate the time step in years on the basis of several known radiocarbon dates. The constant interval time lines on the output maps can then be assigned values in years before present. The model is quite flexible in its ability to simulate various historical scenarios.

Critical Assumptions of the Computer Model

To allow the reader to evaluate the computer model, we present a list of critical assumptions of the model:

1. *The path that wetland sediments follow along the lake bottom can be defined by a steepest descent path.* The assumption is made that even with the disturbance by lake turbulence, a downhill path is an adequate regional representation of the motion of sediments along the lake bottom.

2. *The path that the decaying vegetation travels across the surface of the wetland is also defined by a steepest descent path.* The model actually uses the last steepest descent path defined for deposition in the lake as the path that vegetation travels after the region has become wetland. This assumption is considered adequate for several reasons: (a) the old steepest descent paths reasonably simulate the relationship of interest, i.e., the area of wetland behind the lake edge as a function of distance. (b) the last steepest descent paths should approximate those found on the surface until the region builds peat sediments above the ambient lake level, (c) the distance that sediments travel before completely decomposing is not great enough to add substantial errors to the approximation.

3. *The percentage of vegetation transported from grid cell to grid cell and the percentage of decomposition is constant through time and uniform over the entire surface.* The total amount of decayed vegetation reaching the lake edge therefore may be expressed as the integral of an exponential decay function with respect to distance from the lake edge, or a close discrete approximation, a binomial series. Because we have no evidence to the contrary, this simplest assumption has been adopted.

4. *The profile of peat sediments on the lake bottom follows a constant angle of repose with respect to a steepest descent line.* Again, on average, this seems to be the simplest assumption accurately depicting the present-day lake edge. This is a phenomenon commonly observed for uniform materials under the influence of gravity.

5. *Mixing of sediments occurs at the lake edge, with a fixed percentage of old sediments washed into the lake and a percentage of lake sediments added.* The present lake bottom near the lake edge is composed of very loosely distributed fibrous peat. Below this fibrous peat layer is the transition to the well-consolidated lake sediments. At the lake edge proper, defined by the rooting of wetland vegetation, the peat becomes much more resistant to displacement. Given the intensity of the lake turnover process and storm events, the loosely consolidated fibrous peat is susceptible to mixing and some loss. In addition, during this mixing process lake sediments are added. After mixing, the sediments still retain a constant angle of repose, consistent with assumption 4, and the mixing is assumed regional in nature due to the density of the peat, consistent with assumption 1.

6. *The entire edge of the original lake bay is susceptible to the invasion of wetland vegetation.* The controlling factor for the invasion of wetland vegetation in the bay is assumed to be the profile of the lake sediments. The location of the original lake edge has been defined by the presence of shallow lake sediments under the fibrous peat. The simulations begin with a uniform border of wetland surface area on top of the shallow lake sediments as initial conditions for lack of data to the contrary. The model is easily specified with regional variation if data exist to indicate the border is not continuous.

TESTING THE MODEL

Verification

An important step in any modeling effort is the verification of the model, i.e., making certain that: (1) the conceptual model is adequately translated into a computer model, and (2) the computer model is functioning correctly. Any mathematical representation of a conceptual model has two sets of assumptions affecting the results. The first set has already been discussed, the assumptions of the conceptual model and the simplifications necessary for computer implementation. The second set of assumptions is less obvious but just as important: any mathematical formalism imposes constraints on the results. These assumptions are usually well concealed, and though the model developer may honestly be unaware of their existence, they still may substantially affect the results.

Comparisons between analytic and discrete models

To make certain that these concealed assumptions were not altering the results of our model, we decided to build a second analogue of the conceptual model using a different formalism, the mathematics of differential equations (Friedman 1978). This model does not include all the features desired in the discrete version, but is complete enough to allow comparison of the results of the two versions. The advantages of this dual modeling approach include:

- It is often easier to understand the ramifications of a process description using continuous mathematics due to the large body of literature which exists on the solution of various equation forms.
- The analytic model can be solved exactly, by hand, for simple boundary conditions, allowing one to easily check the results of a numerical algorithm.
- Once the numerical evaluation algorithm of the analytical model has been verified, complicated boundary conditions can be imposed and the results compared to the discrete descriptive version.
- The conciseness and clarity of an analytical description allows one to conceptualize the entire system at one time, rather than as separate process descriptions interacting in a specified manner.

Development of both model versions occurred simultaneously. We experimented with various equation forms in the analytic model first, then applied the results to the discrete version. We followed this sequence for each portion of the conceptual model until the constraints of the mathematics used in the analytic version limited inclusion of several desired process descriptions. The results of the analytic model were verified with boundary conditions that allowed exact solutions. More realistic boundary conditions were then imposed and the numerical solution compared to the results of the discrete model. The results of comparison of these analytic and discrete models showed both to have closely similar outputs for a number of identical boundary conditions, thus lending assurance that the discrete model had been adequately translated from the conceptual model and that the discrete model was functioning correctly.

Sensitivity testing and robustness of the discrete model

Another important step in the verification process is testing the sensitivity of the model to parameter changes and the robustness of the predictions to slight changes in computational algorithms. If the model seems overly sensitive to parameter changes as compared to variation observed in the field, or the output changes drastically with minor computer code changes, an error probably exists in the conceptual model or the computer implementation.

Sensitivity testing. Sensitivity refers to the deviation of some measure of the model's output response with respect to changes of parameter values. Two parameters of interest are the angle of repose of wetland sediments in the lake and the percentage transport and decay of surface vegetation. The sensitivity of the model to changes in these parameters were within ranges of field observation and agreed quite well with the sensitivity of the analytic model evaluated with a simple basin morphometry.

The sensitivity of the model to slight changes in basin profile has also been tested. By updating the morphometry of the lake basin less frequently, the model functionally interacts with an altered system. Alterations of the basin produced by updating the morphometry every other time step produce changes in the output well below the level of resolution of the model. The size of the grid cells used in the model, i.e., the degree of refinement in defining the basin profile, has little effect below a grid cell size of 5,000 m^2.

Robustness of the model. Robustness refers to the deviation of the model's output with respect to small coding or implementation changes. Three sections of the model were tested for robustness: (1) the transport of decaying vegetation across the wetland surface, (2) the procedure to decide which cells were lake-edge cells (cells directly contributing sediments to the lake) and the criteria for removal of a cell from this list, and (3) the algorithm to determine the extent of mixing and lake sedimentation. Multiple representations of the same conceptual process in each case produced changes in the output well below the level of resolution of the model.

Because the simulation model is implemented with an iterative algorithm, the effect of the step size must be determined. Experiments performed indicated that simulations with between 100 to 200 iterations generated time lines of formation nearly identical to longer simulations.

The Difficulty of Ecosystem Model Validation

We shall now discuss two methods for evaluating the model's behavior: (1) a statistical approach, comparing quantitative predictions of behavior to data collected, or (2) a qualitative approach, comparing the general behavior of the model to the scientist's accumulated experience observing the system.

For ecosystem models, the qualitative approach is often chosen for several reasons. Ecosystems are extremely complex with observed responses the result of many different factors occurring at different time scales. Often the desired response is difficult to observe or quantify in the field. Long-term dynamics (e.g., centuries or millenia) are much more difficult to observe than shorter fluctuations (e.g., daily) but may be just as important. Complicating matters further, the inherent variation within and between ecosystems is much greater than in physical and chemical systems. Controlled experimental situations to allow isolation of factors of interest are very difficult and in many cases impossible to construct.

An often-cited paper by Levins (1966) exemplifies the problem many ecologists face when confronted with the task of statistically evaluating the results of their model. Levins lists three characteristics of models: (1) realism, the model describes the qualitative behavior of an ecosystem, (2) precision, the model yields accurate quantitative predictions of the dynamic response of one or more ecosystem variables, and (3) generality, the principles contained within the model are applicable to many ecosystems. Levins points out it is difficult to construct a model that has all three characteristics. A management-oriented model may be quite precise, reasonably realistic, but not at all general. A theoretical population dynamics model may exhibit realism and generality, but no precision of prediction of observed population levels.

Statistical validation of ecosystem models has often been ignored because ecologists have chosen the characteristics of realism and generality as the primary purposes of their model. In a discussion of the validation question, Mankin et al. (1975) state that model validity has two components: (1) adequacy, the fraction of the system correctly modeled, and (2) reliability, the fraction of a model's output that is correct. They conclude that because no ecosystem model can be completely adequate and reliable, it is more pertinent to consider the usefulness of the model, rather than the validity. For most ecosystem modeling efforts, a model is considered useful when the qualitative dynamics correspond with observed ecosystem dynamics, i.e., when some understanding of the system has been gained from the model.

A common theme runs through the papers mentioned: a model constructed to understand the dynamics of an ecosystem may not be the best model for predicting the dynamics. In our opinion, caution must be taken when interpreting these arguments. This is not a justification for disregarding statistical methods in the model building and validation process. Though it is true that a model constructed to understand the dynamics of an ecosystem may not be the best model for predicting the dynamics, a model that cannot predict the dynamics of an ecosystem may not be the best model for establishing whether the understanding gained is credible.

Often statistical methods are the only procedures available for discriminating between two alternative hypotheses of the system's dynamics. Qualitative comparisons of model versus ecosystem behavior may be an adequate test of the model in some situations; in other situations, qualitative comparisons may more accurately be described as verification procedures (making sure the model works as expected) than validation procedures (comparing the model's output to the real world).

Care must be taken so that statistical procedures are considered from the very beginning of the model-building process. If at all possible, a simulation model should be constructed so that the model's output is measurable in the system modeled. Efforts must also be made to insure that an understanding of ecosystem dynamics is not sacrificed. Often the compromise between realism and precision is an artifact of poorly chosen output variables and poorly designed data collection strategies. When a compromise is necessary, included in the balance should be credibility of the model.

