Development of a general ecosystem model for a range of scales and ecosystems

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Note: This version has figures embedded in the text. The quality of some of these bit-mapped figures is inadequate to read them in detail. Original figures are available from the first author.

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ABSTRACT

We have developed a General Ecosystem Model (GEM) that is designed to simulate a variety of ecosystem types using a fixed model structure. Driven largely by hydrologic algorithms for upland, wetland and shallow-water habitats, the model captures the response of macrophyte and algal communities to simulated levels of nutrients, water, and environmental inputs. It explicitly incorporates ecological processes that determine water levels, plant production, nutrient cycling associated with organic matter decomposition, consumer dynamics, and fire. While the model may be used to simulate ecosystem dynamics for a single homogenous habitat, our primary objective is to replicate it as a "unit" model in heterogeneous, grid-based dynamic spatial models using different parameter sets for each habitat. Thus, we constrained the process (i.e., computational) complexity, yet targeted a level of disaggregation that would effectively capture the feedbacks among important ecosystem processes. A basic version was used to simulate the response of sedge and hardwood communities to varying hydrologic regimes and associated water quality. Sensitivity analyses provided examples of the model dynamics, showing the varying response of macrophyte production to different nutrient requirements, with subsequent changes in the sediment water nutrient concentrations and total water head. Changes in the macrophyte canopy structure resulted in differences in transpiration, and thus the total water levels and macrophyte production. The GEM's modular design facilitates understanding the model structure and objectives, inviting variants of the basic version for other research goals. Importantly, we hope that the generic nature of the model will help alleviate the "reinventing-the-wheel" syndrome of model development, and we are implementing it in a variety of systems to help understand their basic dynamics.

INTRODUCTION

Why a general model?

Process oriented ecological models can be useful tools in ecosystem research and management, but there are a relatively large number of models for a relative handful of simulated ecosystem types. Much of the rationale, and necessity, for this perceived redundancy in modeling efforts involves differing research objectives, the scale associated with those objectives, and the varying importance of different ecological processes as one crosses system boundaries. Widely varying ecosystem model objectives may range from those involving predictions on the scale of individual organisms or groups of organisms to models that focus more on theoretical constructs of identifying/quantifying important interactions, feedbacks, and/or cycling in ecosystems. Moreover, model objectives that are similar for different biomes or regions may still involve different physical forcing functions or feedback mechanisms that significantly affect the system behavior. For these reasons, there will continue to be questions in ecosystem research that require the creation of completely new models. However, we feel that there exists a significant void in our understanding of basic ecosystem properties that can be addressed with the aid of a general model of ecosystems, looking for the broad similarities in comparison instead of the unique details. In this paper, we present a computer simulation model that is a step in that direction.

The utility of a generalized ecosystem model for research has been recognized for some time, with CLEANER/MS.CLEANER (Park et al., 1974; Park et al., 1979) and CENTURY (Parton et al., 1987; Parton et al., 1988) being efforts for freshwater and grassland ecosystems, respectively. These models have been usefully applied to a variety of sites of the targeted ecosystem types, alleviating the need to extensively recode the model for each new application. However, central to these and most other ecosystem-level models has been the assumed homogeneity within the system, using lumped (averaged) parameters. Due to the heterogeneity inherent in natural systems, more recent research has accentuated the need for general ecological models that can be reparameterized and applied to different ecosystems for distributed, or spatially explicit, simulation (Costanza et al., 1990; Band et al., 1991; Costanza and Maxwell, 1991). Such models that incorporate the effects of pattern on process, with feedbacks among the physical and biological processes, are needed for the next generation of models that incorporate the landscape, regional and global scales.

A general ecosystem model can eliminate the need for continuous remaking of models for different systems and/or sites and can form the basis of spatially explicit ecosystem process models. Such characteristics logically lead to one of the broader objectives in ecosystem research: with a standard structure for developing a (model) synthesis of a system, comparisons among systems may be facilitated. A model that can be generally applied to ecosystems that range from wetlands to upland forests could provide at least two useful functions in synthesizing our broader understanding of ecosystem properties. One involves using the model as a quantitative template for comparisons of the different controls on each ecosystem, including the process- related parameters to which the systems are most sensitive. Secondly, a simulation model which is general in process-orientation and structure could provide one of the tools to analyze the influence of scale on actual and perceived ecosystem structure. For example, what is the relative sensitivity of different ecosystems to changes in nutrient concentrations? To what extent, and under what set of conditions, are transpiration losses controlled by the fine-scale plant physiology versus field-scale radiative flux? Models that can be consistently applied across systems and across geographic regions would allow different levels of process aggregation to be evaluated, and would allow us to discern the more sensitive parameters of the biological and physical processes that vary in importance with different ecosystems. To this end, with a general ecosystem model as a fundamental building block for analysis and prediction, hypotheses on scaling within ecosystem dynamics could be analyzed (Holling, 1992).

Existing models

A survey of the modeling literature reveals no general ecosystem simulation model that had been developed for use across a wide range of ecosystem types. However, several models have been formulated for general application to a specific type of system. Before presenting the structure of the General Ecosystem Model (GEM) that we have developed, we discuss some of the existing models that we borrowed from, or that parallel our design in some component. In order to present where the GEM fits into the scheme of general ecosystem models, we briefly review some ecosystem level models that have been designed to be general enough to be used for different sites without extensive recoding. Several of these models were intended to be used in spatial applications to accommodate within-site heterogeneity.

Physical hydrology is a critical component of many ecological systems and the hydrologic component of the GEM is an important aspect of the model's generality. Models of water processes operate within a well-understood set of physical constraints that allows these models to be applied to a broad range of landscapes, differentiated by terrain-

related parameters and quantified by physical laws. Thus, hydrologic components may generalize well within a general model of ecosystem processes. The hydrologic models are those which include water movement among storages in aquifers, sediment zones, ponded surface water, and the atmosphere, including the horizontal component of surface water and groundwater flows along hydraulic gradients.

The large number of existing process- based hydrologic models use different spatial/temporal scales and have varying objectives. Compared to changes in living biomass or nutrient cycling, hydrology encompasses fast ecosystem processes: many hydrologic models of small catchments or watersheds work with time scales of seconds to hours to effectively capture fine-scale detail of rainfall events and subsequent runoff or variable infiltration through finely partitioned soil layers. Recent examples (Binley and Beven, 1992; Grayson et al., 1992) of such distributed hydrologic models with fine temporal/spatial scales and high hydrologic process detail are computationally complex and not readily amenable to applications that involve many other ecosystem processes.

Some simpler watershed hydrologic models incorporate some form of chemical or sediment transport and fate (Shoemaker et al., 1992). The CREAMS model (Knisel, 1980) used a variety of process- oriented algorithms to measure runoff and sediment/nutrient transport relatively homogeneous "field"- scale regions using a daily time step. The simpler GWLF model (Haith and Shoemaker, 1987) was a generalized watershed model for nutrient loadings, based largely on empirically- derived loading functions and simple runoff and groundwater relationships. These models incorporated varying degrees of process- and statistically- derived algorithms to describe hydrologic functions, reducing the complexity from that of a more purely process- oriented approach.