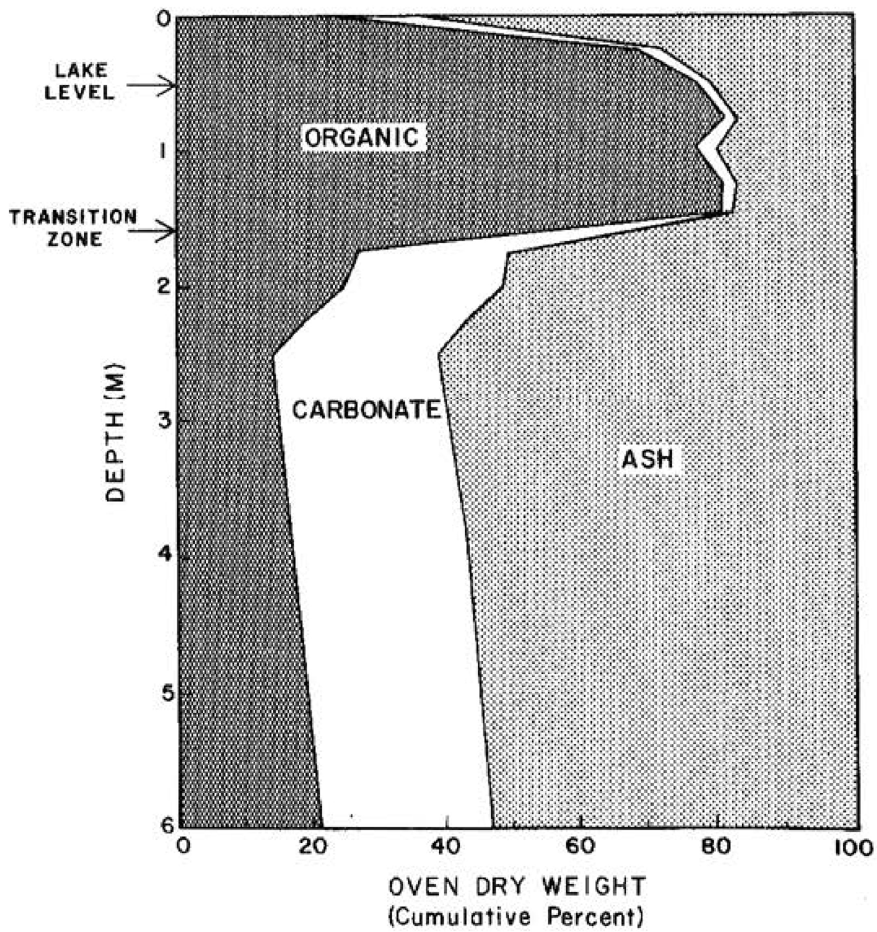
Data to Run the Model

The computer model is a set of process algorithms that interact on the basis of the system morphometry at a point in time. To run the model, one must supply the depths to the transition between marsh sediments (fibrous peat) and lake sediments. The first basin profile mapped was the glacial lake basin, the transition between glacial till and lake sediments. We used a combination of direct coring methods and gravimetric survey techniques (Telford 1976). The glacial lake basin, at its deepest point, is in excess of 30 meters below the lake surface. The depths to the transition between marsh sediments (fibrous peat) and lake sediments were much shallower, reaching a maximum depth of three meters below the present lake surface and averaging 1.5 meters.

Wetland sediments were differentiated from lake sediments by color and texture: the wetland sediments are dark brown and contain fibrous organic matter; the lake sediments are a lighter brownish green with a clay-like texture. Laboratory analysis was used to verify the field technique. The two types of sediment were combusted to determine percentage organic matter and percentage carbonate. Sediments below the transition zone were approximately 20% organic matter and 25% carbonate on an oven-dry weight basis. A sharp discontinuity was noted at the transition zone, with samples above this level averaging 80% organic matter and 1% to 2% carbonate. The uppermost sediments were formed above lake level and contain a lower percentage organic matter, probably due to increased decomposition.

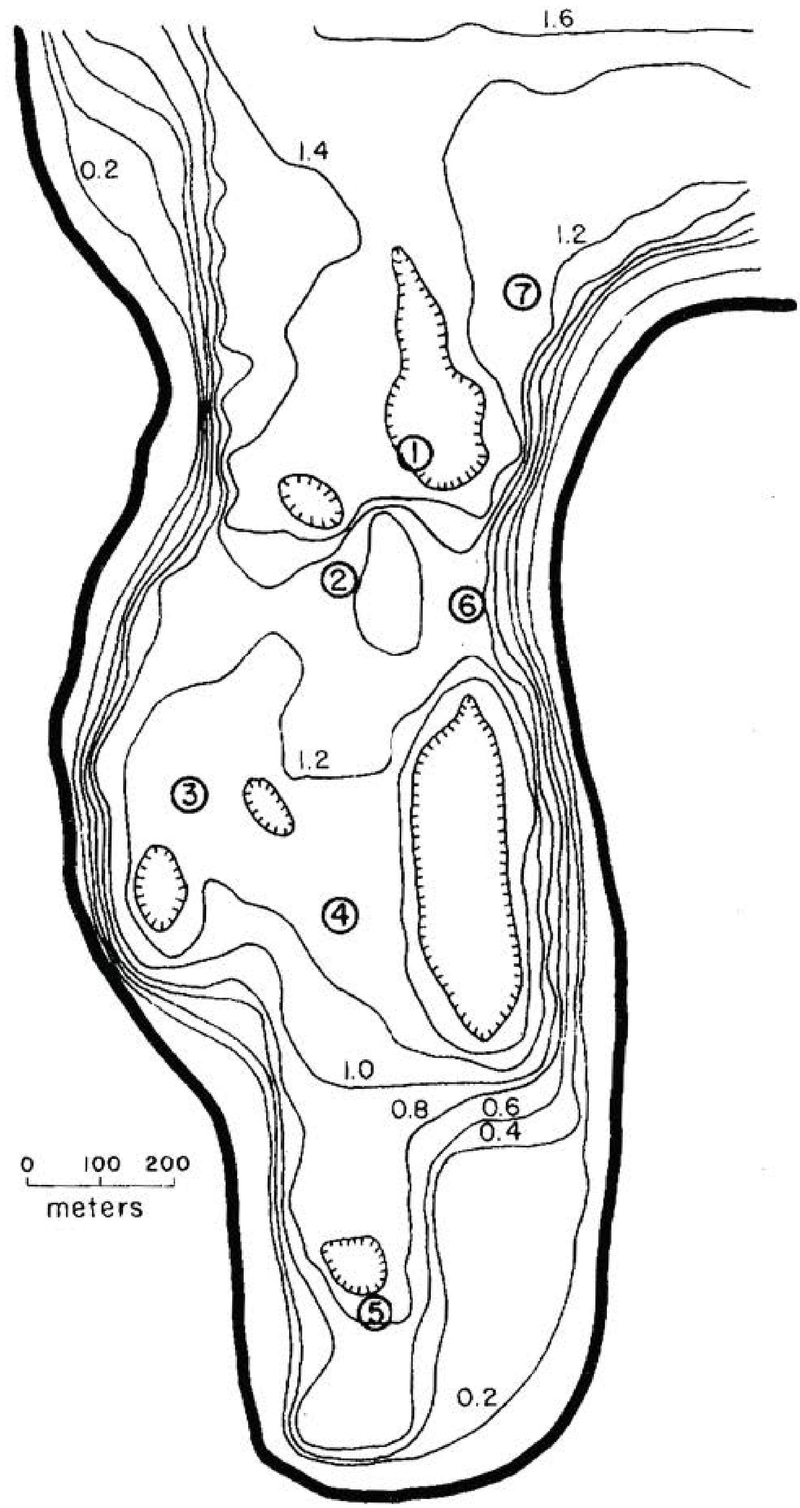
Figure 8 displays the results of the analysis. Samples were oven dried for 24 hours, weighed, heated to 450°C for 6 hours and reweighed, to determine percentage organic matter. The 450°C temperature was chosen to minimize carbonate loss (G. B. Lee: personal communication). Samples were then reheated to 950°C for 3 hours (Wetzel 1970) and reweighed to determine percentage carbonate.

FIGURE 8. Proportion of organic matter, carbonate, and ash content of sediments as a function of depth.



A reference grid with 200-meter spacing was established on the marsh surface. Approximately 75 cores were taken to establish the depth profile of the transition zone. The location of each core was determined in reference to the grid markers. The elevation above mean lake level was determined using a Leitz automatic level. A map of the depth to lake sediments was produced from the 75 data points using an inverse square distance interpolation procedure (Figure 9).

FIGURE 9. Topography of lake-wetland peat interface. Contours indicate depth below lake surface. Contour interval 0.2 meters. Circled numbers refer to location of radiocarbon dates in Table 1.



Parameters of the Model .

The simulation model includes several parameters that correspond to characteristics of the specific system modeled. Estimates of the values of these parameters collected from the wetland system modeled can be used in two ways: (1) specify the field estimates of the parameter values and test how well the model predicts the radiocarbon dates, or (2) determine the values of the parameters that best fit the radiocarbon dates and compare these results to the field estimates. With either approach, estimates of the parameters must be obtained from field observations, data from the literature, or theoretical considerations. Estimates of four parameters necessary to run the model follow.

1. *Net productivity of the vegetation per unit area per time.* The net productivity of the vegetation found at the study site varies considerably. Literature estimates for this wetland type in the midwestern United States range from approximately 1,000 to 2,500 g dry weight biomass/m^2 per yr (Bray 1963; Klopatek 1975; Bernard and Gorham 1978).

2. *Angle of repose of wetland sediments in water.* The depth profile of the lake adjacent to the study site was measured under ice cover for a distance of 300 meters from the lake edge. Two transects were made measuring the depth to fibrous peat using an ice auger. The slope of the sediments is approximately 1 to 200.

3. *Transport and decay constant.* The model assumes that the percentage of vegetation that travels from grid to cell to grid cell in one time step is a function of distance. For example, if 100 units of biomass reach the lake from each lake-edge cell, and the transport and decay constant equals .2 then: $100 \times (.2)^1 = 20$ units biomass reach the lake from each edge cell one cell away from the lake edge; $100 \times (.2)^2 =$ 4 units biomass reach the lake from each edge cell two cells away from the lake edge, etc. Observations of rivulets transporting decayed vegetation during rains when the wetland surface was partially frozen (with some ice cover left to be able to observe movement) revealed overland transport occurring in regions on the order of 100 to 200 meters from streams. Using these estimates as the maximum distance from the lake edge contributing sediments to the lake before complete decomposition, the transport and decay constant falls within a theoretically expected range of 0.3 to 0.5.

4. *Lake sediment addition constant.* The percentage addition of lake sediments to the submerged wetland sediments has little effect on the marsh formation process, but is important for deriving the predictions of the radiocarbon dated samples. Two factors are important: (1) whether the age stratigraphy of the sediments is preserved or mixed by lake circulation, and (2) the extent of lake contribution to the submerged sediments.

The indicator used to determine the magnitude of lake sediment addition to the wetland sediments was percentage carbonate. The results displayed as Figure 8 suggest the percentage carbonate contained within the wetland sediments is approximately 7% of the amount found in lake sediments. From this we conclude that a reasonable estimate for the lake sediment addition constant is approximately .07. No literature data could be found to confirm this estimate. The uniformity of the wetland sediment stratigraphy and the low resistance to disturbance of the suspended peat indicate that mixing most likely occurs.

Data to Test the Model Response

The system response we chose to measure was the extent of the wetland throughout its formational history. The choice of this response allowed us to construct a model that contains our hypotheses concerning the dynamics of formation and is testable with data from the study site. If our hypotheses are correct, we should be able to predict the date a particular parcel of peat was deposited. The peat dating methods we chose were radiocarbon techniques and inspection of pollen stratigraphy.

Seven samples of peat and two of lake sediments were analyzed by the radiocarbon laboratory at the Center for Climatic Research, University of Wisconsin-Madison. The samples were chosen on the basis of: (1) a wide geographical spread to detect regional variation, and (2) a factorial design using depth to lake sediments and distance from an upland edge as factors.

At seven surface locations, a 12.5 cm core was extracted from a depth 6 cm above the transition between wetlands and lake sediments. The sample was taken just above the transition zone to minimize contamination by recent roots. At one location, two additional 12.5 cm cores were extracted at 1 m and 3 m below the transition.

The seven peat samples range in age from 5,060 radiocarbon years B.P. to 1,065 radiocarbon years B.P. The standard deviation of the counting error for the radiocarbon analysis is approximately 65 years. To convert the radiocarbon dates into calendar dates we applied the correction described by Wendland and Donley (1971). Except where otherwise stated all dates referred to are given in calendar years before present. The parameter estimation and experimental design are based on radiocarbon years. Subsequent analysis using calendar years give similar results. Table 1 lists the radiocarbon dates with the corrected calendar dates.

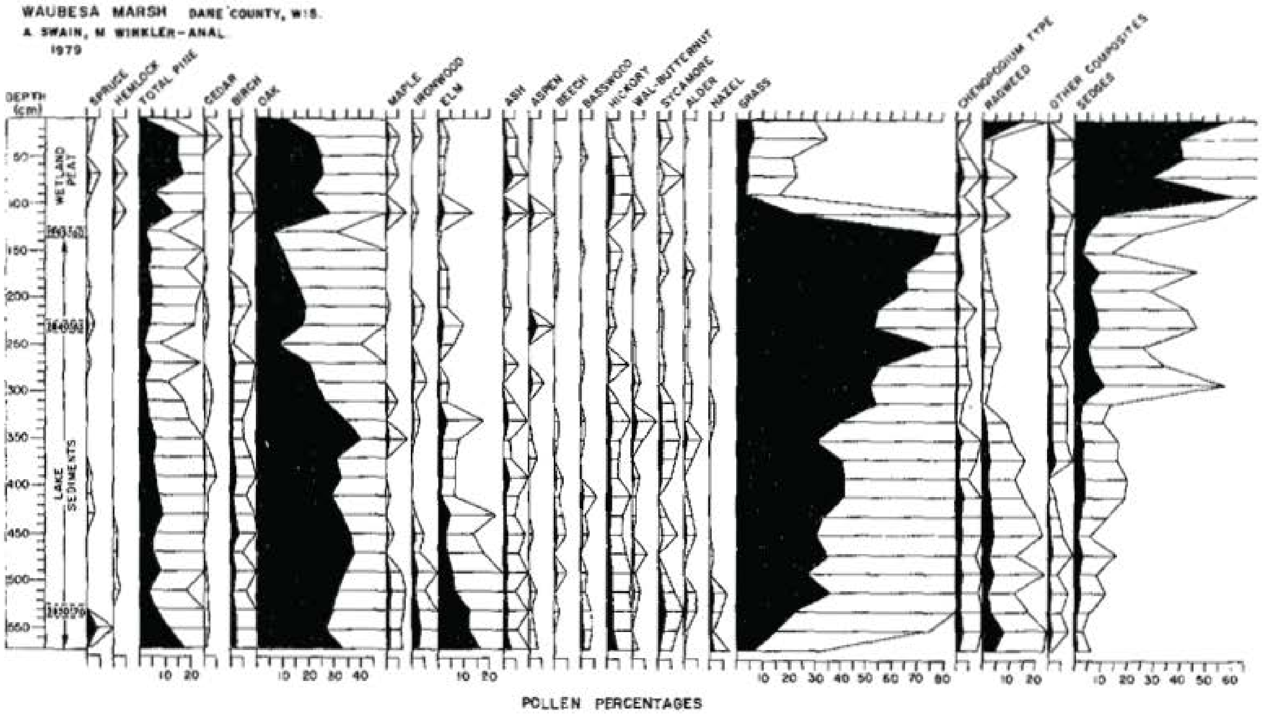
TABLE 1. Radiocarbon dates.

Location*	Reference number	^{14}C date** yrs B.P.	Calendar date***	$\delta^{13}C$ 0/00	Depth below surface m
1	WIS-953	1,915 ± 60	1,960 ± 60	-28.8	1.75
2	WIS-951	1,995 ± 60	2,050 ± 60	-28.4	1.36
3	WIS-967	2,820 ± 65	3,060 ± 65	-29.3	1.90
4	WIS-971	3,425 ± 65	3,830 ± 65	-28.8	1.76
5	WIS-973	5,060 ± 70	5,885 ± 70	-28.8	1.70
6	WIS-974	2,015 ± 65	2,075 ± 65	-29.8	1.32
7	WIS-975	1,065 ± 60	1,035 ± 60	-29.0	1.25
2	WIS-977	2,840 ± 65	3,085 ± 65	-28.8	2.31
2	WIS-978	5,850 ± 70	6,770 ± 70	---	5.30

* Location refers to numbers shown on Figure 9.
** 5,568 half-life.
*** Calculated according to procedure described by Wendland and Donley (1971).

We had hoped that pollen stratigraphy might indicate a regional vegetation change during the formation period of the wetland to enable us to reconstruct the complete wetland edge at some time other than the present. A pollen analysis performed by the Center for Climatic Research (Figure 10) indicates that the wetland has been surrounded by oak-savannah during the entire formational period. The one discontinuity observed, the increase in pine and oak and decrease in grasses, occurs at the transition between lake and wetland sediments. This discontinuity may be an artifact of the substrate change rather than an indication of regional vegetation change.

FIGURE 10. Pollen profile of sediments versus depth. All categories are included in pollen sum. At least 300 grains counted at each level. Hatched area magnifies scale by 5.



Fitting the Model to the Radiocarbon Dates

The simulation is run with arbitrary length time steps. The time steps can be converted to years in two ways: (1) supplying an estimate of the net productivity/m^2 per year of the wetland surface vegetation, or (2) calculating the appropriate time scale by linear regression, minimizing the sum of square errors between the observed radiocarbon dates and the predicted model dates. The second approach is the preferred method because of the wide range in observed productivities of this type of ecosystem. Estimates of net productivity derived from the linear regression fall within the literature ranges presented earlier.

Three other parameters are necessary for running the model:

- The angle of repose of the wetland sediments in water
- The decomposition and transport constant for wetland vegetation
- A constant that refers to the extent of lake sediment addition to, and mixing of, the submerged wetland sediments.

Running the model with parameter estimates from field observations yields regression estimates that are comparable to the errors of the radiocarbon dating technique and reasonable productivity results.

An alternative method for testing the adequacy is to search the response surface of the model with respect to the three important parameters until the best fit of the model to the data is obtained. This response surface ideally exhibits three characteristics:

- The optimum fit of the parameters should correspond to observed or theoretically calculated estimates of the parameters.
- The response surface should be shaped like a bowl with fairly steep sides, to locate the optimum fit within a fairly narrow range of parameter estimates.
- The residual errors from the optimum fit should be random and within range of estimated experimental error.

The three criteria together simply state that a useful model should fit the data fairly well and allow discrimination between realistic and unreasonable parameter estimates.

The response surfaces for the angle of repose versus the surface transport constant for several values of the mixing constant are shown in Figure 11. Three indicators of goodness of fit of the model are given:

- The mean absolute error of the observed minus the predicted dates using six radiocarbon dates.
- The same criterion using all seven data points.
- The predicted date that corresponds to the present-day lake edge.

Regression estimates were calculated using both six and the complete set of seven dated wetland sediment samples because one date seemed much older than expected. We conjecture that this sample was contaminated by old carbon from snail shells. Ordering the prediction errors of the seven dates from multiple simulations indicated the only detectable pattern was that one date was almost always several hundred years older than predicted. Regression estimates were good using both indicators, but we feel the six date indicator is more reliable. The mean absolute error of the predictions may be compared to the two standard deviation confidence interval of the counting error for the radiocarbon dating procedure of 130 years. The errors from the optimum fit simulation were near this value for both the six and seven data point criteria.

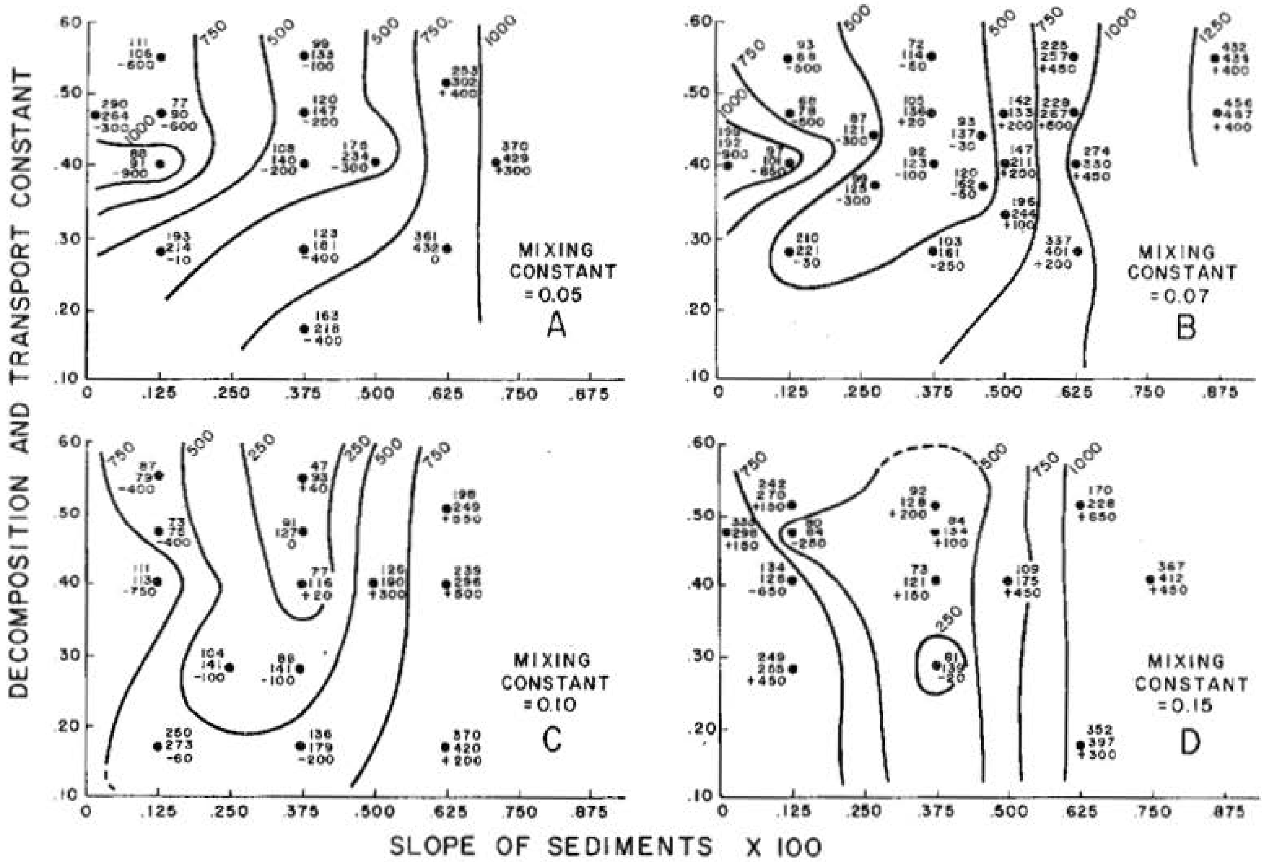
The date predicted for the current location of the lake edge is considered separately because the only criterion that can be imposed is that this date be equal to or younger than the present. As well, the accuracy of this prediction is limited for several reasons:

- The sparse data collected on the depth to transition layer under the present-day lake.
- A somewhat arbitrary algorithm for ending a model simulation.
- The lack of a radiocarbon date very close to the present-day lake edge.