A versatile ecological model for freshwater lakes, CLEANER/MS.CLEANER contained up to 20 biotic state variables including: phytoplankton, macrophytes, zooplankton, fish, and benthic fauna (Park et al., 1974; Park et al., 1979). It also had 20 abiotic state variables including dissolved and particulate organic matter, inorganic nutrients, carbon and oxygen, as well as external environmental forcing functions. According to the authors, the full model complexity was seldom used; normal application required only 20 state variables. Users were able to run parts of the model by specifying the state variables of interest using an editing routine contained in the model package. MS.CLEANER was designed as a user-oriented model with a simple set of commands.

The model CENTURY (Parton et al., 1987; Parton et al., 1988) was used to simulate very long term, regional patterns for plant production in the US central grasslands region. This model evaluated plant growth and the cycles of carbon, nitrogen, and phosphorus using a monthly time step over century- long periods. Soil moisture and
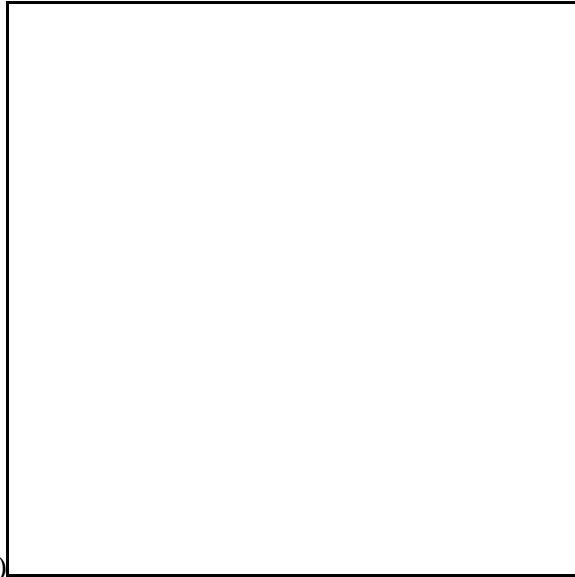
temperature affected decomposition rates of the five organic matter components which had very different turnover times (from 0.5 yr. to 1000 yr.). Soil moisture was a function of the ratio of monthly precipitation to monthly potential evapotranspiration. The plant production submodel simulated monthly dynamics of C, N, and P in live and dead above ground plant material, live roots, and surface and root detritus.

Another model for describing biogeochemistry and plant growth in terrestrial ecosystems (Rastetter et al., 1991) was applied to Arctic tundra and temperate hardwood forested systems. The model contained 23 state variables including four plant compartments and four soil organic compartments. Focusing on monthly changes in distribution of C and N between vegetation and soils, the model simulated the stoichiometric shifts in plant tissues and a had a variety of controls on production, but excluded hydrologic processes. Rastetter et al. (Rastetter et al., 1991) demonstrated that a similarly structured model could capture selected ecosystem dynamics of two rather differently structured ecosystems.

FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991) was a general forest ecosystem model to describe basic components of carbon, nitrogen and water cycling. They used daily time steps for canopy gas exchange and basic hydrology (precipitation and transpiration), with yearly time resolution for carbon allocation, litterfall and decomposition processes. The leaf area index was a prominent control over a number of the process rates involving three compartments for tree biomass; detrital dynamics involve two compartments with different decomposition rates.

A general terrestrial ecosystem model (TEM) with 5 state variables was used in a spatial model of South America (Raich et al., 1991) to estimate primary production for the region. The TEM was intended to be spatially distributed at the continental and global scales, using monthly time steps for decadal output. State variables included organic carbon and nitrogen in both living and dead matter, with a pool of available inorganic N To incorporate feedbacks between moisture and the ecosystem dynamics, a water-balance model (Vörösmarty et al., 1989). was linked to the TEM. The model was calibrated with data for a variety of non-wetland ecosystems from different sites that were assumed to be relatively undisturbed.

Lauenroth   et   al.   (Lauenroth   et   al.,

1993)(1993) recently began linking separate
biotic ecosystem models with abiotic environmental process models. The effort involved
the linking of two individual-based plant models, STEPPE for the (0.1 m^2) scale of plots in
grasslands (Coffin and Lauenroth, 1990) and ZELIG (500m^2) for the scale of forest
assemblages (Smith and Urban, 1988), using the coupling framework of VEGOMAT
(Smith et al., 1989). This in turn is designed to be linked with an existing compartment
model of nutrient cycling and plant production, CENTURY (Parton et al., 1987), and a soil
water model, SOILWAT (Parton, 1978). The design for linking the models will rely upon
running the models concurrently over a network in a UNIX processing environment.
Preliminary simulations linking STEPPE with CENTURY and STEPPE with SOILWAT
demonstrated the rich dynamics that are possible to explore by integrating realistic models
of vegetative dynamics with physically based ecosystem processes.

Our objectives are very similar to those for most general models: we seek to
integrate biological and physical processes in a simulation of basic ecosystem dynamics for
applications to more than one ecosystem. To be most useful, the model should be readily
understood and be used at other sites with minimal recoding. All GEM's, using different
approaches and simulation algorithms, will provide useful comparisons of model
assumptions, design, and results. Furthermore, such models will aid in evaluating and
understanding how scale can affect results (Allen and Starr, 1982).

GEM

The GEM is a physically driven model that incorporates the processes that we
hypothesize are most important in influencing plant production and modify that
ecosystem's properties. For this manuscript, we will first present the basic tools used to
develop, modify, and use the GEM. Following that is a description of the model structure

(variables and pathways of material and information flow) and function (algorithms controlling model behavior). For that presentation, the GEM may be best understood by considering the following.

- We assume homogeneity of the modeled system. Spatial heterogeneity of the landscape is accommodated by replicating this model in a grid-cell array for explicit spatial simulations (Costanza and Maxwell, 1991).
- We assume that hydrology is a critical process of most ecosystems. Thus the model is largely driven by hydrologic algorithms; some are novel, others are patterned after previous work such as Haith and Shoemaker (Haith and Shoemaker, 1987). Three (variable) layers of vertical zonation are established as a minimum for plant response to available water and its dissolved inorganic nutrients.
- Hydrology is a "fast" process (Holling, 1992) which dictates the minimum (fixed) time unit of the model. We chose daily time steps as the minimum that would adequately represent broad, field-scale hydrologic responses to daily rainfall data. Yearly to decadal simulations are feasible depending on data constraints.
- Beyond hydrology, the GEM extends the simple unit ecosystem processes of CELSS (Costanza et al., 1990) by including significantly more explicit process details for both wetland and terrestrial habitats.
- Inorganic and organic components of the sediment are simulated as a determinant of sediment elevation.
- Nitrogen and phosphorus cycling are developed with very similar model functions, aggregating the speciation of each nutrient into one inorganic form. Inorganic nutrient stocks in homogenous zones of the water and sediment/soils are one constraint on plant production.
- Maximum rates of carbon fixation, ingestion, and decomposition are limited by control functions; for macrophyte growth, these are nutrients, water, temperature and light.
- We target plant (macrophytes and algae) production as indicative of the most basic ecosystem dynamic. Trophic dynamics are only crudely incorporated into GEM. Thus, feedbacks resulting from multi-species consumer interactions are implicit.
- Having made the above statement, we hope to show that modularity of the GEM is such that detailed trophic structure *can* be built into GEM to explicitly test hypotheses regarding the relative importance of top-down and bottom-up controls on different wetland and terrestrial systems. The building blocks are there.
- Sectors such as fire dynamics or hydrodynamics may easily be removed (or turned off) from the model just as other components may be replicated or revised.