The parameter values that gave the most satisfactory fits to the data are:

- The tangent of the angle of repose equal to 3.75×10^{-3}.
- The decomposition and transport constant equal to 0.40.
- The lake sediment mixing constant equal to 0.07.

FIGURE 11. Response surface of the computer model. Decomposition and transport constant versus slope of sediments. Goodness of fit criteria in descending order: six date, seven date, current lake edge. Errors are in ^{14}C years. Contour lines indicate the sum of the absolute values of the three criteria. Lake mixing constants of (A) 0.05, (B) 0.07, (C) 0.10, and (D) 0.15.



The mean absolute errors of the predictions as compared to the radiocarbon dates are 92 and 123 years for the six and seven data criteria, respectively. The current location of the lake edge is predicted by the model as corresponding to 100 years into the future. All these values are within the accuracy of the data and approximately twice the resolution of the model.

Several simulations were comparable or better (e.g., 47 years average error), but the increment of improvement is negligible given the accuracy of the data. The parameter values listed above were chosen as the reference simulation because these values most closely approximated measured or theoretically expected parameter estimates. The measured value of the angle of repose was 5×10^{-3}, which might be slightly high due to dredging of the lake edge in the 1930s. The expected range of the decomposition and transport constant is 0.3 to 0.5, and the measured value for the mixing constant was 0.07. The net productivity of the wetland vegetation is predicted to be between 1,000 and 2,000 g dry weight biomass/m^2 per yr, (the wide range is due to uncertainty of the decomposition rate of the submerged wetland sediments), within range of literature estimates.

The response surface is reasonably smooth and steep enough to distinguish between realistic and unreasonable parameter estimates in most regions. Examination of Figure 11A-D shows that the model has the greatest difficulty distinguishing between moderate and high values of the decomposition constant. The next section presents an experimental design procedure that we hope will remedy this problem.

Experimental Design

The first seven radiocarbon dates were chosen on the basis of a factorial design to insure that (1) the complete time span of the marsh formation process was sampled, and (2) a range of morphometric conditions was sampled. The results from the seven dates seem quite favorable, but more radiocarbon dates would allow a more rigorous test of the model. To obtain the maximum effectiveness from each expensive, time-consuming radiocarbon analysis, we have used an experimental design procedure to choose five more locations to sample.

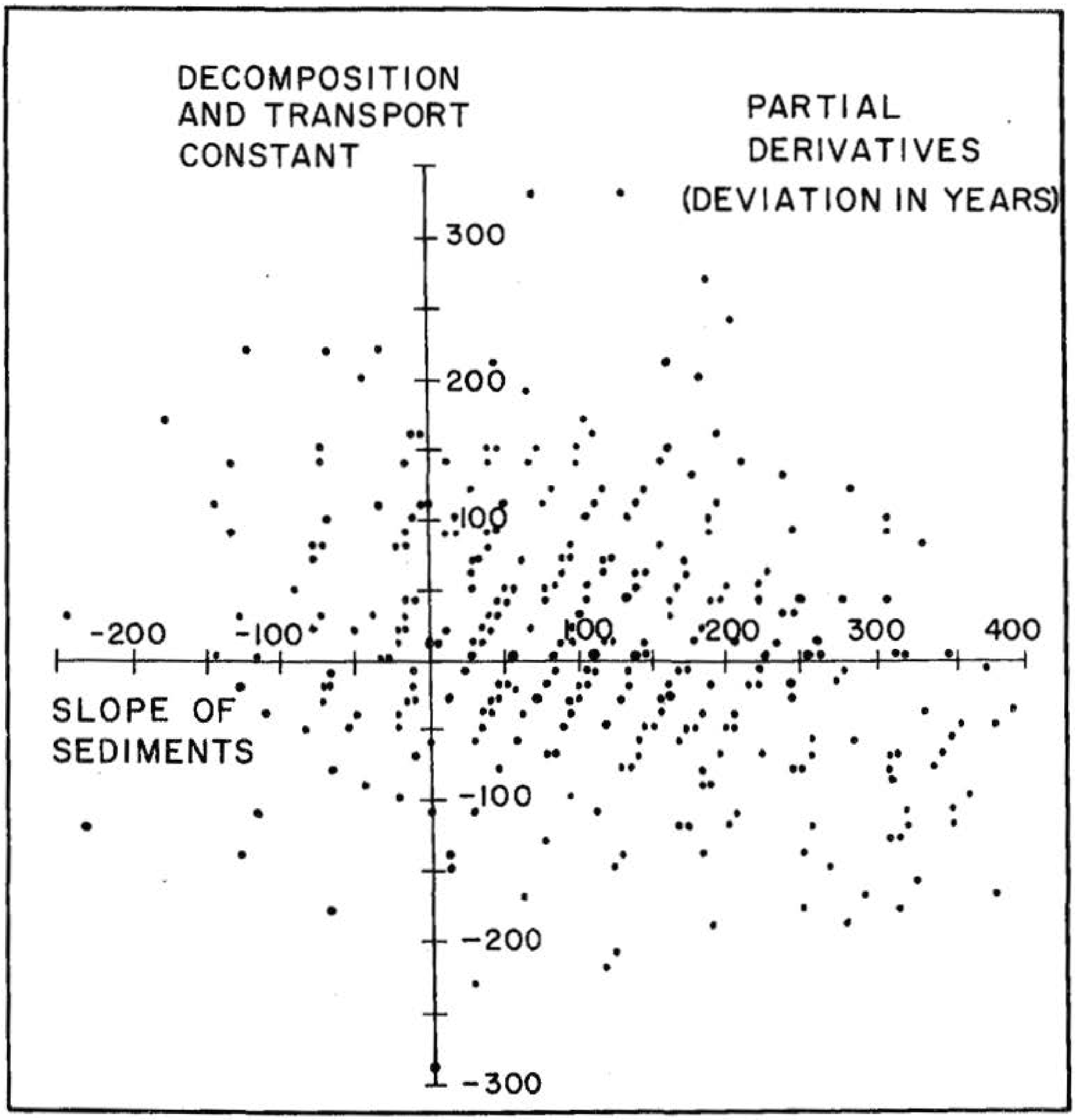
The technique, developed by Box and Lucas (1959), selects the sampling points that will minimize the size of the confidence region of the model parameters, given prior estimates of the parameters. The procedure is quite helpful for testing a model because not only do we desire accurate predictions of the data, but we want to be able to discriminate between realistic and unreasonable parameter estimates. For a clear, concise explanation of this technique consult Berthouex and Hunter (1971). We have modified the experimental design procedure slightly to fit the needs of a simulation model.

The experimental design criterion is to choose the sampling points that maximize some function of the partial derivatives of the model with respect to the parameters, evaluated at a prior estimate of the parameters (for example, the values from the reference simulation mentioned previously). The partial derivatives were evaluated numerically as two-sided partial derivatives around the reference values for the angle of repose and the decomposition constant. The state space diagram of the deviations in years at each point on the wetland surface is displayed as Figure 12. We wish to choose the five points in the 'cloud' of points shown in Figure 12 that maximize the design criterion.

The properties of the design criteria are such that the optimal points are located on a boundary line that encloses the points. This makes sense intuitively, because we wish to choose sampling points that have the largest effect on the model's response. We wish to avoid sampling points that have little capability for improving the parameter estimates.

We have been quite conservative with the choice of boundary (a circle with a radius of 200 years deviation centered at the origin) to insure that several surface locations would correspond to the chosen value of the partial derivatives. The design criteria is optimized by choosing sampling locations that correspond to (1) maximum partial derivatives (positive or negative) with respect to one parameter and zero with respect to the other, and (2) the pair of partial derivatives with the maximum absolute values that are equal. The search algorithm used to find the optimal sampling points was based on the Fletcher-Reeves method for constrained optimization (Walsh 1975). Surface locations that correspond to these values were determined using overlay maps.

FIGURE 12. State space diagram of partial derivatives of the computer model with respect to the sediment slope versus the partial derivatives with respect to the decomposition and transport constant.



ECOLOGICAL INFERENCE

A Reconstruction of the Historical Sequence

Figure 13 displays model predictions of the extent of wetland formation at the study site at 1,500-year intervals. We can reconsider the historical overview presented in the introduction in light of these results and the stratigraphic and radiocarbon data collected.

From the time of the glacier's retreat from this region until 6,500 years ago, the present-day wetland was a bay in Lake Waubesa receiving considerable lake sediment input. During this period, the deepest portion of the bay filled from a depth of 30 meters to about 6 or 7 meters. Approximately 6,500 years ago, the shoreline slopes became gradual enough to allow the invasion of wetland vegetation along the edges of the bay. The newly established vegetation produced peat sediments, which as they accumulated, provided new habitat suitable for the spread of wetland vegetation. This vegetation, in turn, was the source of more organic sediments (peat), which in combination with the continued lake sedimentation, altered the configuration of the lake bay. The upper left map in Figure 13 illustrates the extent of wetland formation from 6,500 to 4,500 years B.P.

The wetland expanded primarily into the shallower areas of the basin, the southern and eastern edges of the lake bay. By approximately 3,000 years ago, the bay had shortened and narrowed considerably. The most rapid expansion of the wetland occurred during the period from 3,500 to 2,000 B.P. The shallow, isolated bay surrounded by an expanse of wetland provided optimum conditions for the continued formation. By 1,500 B.P. most of the present-day wetland had already formed. The wetland continued to expand, but at a slower rate as the edge approached the main body of the lake. The combination of the present morphometry of the lake basin, the circulation patterns within the lake, and the activities of man (artificial lake level manipulation, dredging, etc.) all serve to maintain the presnt extent of the wetland.

A more detailed illustration of the pattern of development is presented as Figure 14. This is a map of the study site with isochrons (time lines) of the extent of the wetland edge superimposed. This illustration will be helpful for interpreting the results presented in subsequent sections.

Ecosystem Level Energy and Nutrient Dynamics

The conceptual model we have used to simulate the dynamics of wetland formation emphasizes the spatial interrelationships which determine the process. The simulations we have presented are the response of the system to a changing morphometry. Though it is the wetland itself that is responsible for the morphometry changes, the landscape and lake basin in which it forms imposes constraints on the process.

FIGURE 13. Reconstruction of the history of formation of Waubesa wetlands.

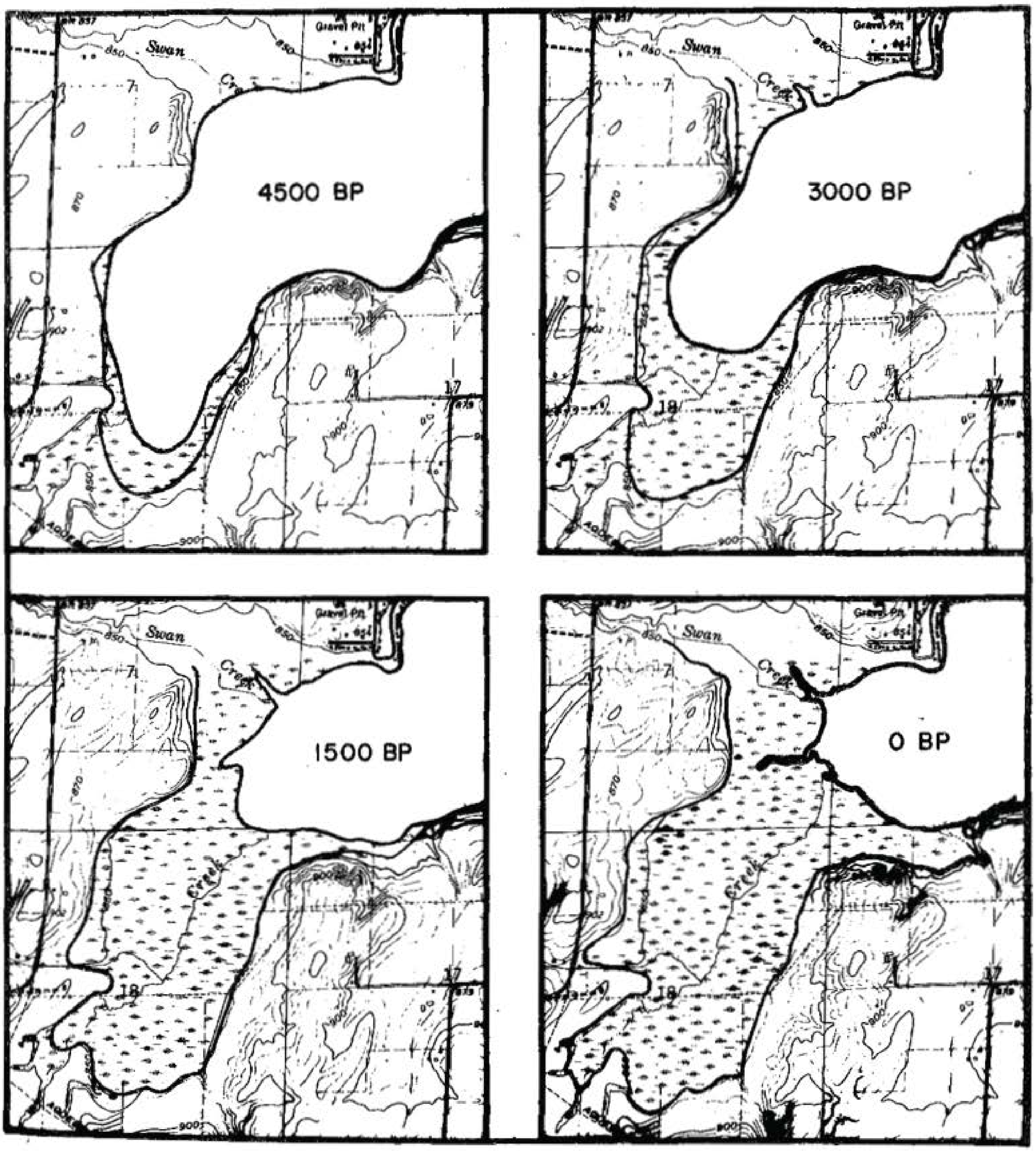
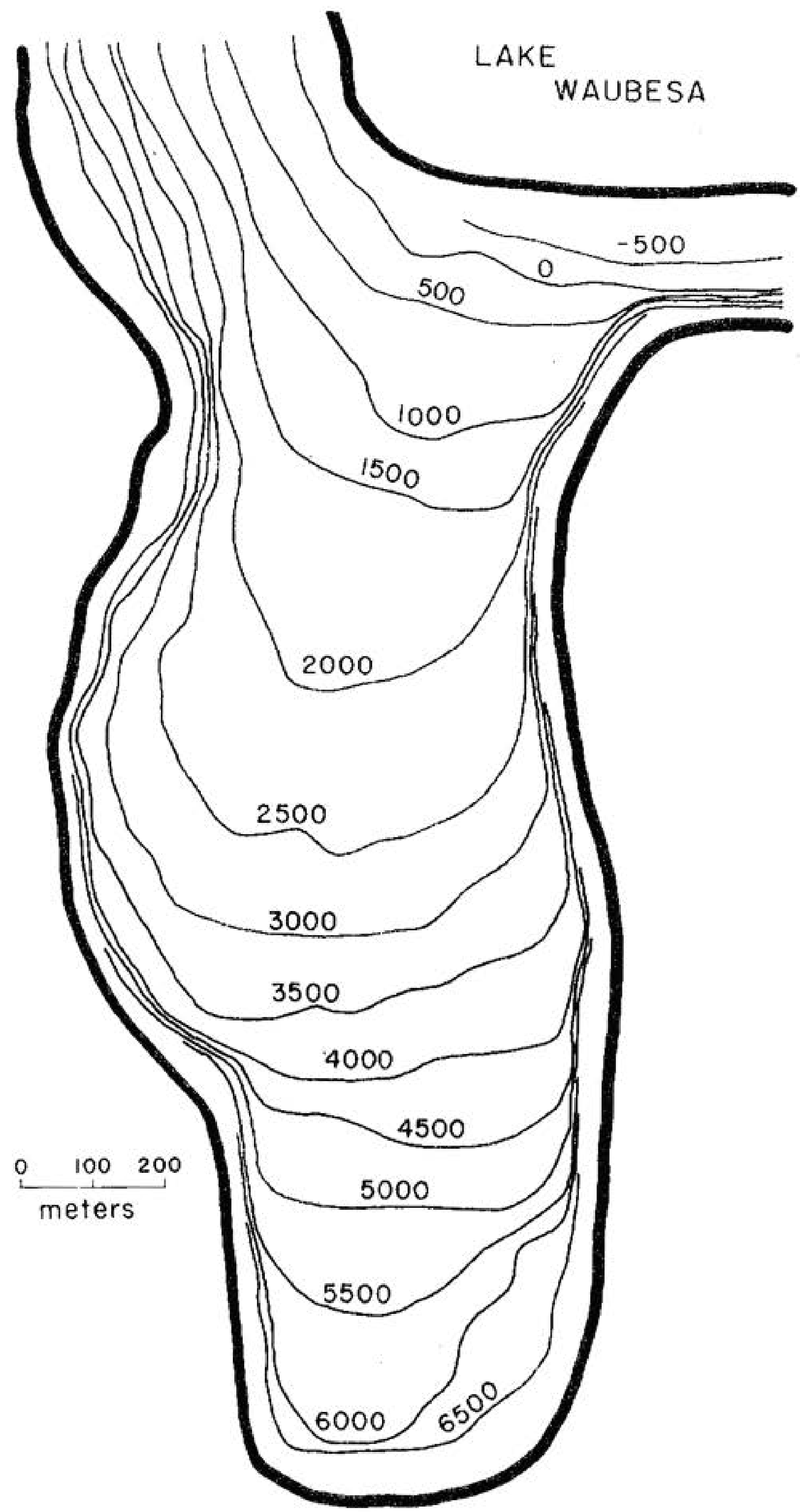


FIGURE 14. Map of the extent of the wetland versus time: reference simulation. Time in calendar years B.P.



E. P. Odum (1969) has presented trends of the energetics of ecosystems through time. Odum relates the patterns of nutrient storage and gross and net productivity of an entire ecosystem to the successional stage of the ecosystem. Using the simulation model we have developed, we can construct similar diagrams, but from a totally different perspective. The total ecosystem energy relationships illustrated in Figures 15 through 19 are not the result of successional (vegetation) changes but are a response to the changing system morphometry. These graphs may be interpreted as stages of ecosystem development, with the stages determined by the landscape or environment that supports the formation, rather than internal successional control.

FIGURE 15. Total biomass stored versus time.

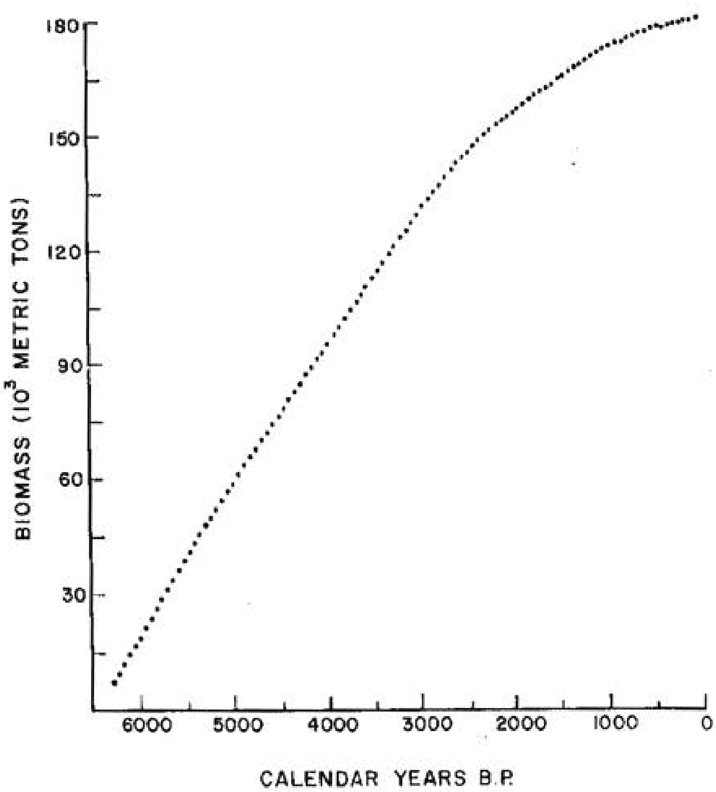


FIGURE 16. System productivity (after decomposition) versus time.