After the complete description, we present some sensitivity analyses of the type that could be useful in determining the level of process aggregation for a site and its parameterization. These simulation results are indicative of the model's internal feedbacks and constraints within biotic and abiotic sectors for habitats representative of different ecosystems of the Everglades in south Florida. From there we indicate the future directions for this model in terms of its use in comparative ecosystem ecology and research in ecosystem- and landscape- level dynamics via modeling.

MODELING TOOLS

Model development environment

Central to the GEM modelling framework is the use of STELLA[1] as a model development tool. This program is a graphically based simulation development environment that alleviates the need for being expert in a high level programming language in order to develop new models or understand existing models (Costanza, 1987). The extensive amount of code needed to execute a large ecosystem level model inevitably is difficult for a potential user to fully understand and modify. STELLA allows for rapid conversion of concepts to logical and mathematical expressions, while providing graphical information maps of the linkages among variables. Importantly, a STELLA model can be divided into functional submodels called sectors that can be run independently or as a part of the whole model. Such modularity allows convenient revision, and facilitates the development/debugging phase for individual process components. The advantage of communicating both general model structure plus specific mathematical algorithms - in a runtime environment with graphical and tabular output - is important for a model that is intended to be communicated to other people and actually get used.

Models developed using STELLA may be run under the Macintosh or MS DOS (using Windows 3.1) operating systems with no translation. Acceptable performance with GEM, however, dictates the use of strictly high end processors for these machines. For those familiar with the C programming language, the GEM may be converted into C code using an existing translator, and executed using drivers for a variety of different computer platforms [Maxwell, in press #51].

Linked databases

A vital component of any model is the data used in its parameterization. For a general model designed to run in different systems with different parameter sets, database access for reviewing simulation parameters and implementing a simulation becomes even

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[1] STELLA® is available from High Performance Systems, Inc. 45 Lyme Road, Hanover, NH 03755.

more important. The GEM has 103 input parameters that vary among ecosystems (Table 1). The model varies in sensitivity to these ecosystem/habitat- specific parameters, all of which are not necessarily needed for each project objective.   These data include rate parameters, initial conditions, threshold values, and other parameters that are used in the GEM and that vary from one habitat or ecosystem type to another. When the GEM is run to compare different habitats or in a spatial context within a heterogeneous landscape [Maxwell, in press #51], the efficient compilation and organization of the data is critical. We have designed a set of linked databases in order to automate the transfer of the parameters to the model.   The database parameters for different habitats are dynamically linked to the model using calls in the Macintosh operating system, with each habitat-specific data set being selected by changing the value of the model's habitat variable.

The databases are organized to match the sectors of the unit model, with a separate database for each sector such as Macrophytes, Hydrology, or Dissolved Inorganic Nitrogen.   Within each sector's database, we provide the user with three different perspectives on viewing information about the data. These include the parameter value and name as it is used in the STELLA unit model, documentation from the model regarding how the parameter is used, and a field for the user to provide comments that include the source of data and any assumptions involved in its use. Moreover, we provide a numeric (range=1-5) grade attribute, whereby the subjective quality of the data can be evaluated [Costanza, 199x #88]. For example, a plant's carbon:nitrogen:phosphorus ratio that was measured in the modeled region during four seasons may be considered high quality information and ranked 1 or 2. Conversely, growth data obtained from the literature for a congener plant species in a climatic region different from the model area would be ranked intermediate (3) to poor (5) in grade depending on an evaluation of the assumptions involved in the data utilization. This system provides users with full access to the critical model data in a format that allows one to easily focus on and evaluate particular areas of interest. Importantly, anyone can view the data, its source and perceived quality, and subsequently further evaluate that aspect of the model.

Revision control software

Because by design the GEM and its databases will change with refinements or different user objectives, we felt that it was important to track the model and databases as such changes are made. The current version of GEM is the basic building block for model development, and is functional as it stands. However, refinements in algorithms and sector enhancements will result in new versions and variants of the basic model. Revision control

software (Voodoo[2]) manages the structure and sequence of changes as they occur within a user's site; new versions during a development/debugging process are stored (with changes in compressed form) along a development path. Moreover, completely new variants of the model project may branch off of the main development path. This management scheme allows effective organization of the development and implementation of the GEM and associated databases in different projects with varying objectives.

MODEL IMPLEMENTATION

GEM Structure

The structure of the model is designed to capture the feedbacks among abiotic and biotic components. The (primary) ecosystem process feedbacks in the model are outlined in (Figure 1). Nutrient availability and changes in surface and subsurface water have explicit controls on algae and macrophyte growth, whereas the macrophytes affect hydrology via the surface roughness and transpiration. Plant mortality and consumer dynamics alter detrital storages, and mineralization of this organic matter of different quality is influenced by hydrology, which also transports nutrients. Fire may be one of the major disturbance that alter many of the system components. These direct and

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[2] Voodoo Lite is a shareware version of Voodoo (Versions of Outdated Documents Organized Orthogonally), available from anonymous ftp sites or the author: ChRei@soft.uni-linz.ac.al.
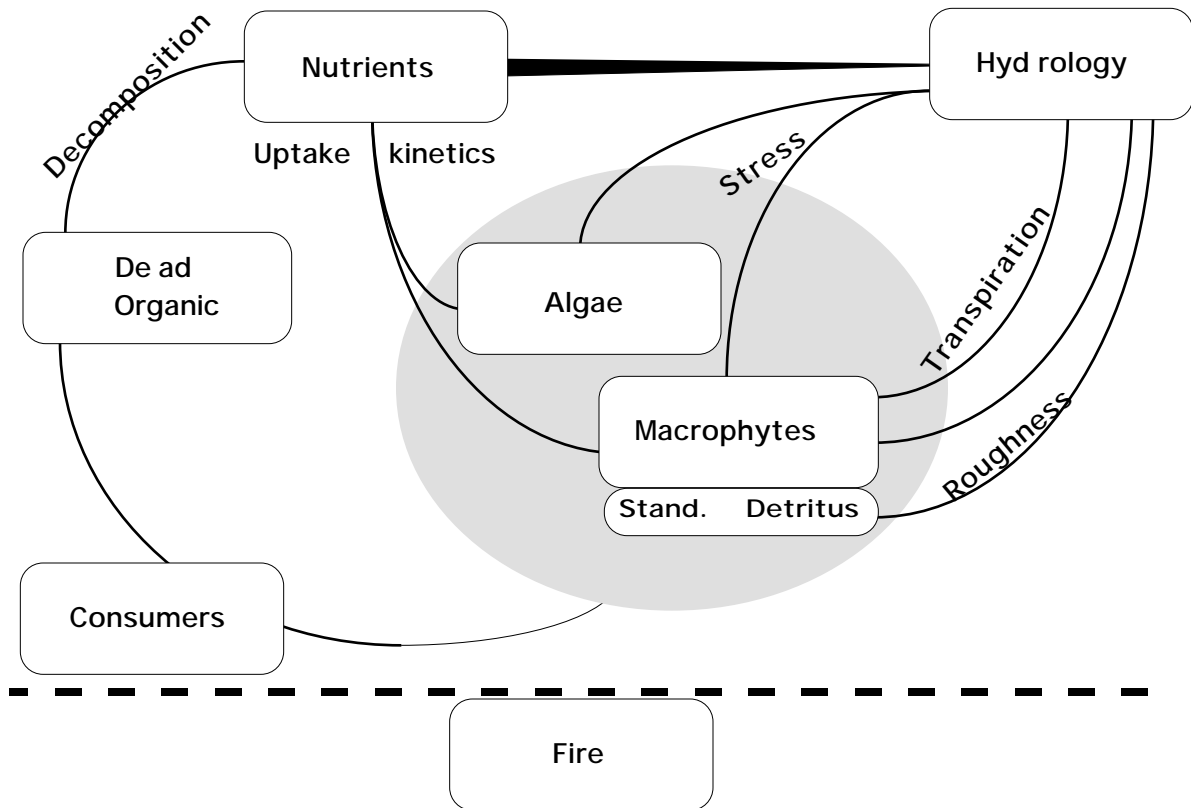
Figure 1. The process- oriented feedbacks among the biotic and abiotic sectors of the GEM. Dynamics of live and standing dead macrophytes alter surface water runoff through changes in structure and thus surface roughness. Water losses via transpiration vary with changes in biomass (leaf area index) and physical canopy structure. Availability of water in surface, unsaturated and saturated storage is one control on plant growth and mortality. Hydrologic algorithms also transport dissolved nutrients and control their remineralization, while nutrient availability and uptake kinetics can control plant growth. Dead organic matter, in different forms of storage and with different C:N:P ratios, is the source for nutrient cycling. Consumers sequester plant biomass, delaying its incorporation into detrital pools. Fire may generally affect the whole system.

indirect interactions built into the model provide a rich variety of dynamics, directly coupling biological and physical components of the whole system. A diagram of the model structure is provided in Figure 2, including most of the linkages among state variables (excluding hydrology). Also indicated is the distinction between above- and below-sediment zones. We describe the model in order of sectors that distinguish among fundamental physical and biological processes within the system. The following descriptions of the different sectors of the model incorporate many of the principal equations that describe the fluxes associated with state variables and the functions that provide feedbacks to some of the biological and/or physical processes. The text descriptions present the logic of many of the algorithms that are used in the model to
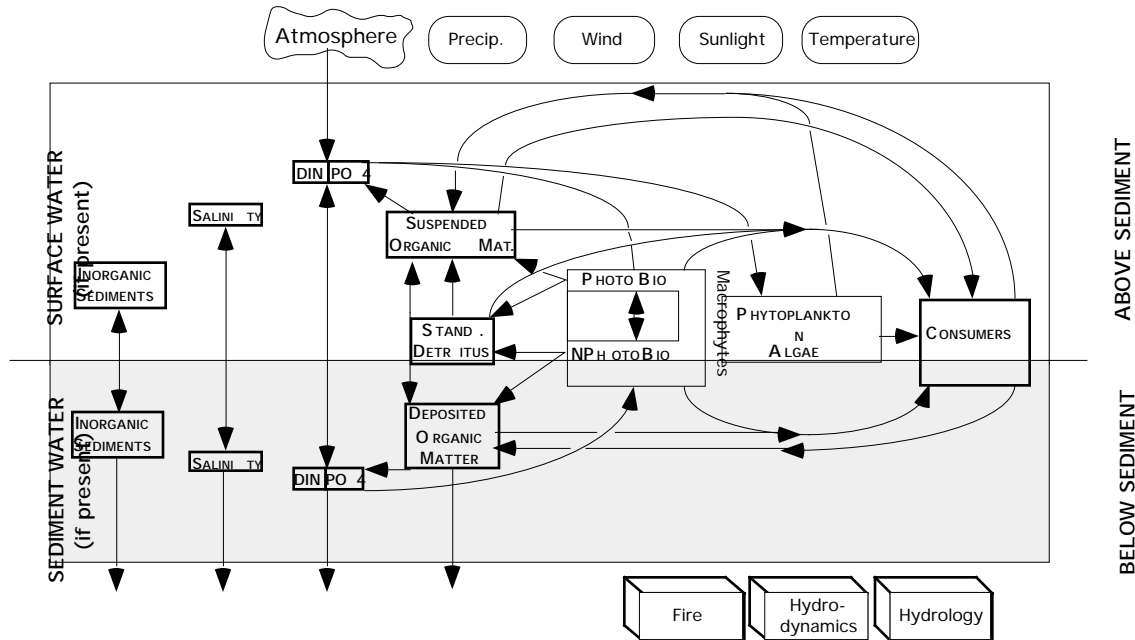
Figure 2. The state variables and most of the linkages of material or information in the GEM, excluding hydrology (Figure 3). Hydrology drives many of the vertical fluxes shown and the unshown horizontal fluxes of materials into and out of the system (cell). State variables are enclosed within rectangles in ALL_CAPS.   Environmental forcing functions are in oval boxes; simulations of fire, hydrology, and hydrodynamics affect model dynamics. Metabolic sinks are not indicated. Dissolved Inorganic Nitrogen (DIN) and PO4 are separate state variables with slightly different dynamics.   Although not shown, both nutrients are involved in uptake and mineralization processes.

generate the flow of material or information. In order to maintain a seamless link between the STELLA model and the description, we maintain the full variable names in accordance with their use in the STELLA model.   The system of non-linear and linear equations employs a variety of built-in logical and mathematical functions that are built into STELLA. The software carries out the solution of the finite difference equations using the Euler integration technique and provides graphical and tabular output of results.

We assume that the area included in the model boundaries is homogenous in most respects. The model boundary area is referred to as a cell, in reference to the typical situation where the GEM is a unit model embedded in a cell of a spatial model. The vertical dimension varies dynamically according to changing sediment and water levels as indicated in the descriptions below.

Text in ALL_CAPS indicates a state variable, and is given in this format when first defined in the text and in all equations. Auxiliary variables and parameters are *italicized* when first defined within a sector and when used in equations. Parameters preceded by *rc_,* such as *rc_alg_prod*, are rate constants; variables appended by *_cf* are control

functions. Within the equations, **bold** standard text represent common intrinsic functions that are defined in STELLA software.

Global Inputs Sector

The GEM used daily rate coefficients and a time step of 0.5 day or less. The area of the modeled system is input by the user, but the example simulations here use a 1.0 km^2 cell size. Daily precipitation and temperature data are required, with humidity data useful, but not essential. Daily solar radiation is simulated using an algorithm derived from Nikolov and Zeller (Nikolov and Zeller, 1992), that begins with a calculation of daily solar radiation at the top of the atmosphere based on Julian date, latitude, solar declination, and other factors. For the GEM, mean monthly cloud cover is calculated using a regressed relationship based on daily precipitation, humidity, and temperature. This monthly cloud cover value is used to attenuate the daily radiation reaching the surface. Daily radiation (*SolRadGrd* in cal•cm^{-2}•d^{-1}) received at the earth surface at a particular elevation, latitude, or time of year in the northern hemisphere is calculated using the Beer's law relationship to account for attenuation through the atmosphere (Nikolov and Zeller, 1992). Other components of their radiation model can accommodate slope and aspect of mountainous terrain, but are not used in this GEM version.