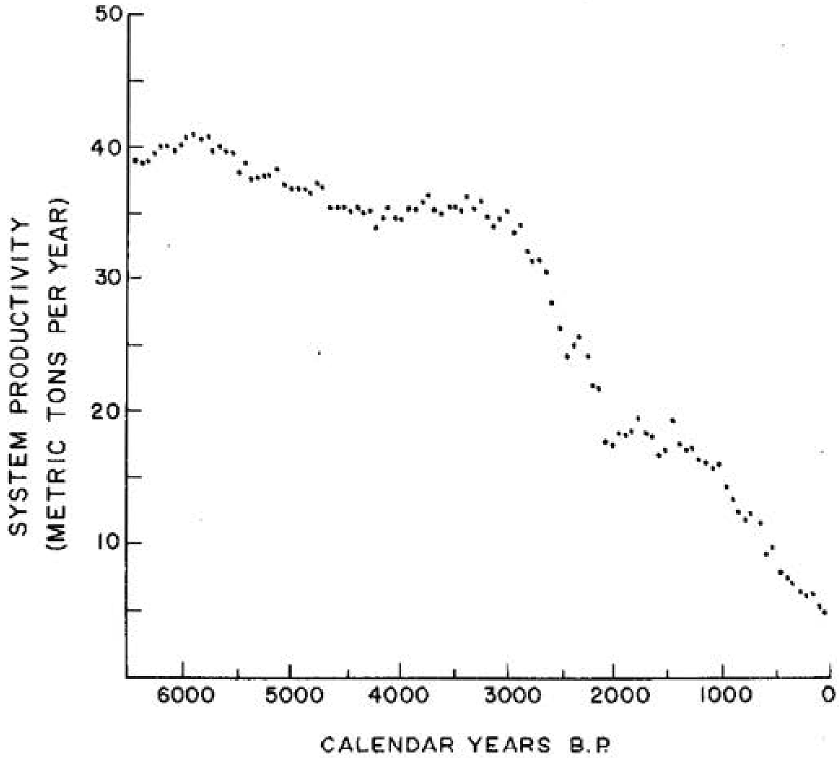


FIGURE 17. System productivity normalized to length of lake edge versus time.

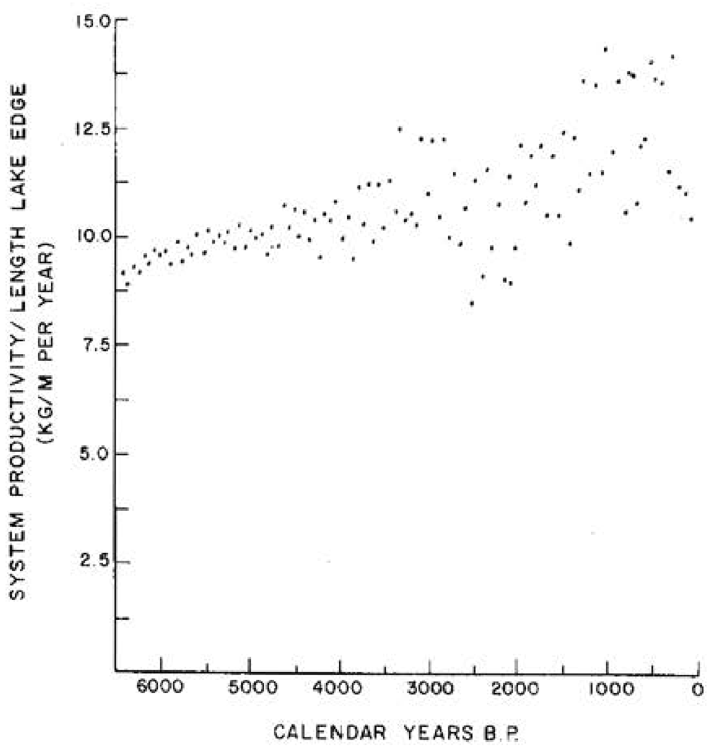


FIGURE 18. Primary productivity (entire surface area) versus time.

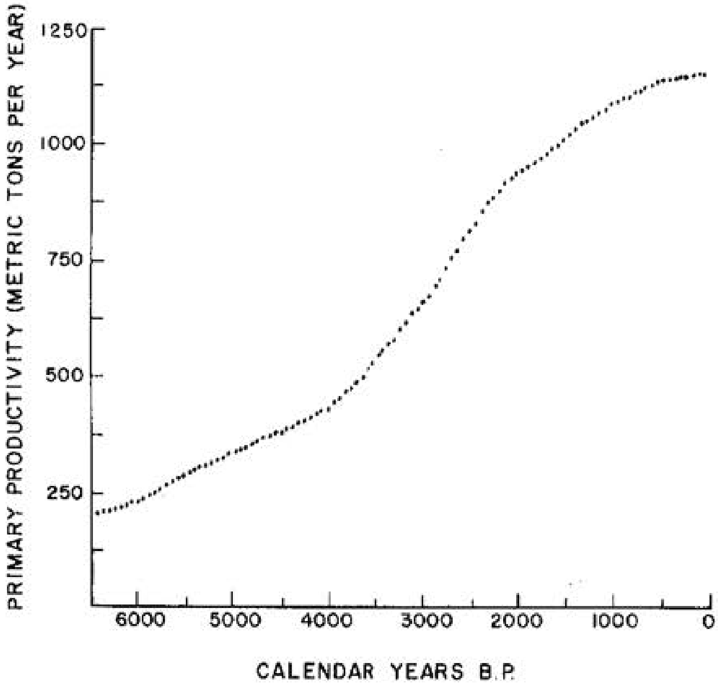


FIGURE 19. Ratio of the rate of change of primary productivity to rate of system productivity plotted as function of time. Dashed line drawn from smoothed data.

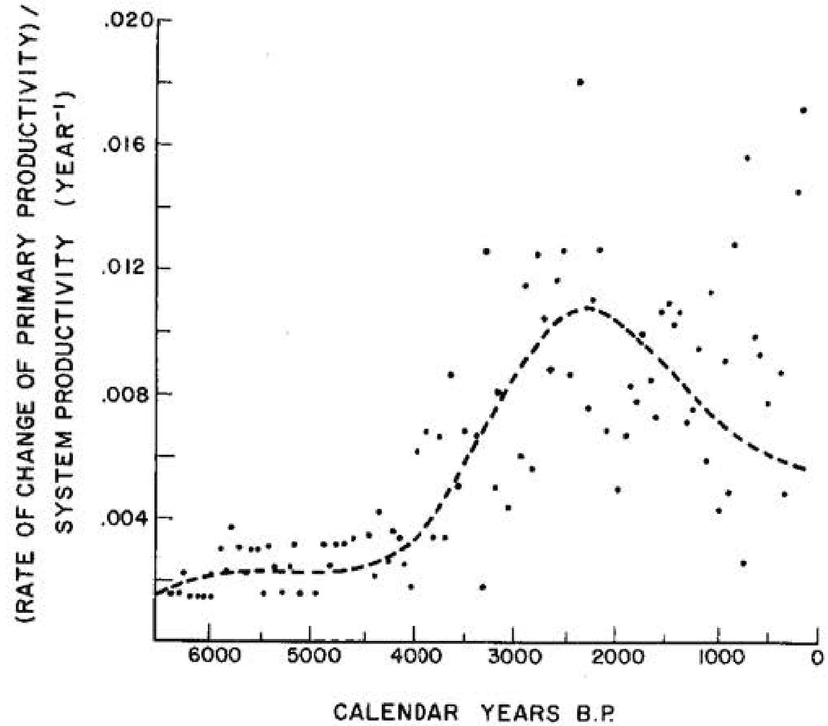


Figure 15 illustrates the biomass stored by the wetland throughout the 6,500 year formational history. This is the amount of organic matter that remains as a result of the formational process described; it does not include the amount of peat that results from paludification processes (accumulation of peat above the lake level due to a raising of the groundwater level). The inclusion of peat formed by paludification might double this figure.

The derivative of this curve, the rate of peat accumulation or the system productivity is shown as Figure 16. This curve should, of course, begin at zero at some time before 6,500 years, but the initial conditions of the model assume a uniform border of wetland surrounding the lake bay due to lack of data to the contrary. The rate of system productivity peaks at approximately 5,800 B.P. and then gradually declines over the next 1,100 years to a plateau that remains from 4,700 B.P. to 3,000 B.P. The peak and gradual decline corresponds to the filling of the southernmost portion of the bay (as seen in Figure 14). The uniform plateau of system productivity occurs when the wetland begins filling the central portion of the bay.

The next prominent feature of the system productivity graph is the rapid decline from 3,000 B.P. until 2,000 B.P. This corresponds to the rapid filling of the central region of the lake bay due to the shallow depths resulting from previous years accumulation. The system productivity drops as the length of the lake edge decreases, reducing the area of wetland that is close enough to the lake to allow contribution of sediments. Another plateau in system productivity occurs after 2,000 B.P. as the wetland expands past the north-central neck of the basin. Following this is another decline in system productivity until the present-day extent of the wetland is reached.

Figure 17 shows the rate of system productivity normalized to the length of lake edge. The relationship seems to be reasonably linear. The explanation for the rising trend is the increased area behind the lake edge that contributes decayed vegetation to the lake. A slight drop occurs as the wetland expands past the north-central neck of the basin, due to decrease of lake edge behind the central part of the basin. As the northern part of the wetland expands, this indicator increases once again. The wide scatter of points is a function of minor convolutions of the lake edge, and should be considered as only artifacts of the model.

The last three graphs relate the history of energy storage by the entire system. Of interest as well is the net productivity of the vegetation before decomposition (Figure 18). This graph illustrates the changes in primary productivity resulting from increases in surface area of the wetland. Comparing Figure 18 with Figure 16, one can see that in the later stages of formation, most of the vegetation decomposes before it can reach the lake edge. The curve is sigmoid shaped, with the most rapid rate of increase of primary productivity corresponding to the filling of the central basin.

The last system energy relationship we will present may be used to interpret the sigmoid nature of the primary productivity curve. Figure 19 is a graph of the ratio of the rate of change of primary productivity with respect to system productivity. This can be considered as the rate of change of area with respect to the rate of change of volume of the wetland. This indicator, with units $time^{-1}$, is a composite morphometric indicator of length of lake edge, area behind the edge, and depth of the basin. The curve gradually increases until 4,000 B.P., rapidly rises to a peak at approximately 2,200 B.P., and then declines. These stages correspond to the formation of the wetland primarily in the southern, central, and northern parts of the basin, respectively.

Associated with the storage of peat is the retention of nutrients by the ecosystem. In wetlands such as the study site, the retention of nutrients in the sediments lowers the nutrient input to the adjacent lake. Analysis of the trends presented in Figures 15 and 16 can yield information on the role of wetlands as nutrient sinks.

Haselow, Watson, and Walland (1976) measured the total phosphorus of peat samples from the study site and obtained a range of 0.05% - 0.12%. Changing the units of the ordinates of Figures 18 and 19 from metric tons biomass to kg total phosphorus shows the magnitude of nutrient storage of the wetland. These estimates might double when peat due to paludification is included. To put these figures into perspective, we can compare the rates of phosphorus storage by Waubesa Wetlands to loading rates that lead to eutrophication of neighboring Lake Waubesa. Using a procedure of Vollenweider (1976), we calculate 850 kg total phosphorus per year as the critical loading level. Waubesa Wetlands stored approximately 10% of this critical annual loading of phosphorus for thousands of years.

Alternative Hypotheses

Due to the flexibility of the model, different sets of assumptions about the dynamics of the wetland formation process may be specified and simulated. We use this capability of the model to specify a set of null hypotheses, i.e., determine if the radiocarbon dates can be predicted as accurately when various spatial interrelationships hypothesized are omitted from the model. The scenarios given below all address the major components of the conceptual model. A summary of the prediction errors for the five scenarios can be found in Table 2. Figures 20 through 22 are maps of the location of the lake edge through time that may be compared to the reference run (Figure 14).

1. The importance of the angle of repose of the submerged wetland sediments. Two alternative hypotheses are presented:

    - The wetland edge advances as a mat with a distinct vertical edge (tangent of the repose angle equals 0.125, Figure 20A)

    - The slope of the sediments is very shallow with the basin filling almost vertically (tanget of the repose angle equals 0.00025, Figure 20B).

FIGURE 20. Steep and shallow angles of repose scenarios. Maps of the extent of the wetland versus time for (A) steep angle of repose and for (B) shallow angle of repose. Time in calendar years B.P. Contour interval 500 calendar years.

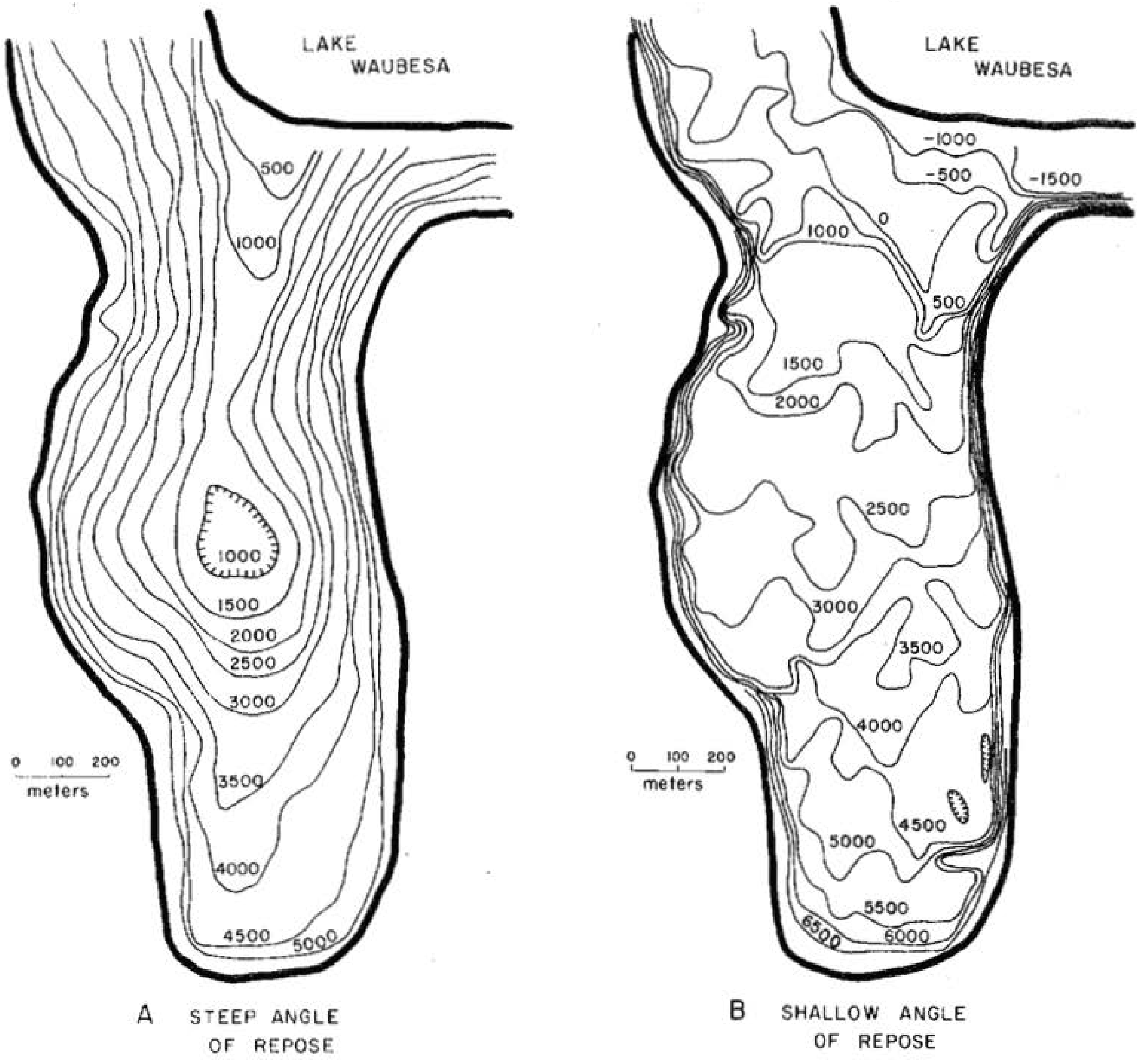


FIGURE 21. Reduced and increased sediment transport scenarios. Maps of the extent of the wetland versus time for (A) reduced sediment transport and for (B) increased sediment transport. Time in calendar years B.P. For (A) contour interval 500 calendar years; for (B) contour interval 1,000 calendar years.

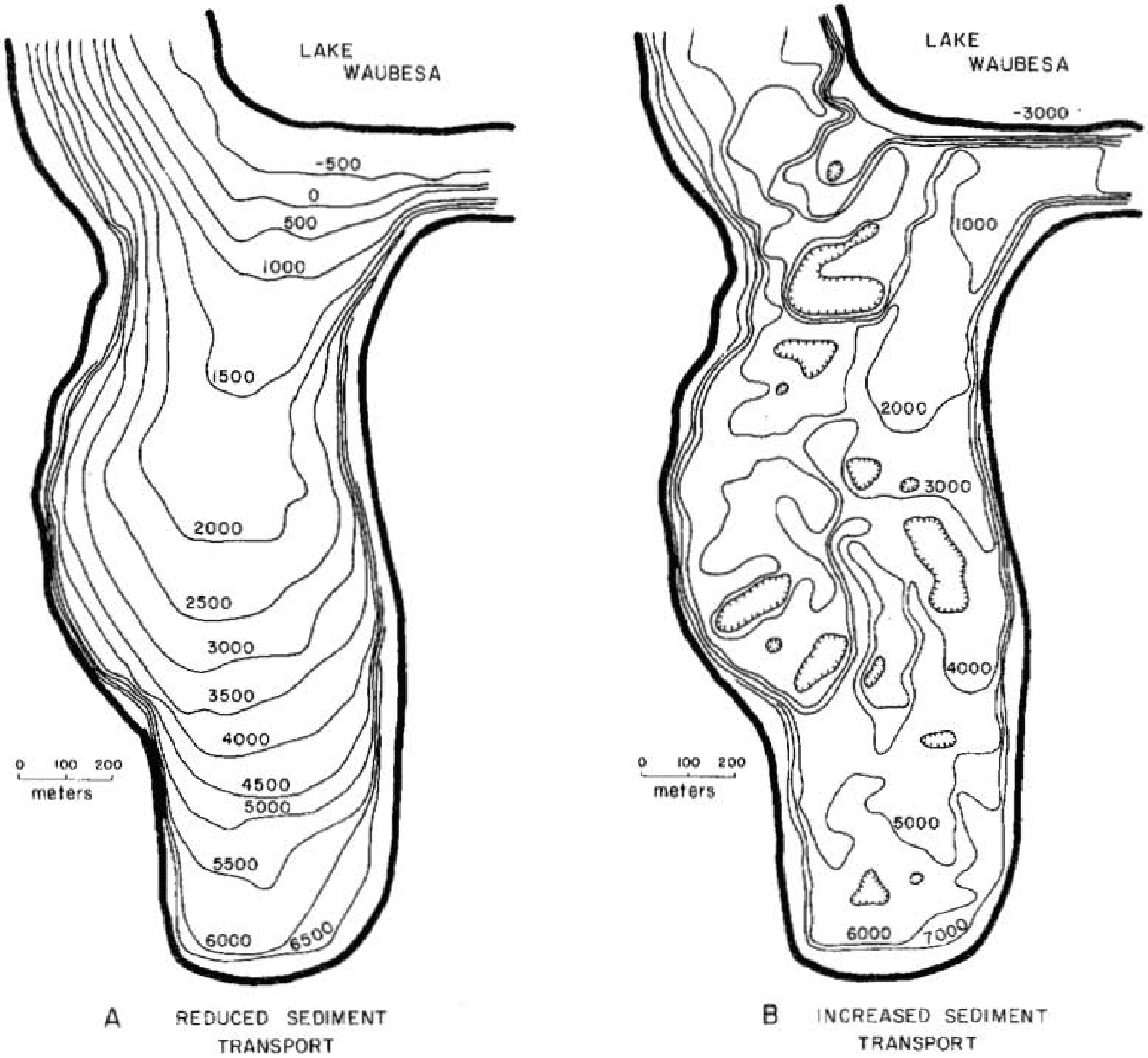
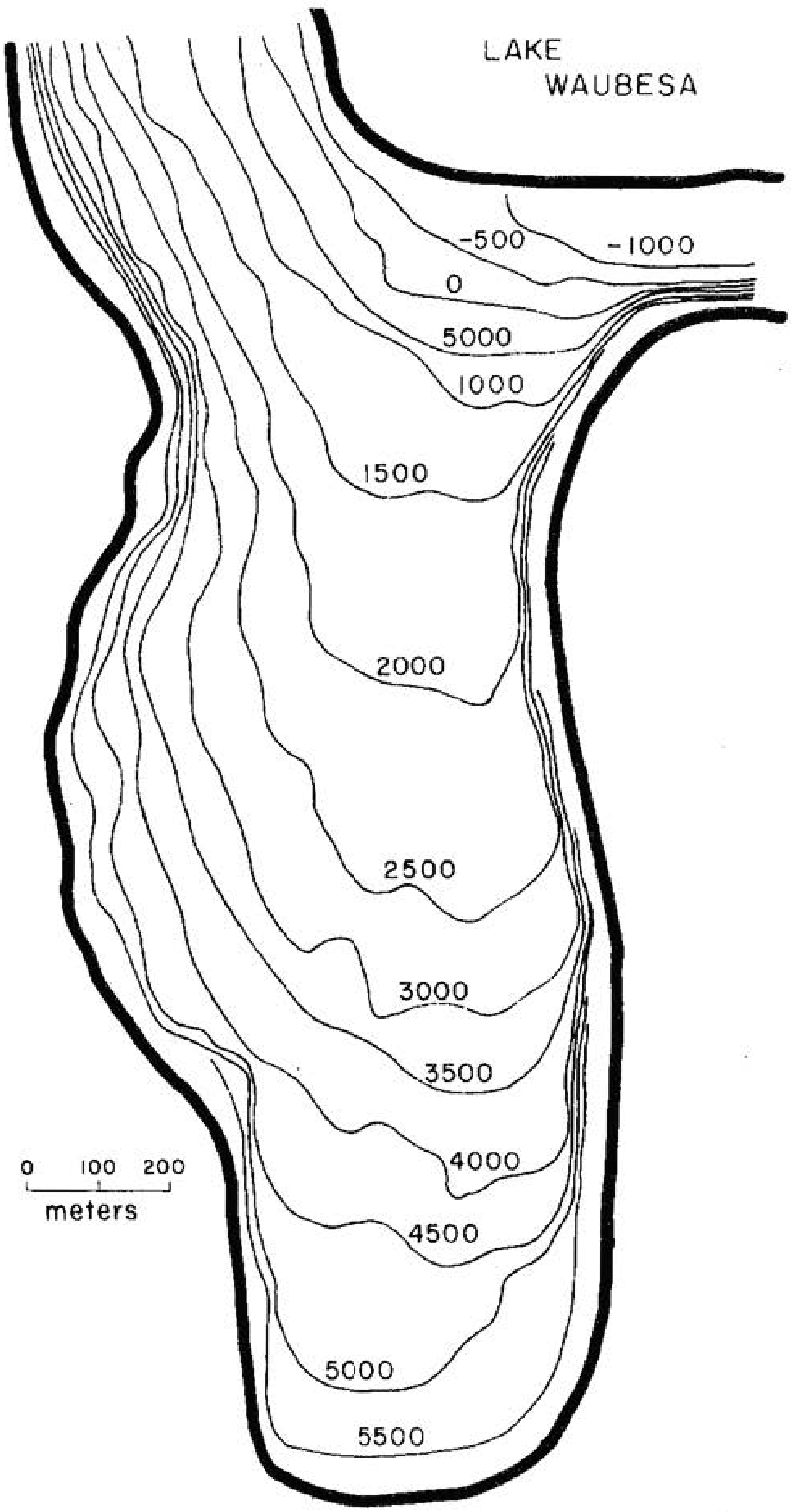