Hydrology Sector

Water is held in three state variables: 1) SURFACE_WAT is water that is stored above the sediment/soil surface; 2) UNSAT_WAT is stored in the pore spaces of the sediment/soil complex, but not saturating that zone; and 3) SAT_WAT is water saturating the pore spaces of the sediment/soil complex. Simulating the fluxes among variables (Figure 3) allows the depiction of wet, moist and dry environments by simulating the water movement between storages and calculating the water level movements above and below the sediment/soil level. Flux among the variables depends on a variety of processes. Horizontal flow of surface and saturated ground water, evaporation, infiltration, and saturated/unsaturated water transpiration are some of the more critical fluxes for accurate simulation of water storages at daily time scales. We ignore details of processes that occur on a time scale faster than the daily time step, such as vertical movement of a saturated wetting front in infiltration events. The longer-term results of storage in a small landscape can be effectively captured within the day-to-weekly time scale.

Surface water -- The volume of surface water that is runoff from the cell in one time step is calculated first. Runoff is determined using the Manning's equation (Chow, 1964) for overland flow which is based on the hydraulic head difference between the current cell and external cells. We provide only one directional pathway of net flow to/from the
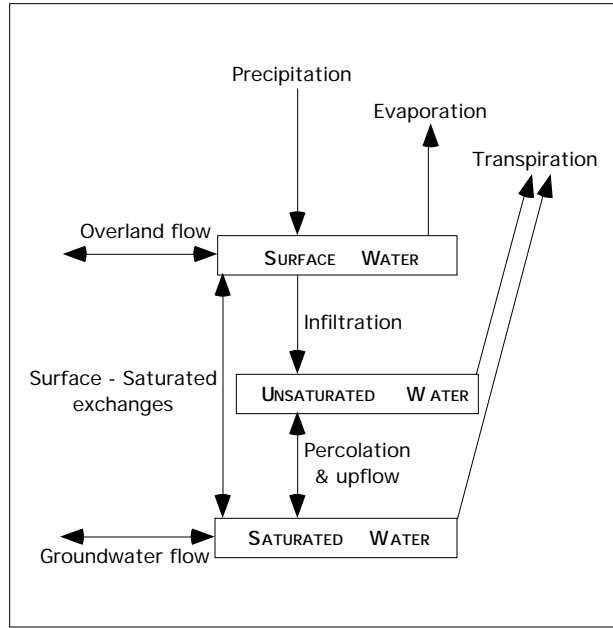
Figure 3. Simplified diagram of water storages and flows for the Hydrology sector. The depths associated with water in surface, unsaturated, and saturated storages all vary dynamically, and calculations determine the variable soil moisture proportion of the unsaturated zone.

external environment for simplicity. In the spatial modelling context, the flux equations would operate in the four directions of the compass. Flow associated with the current cell is:

$$Sf\_wt\_flow = \sqrt{\frac{Sf\_wt\_head - Sf\_wt\_headExt}{cell\_width}} \cdot \frac{Sf\_wt\_avg^{5/3} \cdot cell\_width}{Mannings\_coef} \tag{1}$$

where Sf_wt_flow is the net flux of water ($m^3 \cdot d^{-1}$) into or out of the cell, $Sf\_wt\_headExt$, Sf_wt_Head, and Sf_wt_avg are the hydraulic heads (m) of the external cell, of the current cell, and their average, respectively; $cell\_width$ is the width (m) of the square cell that is uniformly covered with water; Sf_wt_depth is the depth of the surface water (m), and $Mannings\_coef$ is Manning's coefficient of surface roughness.

The Manning's roughness coefficient is a function of the sediment type and the interaction of the vegetation height/density and water depth.

$$Mannings\_coef =$$

$$-\left| (Mac\_max\_rough - sed\_Material) \cdot 2^{\left(1 - \frac{Sf\_wt\_depth}{mac\_height}\right)} - 1 \right| + Mac\_max\_rough) \tag{2}$$

The *sed_Material* roughness is the minimum Manning's coefficient for a vegetation-free cell, the *Mac_max_rough* is the maximum roughness associated with the (dynamic) vegetation density in the cell, and *mac_height* is the (dynamic) height of the macrophytes in the cell. This function (Figure 4) returns a positive roughness coefficient whose value ranges from a vegetation-free minimum to a maximum at the point of full plant immersion (Petryk et al., 1975). As water depth increases over that of the macrophyte height, the roughness decreases to an asymptote at the baseline sediment roughness (Nalluri and Judy, 1989).
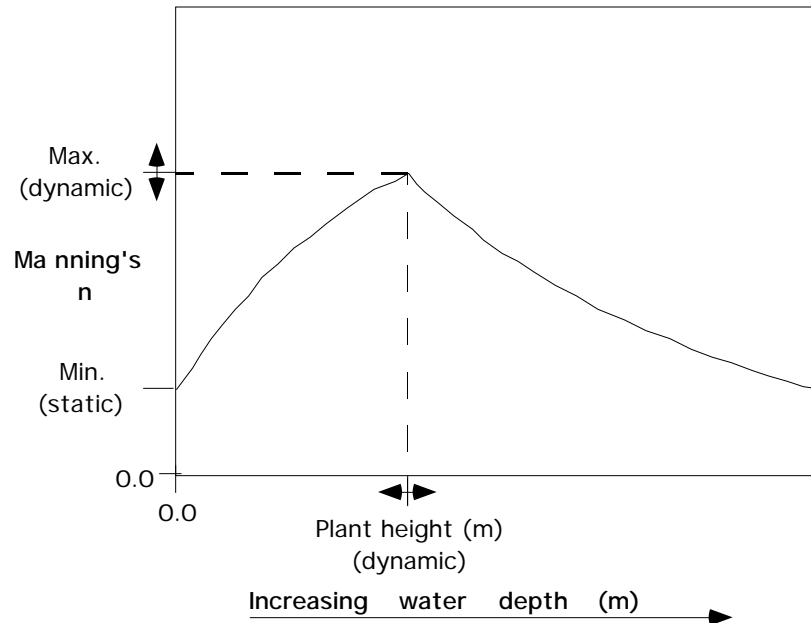
Figure 4. The relationship between Manning's roughness coefficient "n" to water depth and to plant height, both of which change dynamically in the model. The maximum Manning's n varies with the plant density; the minimum Manning's n is fixed for a vegetation-free cell. Maximum roughness for a given plant density occurs when water depth equals the plant height.

Surface water loss to storage in the sediment/soil is determined after runoff and can occur via two pathways: 1) infiltration from the surface water to an unsaturated soil water zone, based on measured infiltration rates for different soil types, and 2) surface water flow to the saturated water storage at a rate that depends on the rate of water loss in saturated storage. Both of these vertical flows are explained in more detail in the next section.

Any remaining surface water is available for evaporation. Surface water evaporation is simulated separately from water loss due to transpiration by plants. Potential evaporation $(m \cdot d^{-1})$ is calculated from Christiansen (Christiansen, 1968). The model uses temperature, solar radiation, wind speed and humidity as the independent variables such that:

$evap\_pot = 0.0000482 \cdot C_T \cdot C_W \cdot C_H \cdot SolRadGrd / 585$, where

$$C_T = 0.463 + 0.425(T / T_0) + 0.112(T / T_0)^2,$$
$$C_W = 0.672 + 0.406(W / W_0) - 0.078(W / W_0)^2,$$
$$C_H = 1.305 + 0.240(H / H_0) - 0.275(H / H_0)^3,$$

(3)

585 cal/g is the latent heat of vaporization to convert solar radiation from cal•cm^{-2}•d^{-1} to it's water equivalent of cm•d^{-1}, and C_T, C_W, and C_H are coefficients related to temperature (T in ˚C), wind speed (W in km/hr), and humidity (H, proportion from 0-1), respectively. Parameters subscripted with 0 (such as T_0) are reference values in Christiansen's (Christiansen, 1968) model.

Saturated and Unsaturated water -- Vertical fluxes of water occur among all three of the water storage compartments. If surface water from precipitation is present, and there is available volume in the unsaturated storage of the sediment, then water infiltrates into the unsaturated zone at a rate determined by the infiltration rate (m•d^{-1}) for the habitat type multiplied by the *cell_size* (m^2). The available capacity of the unsaturated zone is calculated from the porosity and current volume of water in unsaturated storage, which also determines the moisture proportion in unsaturated storage (*unsat_moist_prp*). We assume that the water in unsaturated storage is distributed homogeneously within that zone, ignoring the presence of any wetted front and the heterogeneities associated with processes occurring on faster time scales than the daily time step used in the GEM.

When the sediment is fully saturated, surface water may flow into the saturated layer to replace outflow from the saturated storage at the rate determined by the loss of saturated water. We assume that the rate of vertical movement of water from the surface to the saturated zone is at least as fast as that of losses from saturated storage via horizontal flow, transpiration, and deep aquifer recharge. Similarly, water from the saturated storage zone flows into surface water storage when the total capacity of the sediment is exceeded. Because the unsaturated zone varies in depth, the GEM has a function to determine the relative degree to which surface water flows towards the unsaturated and saturated storage zones in the transition from significant depths of ponded surface water to little surface water and increasing depths of unsaturated storage:

$sat\_vs\_unsat = 1/ \mathbf{exp}(100 * \mathbf{max}((Sf\_wt\_depth - unsat\_depth),0))$.

(4)

This equation allows for the presence of a vanishingly small unsaturated depth (*unsat_depth*) in the presence of small depth of overlying surface water (*sf_wt_depth*). The function **max**(x,y) returns the greater of either argument x or y, and **exp**(x) returns e raised to the x power. The equation returns a (dimensionless) value near 0.0 for a small

unsaturated zone, resulting in most water flux to the saturated zone; the function rapidly approaches 1.0 as the unsaturated depth becomes significant, resulting in all surface water infiltration to the unsaturated layer.

Any moisture in excess of field capacity may percolate from the unsaturated storage to saturated storage, determined by the hydraulic conductivity of the sediment for unsaturated conditions. The unsaturated hydraulic conductivity ($m \cdot d^{-1}$) for each habitat (sediment) type is decreased from the saturated hydraulic conductivity as a function of decreasing sediment moisture (*unsat_moist_prp*). This (0-1) multiplier varies with soil type (Dominico and Schwartz, 1990) as shown in Figure 5.
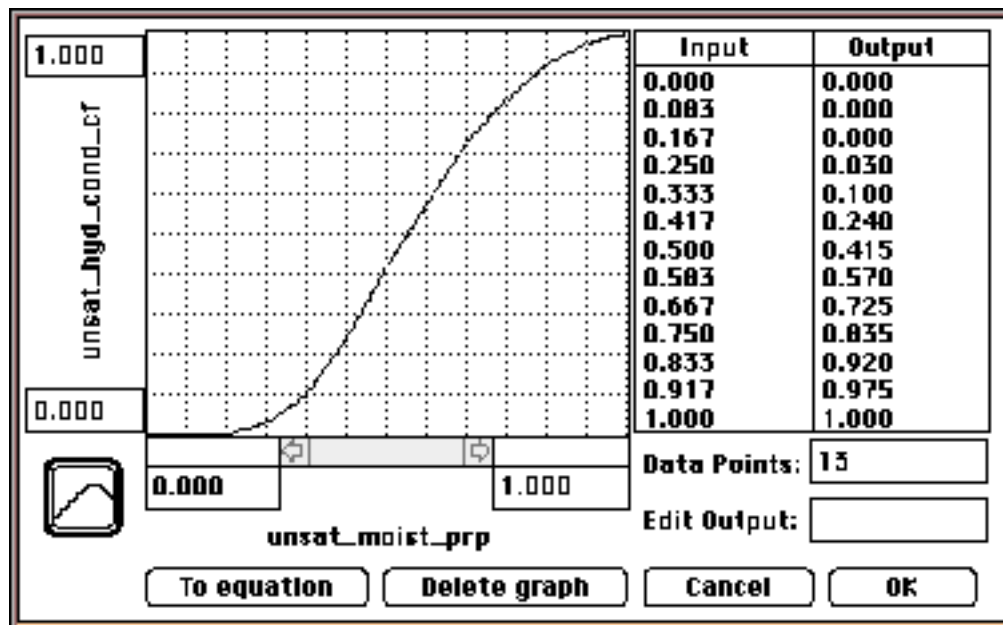
Figure 5. An example of a control function that is determined by data, graphically represented in a STELLA dialog box. The unsaturated hydraulic conductivity (0-1) multiplier (*unsat_hyd_cond_cf* along the Y axis and listed in the Output column of data) is a function of the (0-1) unsaturated moisture proportion (*unsat_moist_prp* along the X axis and listed in the Input column). The multiplier reduces the value of saturated hydraulic conductivity for the current soil moisture; STELLA performs a linear interpolation between data points. The user may input tabular experimental data or manipulate the curve to some hypothesized relationship between the X and Y variables.

Downward percolation, then, is simply the calculated hydraulic conductivity multiplied by the *cell_size* (m^2). When the water table rises (due to groundwater inflow or percolation), the volume of water held in pore space in the previously unsaturated zone is incorporated into saturated water storage. Thus, the total flux of water from the unsaturated to saturated zone ($m^3 \cdot d^{-1}$) is the sum of percolation and that due to groundwater inflow.

Loss of water by plant transpiration occurs either from the unsaturated or saturated water storages depending on the presence/absence of roots within the zone. The GEM has a gradation between physical and biological controls on this flux term, dictated by the vegetation type, water availability, and model scale. There are two basic mechanisms of evaporative loss through the plant canopy. First, the degree of coupling of air masses in the canopy and the lower atmosphere influences the degree to which purely physical processes (Equation 3) drive the transpirative loss. Secondly, the degree to which water is limiting, and thus stressing plants, simulates the reduction in transpiration (and thus primary production at some point) due to stomatal closure and changed canopy conductance.

In the general sense, transpiration is controlled by canopy conductance, net radiation, the air saturation deficit, temperature, and wind speed. The algorithm used in GEM depends on several factors associated with the plant assemblage and with the physical environment. Total transpiration is determined along a continuum of the relative importance of the physical versus the plant-related factors for the given ecosystem. First, we calculate the part of the potential transpiration that is based on the leaf canopy conductance, the water saturation deficit of the local (canopy) environment, and water stress of the plant. Next, the potential evaporation model (Equation 3) is used to determine the potential rate of evaporative flux given the solar radiation, temperature, humidity and wind speed. For the GEM, the degree to which these two processes control the total transpirative flux depends on the extent to which the saturation deficit at the canopy surface is decoupled from the saturation deficit in the atmosphere above the boundary layer of the canopy (Jarvis and McNaughton, 1986), here taken to be the mixed Planetary Boundary Layer on the order of hundreds of meters in height. This (0-1) decoupling factor is an approximate scaling measure that varies with gross canopy morphology, with forests generally being near 0.2 and grasslands being near 0.8 (strongly decoupled). The decoupling factor will be discussed further in the context of sensitivity analyses.