FIGURE 22. Alteration of initial conditions scenario. Map of the extent o: the wetland versus time: alteration of initial conditions. Time in calendar years B.P. Contour interval 500 calendar year:



The shallow angle of repose results in the wetland forming almost exclusively from a south to north direction. The steep angle results in just the opposite, the wetland forms from the sides, i.e., west to east and east to west. The reference simulation is a compromise, but looks more similar to the shallow angle of repose scenario. The fit to the data is much better for the shallow angle scenario than the steep angle of repose simulation, but both are greater than experimental error. Estimates of productivity decrease and the ending date extends into the future for the shallow angle scenario. Again, the opposite occurs in the steep angle scenario.

2. The importance of the transport of vegetation across the wetland surface. Two alternative hypotheses are presented:

   - Wetland formation is a result of peat sediments that originate exclusively from the lake edge (decomposition and transport constant equals 0.0, Figure 21A)

   - Decayed vegetation travels across the entire surface to form new sediments (decomposition and transport constant equals 0.99, Figure 21B).

   The first scenario (sediments originating exclusively from the lake edge) results in more rapid expansion of the eastern and western edges as compared to the reference simulation. Productivity increases and the position of the current lake edge is predicted into the future, as is to be expected to compensate for the decreased area contributing sediments. The prediction errors are greater than experimental error.

   The second scenario, transport of vegetation across the entire surface with no loss, has been included for completeness. The time lines illustrated in Figure 21B show that in the southern part of the basin, expansion is extremely rapid in the south to north direction as compared to the reference simulation. The northern part of the basin illustrates only the results of a poor simulation: because sediments travel the complete length of the basin, the second half of the simulation accumulates and magnifies all previous errors. All other simulations allow sediments to travel through at most six surface cells, eliminating this problem.

3. Extent of the original basin. Wetland sediments are found in the study site in areas where the substrate is above the present lake level. These sediments might have been formed in two ways: (a) the lake was higher in the past, allowing these sediments to accumulate by the processes simulated in the model, or (b) these sediments formed by paludification, i.e., formed above the present lake level due to the peat raising the groundwater table.

In this last scenario, we included the area of wetland with the bottom of the peat layer above current lake level as part of the initial conditions. These sediments do not have a layer of lake sediments below them, supporting the second hypothesis.

The results of the simulation are shown as Figure 22. The western edge of the wetland advances more rapidly than in the reference simulation. The simulation gave very poor fits to the radiocarbon dates and the current lake edge was predicted into the future. The hypothesis simulated in the reference simulation seems more probable, with paludification the explanation for the expansion of the wetland into the uplands.

Summarizing the results of the alternative scenarios, we conclude that the reference simulation, the implementation of the complete conceptual model, is the most satisfactory description of the wetland formation process. Table 2 shows that the reference simulation provides the best fit to the radiocarbon dates, the only scenario with errors within range of experimental error. Figures 20 through 22 illustrate the reason for poorer fits of the alternative scenarios: the altered spatial patterns of formation cannot simultaneously predict the widely scattered data points. These results support our hypothesis that a spatial model is necessary to understand the dynamics of the formation process.

TABLE 2. Prediction errors for alternative scenarios.

	Mean absolute error			
	6 date	7 date	End date	Net productivity
	years	years	yrs B.P.	Δ%
Reference run*	136	161	- 800	---
Slope = .125	1,090	1,125	+ 430	10
Slope = .00025	290	273	-1,750	- 9
Decomp = 0.0	281	342	-1,000	20
Decomp = .99	395	524	-3,300	-33
Extent of marsh	453	445	-1,230	- 7

* Reference run parameter values: Slope = 0.00375
Decomp = 0.4
Mix = 0.07

Summary: A Reconsideration of the Goals, Problem Statement, and Methods of the Research

The goal of the research was to gain an understanding of the ecological processes controlling lake-edge wetland formation. The formal problem statement expressed earlier contains a set of hypotheses concerning both the processes involved and research methods appropriate for understanding these processes. The problem statement was expressed as the question, "Can the developmental history of a wetland ecosystem be quantitatively reconstructed: (a) at the level of resolution of the ecosystem itself, (b) dynamically, and (c) spatially?" The statement led us to the development of an appropriate simulation model augmented by statistical techniques and laboratory and field data collection.

The three points in this problem statement are not separable, rather they express the hypothesis that the formation of a wetland is a total system response to the landscape in which it forms and the history of past responses. The most meaningful way to characterize this response, given this hypothesis, is to simulate the size and shape of the wetland as a 3-dimensional entity through time. By adopting this approach, we have relied on a system-level response for testing our hypotheses of the important dynamics of the formation process. An alternative strategy would have been to test each component separately and to draw conclusions accordingly. The systems level approach we have taken follows from a recognition that the structure of the system (i.e., how the components interrelate) is as important as the state of the components.

The choice of a wetland site for the research aided our ability to simulate the dynamics on the basis of the structure: (1) the morphometry of the basin was complex enough to exhibit different responses given different structures, but not too complicated to analyze. (2) There was no evidence to suggest drastic climatic changes (the pollen stratigraphy exhibits no upland community changes) so that net productivity and decomposition rates have probably remained fairly uniform. (3) Nutrient influx has probably remained fairly constant for the same reason. In an area with changing climatic and nutrient regimes, or when comparing one wetland type to another it would have been necessary to specify the response of the vegetation (growth and decay) to these changing conditions.

The capability of defining the system structure is a result of the modeling methods used. The spatial constraints that define the system structure are simple in abstraction:

- decomposition and transport of decaying vegetation is related to the distance away from the lake edge

- sediments travel downhill

- the angle of repose of sediments in water is constant in the downhill direction

- the wetland can expand only as fast as new sediments are exposed

- the rate at which new sediments are exposed is constrained by the basin in which they are deposited.

The complexity of the model results from specifying the magnitude of the interactions given a particular system morphometry and modifying the morphometry accordingly.

Separately describing the morphometry of the system and the processes that occur within the system has several advantages:

- the conceptual model of the process, i.e., the general principles, is isolated from a specific morphometry to aid the understanding of the process

- the conceptual model is easily altered to include other relevant ecological processes

- the model is easily transferred from study site to study site.

And, the choice of the simulation language SIMULA has helped us implement the model structure by providing a large number of system simulation options and efficient handling of data structures and calculation.

The simulation model of the formation process is based upon our hypothesis of the structure of the formation process; the structure we have hypothesized is based on the constraints imposed by the morphometry of the system. The division of the system into parts has been quite minimal, separating only the vegetation and the sediments. The dynamics of each part that we consider is also a small subset of the dynamics we know are occurring within the system: the vegetation grows and dies, the decaying vegetation is transported to the lake edge, travels through the lake, and eventually forms more sediments on which new wetlands vegetation can grow.

We know that the system has more parts and we know the parts identified are involved in more complicated dynamics; the question we ask, however, is whether given this subset of parts and dynamics can we adequately reconstruct the system response? Our simulation model uses these components and dynamics, and through the specification of the system's structure as a set of spatial interrelationships, predicts a time and space response surprisingly well. The success of our model comes from, in part, the identification of appropriate system variables and dynamics, but more important, the identification of the pertinent structure (constraints) of the wetlands development process.

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