The below equation determines the relative importance of these controls in determining potential transpiration ($m \cdot d^{-1}$) for a unit area of plant canopy:

$$transp\_pot = \frac{transp\_canop(1 - mac\_canop\_decoup) \cdot mac\_wat\_str\_cf}{+evap\_pot \cdot mac\_canop\_decoup} \cdot mac\_LAI \qquad (5)$$

where *transp_canop* is the canopy conductance ($m \cdot d^{-1}$), which varies from a plant's maximum rate depending on the atmospheric saturation deficit. The mac_canop_decoup *is* the dimensionless decoupling factor for the macrophyte canopy, *mac_wat_str_cf* the dimensionless (0-1) control function indicating the relative extent of water stress of the

plant, *mac_LAI* is the variable (linked to biomass) ratio of plant canopy surface area to ground area, and *evap_pot* is the calculated (Equation 3) potential evaporation (m•d^{-1}). Thus, transpiration potential may be significantly controlled by plant responses to water limitations on one extreme of canopy morphology, but respond primarily to radiative heat flux when the canopy is strongly decoupled.

Actual transpiration is a function of available water in the saturated and the unsaturated zones, partitioned relative to the depth to which roots exist. When the root zone depth is greater than or equal to the depth to the saturated zone, all transpiration flux is assumed to be from the saturated zone. As the saturated water table drops below the root zone, the roots draw water from the saturated zone via capillary action in an exponentially decreasing amount, with the remainder being drawn from the soil moisture in unsaturated storage:

$$sat\_wt\_transp = transp\_pot \bullet cell\_area$$
$$\bullet \mathbf{exp}(-10 \bullet \mathbf{max}(Unsat\_depth - NPhBio\_root\_depth, 0))'$$

(6)

where *sat_wt_transp* is the actual transpiration flux from saturated storage (m^3•d^{-1}), *NPhBio_root_depth* is the root depth (m), and *transp_pot* is the potential flux (m•d^{-1}); a complementary relationship exists for flux from the unsaturated storage.

In the GEM, horizontal flow of water in saturated storage is assumed to be steady, unidirectional flow in an homogenous, unconfined aquifer. The basic Darcy equation is applied to flux between two cells as follows:

$$Sat\_wt\_flow = \frac{\left(tot\_water\_head - tot\_wat\_headExt\right)}{cell\_width}$$
$$\bullet sat\_hydr\_conduct \bullet cell\_width \bullet sat\_avg\_hd$$

(7)

where *Sat_wt_flow* is the net flux of water (m^3•d^{-1}) into or out of the cell, *tot_water_head* is the total hydraulic head (m) and is the sum of the saturated water head plus the surface water depth, for the case when the saturated water height reaches the sediment surface. The *tot_wat_headExt* is the analogous total water head (m) of an external cell, *cell_width* is the width (m) of a square grid cell, *sat_hydr_conduct* is the saturated hydraulic conductivity (m•d^{-1}), and *sat_avg_hd* is the average hydraulic head of the water in saturated storage (m) in the two cells. The total water head is used to accommodate any difference in elevation among two cells when surface water is present to alter the hydraulic gradient.

Hydrodynamics Sector

In shallow surface water (<~3 m), the GEM simulates the hydrodynamics associated with the transfer of wind energy to water and calculates the stress effect of wave- and current- induced turbulence near the bottom sediments. This turbulence drives

the suspension and deposition of sediments, which in turn affects water clarity within the system. We envision the GEM as a terrestrial and wetland modelling system, and therefore assume that 1) water density is constant; 2) surface tension is negligible; 3) Coriolis force is negligible; 4) only one set of waves is considered at a time; 5) the sediment surface is a horizontal, fixed boundary that does not absorb energy; and 6) wave amplitude is small and the wave form invariant within the time and space scales considered. While the first three assumptions are reasonable for most situations, assumptions 4 through 6 involve issues of the area considered in the model, and can be considered reasonable in most situations if sufficiently small cells are used in a spatial model. Factors within the equations of motion not relevant to coastal and shallow water conditions are not considered. Wave predictions and formulae are based on the axioms of linear wave theory (USACOE, 1984).

       Wave and current simulation -- Wave dynamics in GEM are estimated by wave prediction equations for transitional water depth in which the depth:wavelength ratio is between 1:25 and 1:2 (USACOE, 1984). These equations are used to estimate significant wave heights based on fetch within a grid cell and wind speed. Linear wave theory makes use of these wave heights to calculate wave dynamics such as orbital velocities and wave energy. We use USACOE (USACOE, 1984) for determining the wave height and period in the following series of Equations (8-10). After determining the fetch distance for a given wind direction within the cell, a local wave height is calculated based on wind speed, fetch distance and water depth.   Both of the latter corrections convert distances into dimensionless parameters using the gravitational constant. For instance, the dimensionless depth parameter used in determining local wave height is determined by:

$$D\_less\_depth = \frac{Sf\_wt\_depth \bullet G}{Wind\_speed^2} ,$$
(8)

where *D_less_depth* is the dimensionless fetch parameter, *Sf_wt_depth* is the distance of open water over which waves travel (m), *G* the gravitational acceleration (m·sec^{-2}), and *Wind_speed* is in m·sec^{-1}. We developed a graphical algorithm to approximate an intrinsic hyperbolic tangent function needed in the calculation of wave height, tanh(X), where X is any expression. This algorithm is then used to calculate intermediate parameters involving depth and fetch parameters, solving the following relationship:

$$depth\_H\_corr = \mathbf{tanh}\left(0.530 \bullet D\_less\_depth^{0.75}\right) ,$$
(9)

where *depth_H_corr* is the intermediate result involving the hyperbolic tangent of the dimensionless depth parameter; **tanh**, the hyperbolic tangent function; and 0.530, an empirical constant. A similar technique is used to determine a second intermediate result

involving fetch, *fetch_H_corr*. These intermediate results are then used in solving the
following equation for local wave height:

$$Loc\_Wave\_height = \frac{0.283 \cdot Wind\_speed^2 \cdot depth\_H\_corr \cdot fetch\_H\_corr}{G} ,$$ **(10)**

where 0.283 is a dimensionless empirical constant.

This local waveheight is then expressed as wave energy (USACOE, 1984).   The
actual wave height *(Wave_height)* within the system is calculated by combining the local
waveheight with wave energy propagated from outside the cell, and energy dissipated due
to bottom friction.

The wave period is determined from algorithms similar to those used in wave height
calculations (USACOE, 1984). The wave period is determined by:

$$Wave\_period = \frac{7.54 \cdot Wind\_speed \cdot depth\_T\_corr \cdot fetch\_T\_corr}{G} ,$$ **(11)**

where *depth_T_corr* and *fetch_T_corr* are the intermediate results involving depth and
fetch. The *wave_Length* is also calculated based on USACOE (USACOE, 1984). We
then determine the wave orbital velocity for waves in water of transitional relative depth
using (USACOE, 1984).

$$Wave\_orbit\_velo = \frac{Wave\_height \cdot G \cdot Wave\_period}{2 \cdot Wave\_Length}$$
$$\cdot \frac{2}{\exp \frac{2 \cdot PI \cdot Sf\_wt\_depth}{Wave\_Length} + \exp \frac{-2 \cdot PI \cdot Sf\_wt\_depth}{Wave\_Length}} ,$$ **(12)**

where *Wave_height* is the actual wave height (m), and *Sf_wt_depth* is the depth of the
surface water (m).

Shear stress -- Shear stress is used to calculate the amount of sediment suspended above
threshold resistances in the Inorganic Sediments Sector and the Deposited Organic Matter
Sector. This version of GEM does not account for erosional and depositional processes in
streams. Shear stress is calculated as a function of the wind-induced wave orbital motion
modified by any current (Grant and Madsen, 1979).

$$Shear\_stress = 0.5 \cdot fric\_coef \cdot Fluid\_density$$
$$\cdot [1.0 + current\_corr^2 + 2.0 \cdot current\_corr$$
$$\cdot \cos((\mathbf{abs}(Current\_direction - Wind\_direction) \cdot 0.8))]$$ **(13)**
$$\cdot \mathbf{abs}(Wave\_orbit\_velo),$$

where *fric_coef* is the friction coefficient that varies with the extent to which the turbulence is due to wave rather than current velocities, *Fluid_density* is the density of water (kg•m^{-3}), *current_corr* is the ratio of current velocity to wave orbital velocity, and **abs**(expression) is the function that returns the absolute value of the expression in parentheses.

Inorganic Sediments Sector

This sector includes a state variable for deposited (DEP_INORG_SEDS) and for suspended (SUS_INORG_SEDS) sediments that represent an aggregate of all sizes of mineral particles. Deposited inorganic sediments are suspended in the presence of surface water as a function of the shear stress calculated in the Hydrodynamics Sector. As described in the Hydrodynamics Sector, a shear stress due to waves and currents is determined for each time step. This shear stress on the sediments is compared to a shear resistance value. Soil shear resistance varies with habitat and is expressed using an algorithm composed of the root density of macrophytes and the inverse of the proportion of organic material in the sediments. Sediment suspension depends on the extent of erosion during the prior time step. If the potential erosion at time t_i is less than that which occurred one time unit previously t_{i-1}, then no erosion will occur (sediments underlying the eroded material are assumed to be more consolidated and less erodable). However, a layer is subject to erosion if the erosion potential is greater than that during the prior time step:

$$eros = \mathbf{max}[Pot\_Eros - \mathbf{delay}(Pot\_Eros,1), 0] \bullet cell\_area, \tag{14}$$

where *eros* is the volume (m^3) of (organic and inorganic) sediment that is actually eroded in one time unit, *Pot_Eros* is the depth (m) of (organic and inorganic) sediment that may be potentially eroded due to the difference between shear stress and shear resistance, and *cell_area* is the surface area (m^2) of the cell. In this example, the **delay** function, which is intrinsic to STELLA, returns the value of *Pot_eros* from the prior (1) time unit. The mass of inorganic sediments eroded are determined by *eros* by the proportion of sediments that are inorganic, and their bulk density.

Suspended inorganic sediments that enter a cell as a function of the surface water inflow and outflow can be deposited from the suspended stock when shear stress is less than fluid yield. The fluid yield is the minimum shear stress value at which a particular mud/sediment concentration can be kept in suspension. To obtain this fluid mud yield, the concentration of mud is multiplied by 10 to account for increases in concentration when the water column becomes stratified during low energy conditions.

The sediment depth may change due to decomposition of organic material and the suspension/deposition of sediment/soil. We dynamically determine sediment elevation depending on the sediment volume. The volume of the organic and the inorganic sediment

(without pore space) is determined from the mass and the standard density of the organic and of the inorganic constituents. The total sediment volume is then the sum of the volume of inorganic sediment/soil, plus the volume of the organic component, plus the pore space volume. Over long time scales, sediments can also downwarp, moving part of the sediment/soil down below the base datum of reference, thus effectively being lost from the system. We describe this as a simple constant rate:

$$DIS\_dn\_warp = rc\_downwarp \bullet cell\_area \bullet (1.0 - Porosity) \bullet DIS\_part\_density, \tag{15}$$

where *rc_downwarp* is the rate of geologic downwarping (m•d^{-1}), *porosity* is the proportion of sediment/soil structure that is occupied by pore space, and *DIS_part_density* is the average density of inorganic material in the sediments (kg•m^{-3}). These dynamics of sediment elevation are most important in coastal areas in relation to the height of the surface (sea) water.

Chemical Constituent Sectors: General Dynamics

The three model sectors involving salts, inorganic nitrogen, and orthophosphate share a variety of common structures and logic. Each is divided into those portions that are dissolved in surface water (*constituent*_SF_WT) and those that are dissolved in sediment/soil pore water (*constituent*_SED_WT), the latter being the total of saturated and unsaturated water storage stocks. The concentration of dissolved constituents is assumed to be distributed homogeneously through their storage volumes. All constituents dissolved in surface water and saturated water can move into and out of the cell determined by their concentration in the water volumes of the horizontal water flows described in the Hydrology Sector. Similarly, advective vertical movement of dissolved constituents are controlled by calculated water flows, in addition to diffusion across the surface water - sediment/soil water gradient. Diffusion is generally small relative to the advective fluxes, and is modeled by the difference in concentration multiplied by the diffusion coefficient for the constituent across a 1 cm distance.

We assume that the vertical fluxes of dissolved constituents between the unsaturated and saturated zones is rapid enough for equilibrium to occur between the different dissolved components in the vertical sediment/soil profile. Because of the assumed homogeneity of concentration in both the saturated and unsaturated water components, a loss of chemicals such as nutrients via saturated (groundwater) flow also decreases the concentration in the unsaturated water zone.

Salt Sector

The dynamics in this sector are those described above for the general model of constituent flows. Although salts are not actively taken up or released by the biotic

components in the GEM, they may affect certain biological processes and the habitat type. This is one example of where a sector structure is established for future use, e.g., salinity constraints on macrophyte growth.

Orthophosphate Sector

Phosphorus is one of two nutrients that can potentially limit the growth of plants in a GEM simulation. Available inorganic phosphorus is simulated as orthophosphate. In addition to the general constituent dynamics outlined above, there are losses due to plant uptake and gains due to decomposition of organic material.

Phosphorus dissolved in surface water (PO4_SF_WT) may increase as a result of the nutrient concentration in rainfall. PO4_SF_WT uptake is directly linked to the amount of carbon fixed by algae (see the Algae Sector) and its carbon to phosphorus (C:P) ratio. Likewise, the rate of decomposition of organic material suspended in the water column (Suspended Organic Matter Sector determines the rate of remineralization of PO4_SF_WT via the C:P ratio of the organic material. Currently, the detrital and algal C:P ratios are not temporally dynamic in the model and vary only by habitat type.

Uptake and mineralization of phosphorus in the sediment water (PO4_SED_WT) are determined by means analogous to those for surface water phosphorus, with the replacement of algae and suspended organic matter by macrophytes (Macrophytes Sector) and deposited organic matter (Deposited Organic Matter Sector), respectively. Mineralization and biotic uptake of nutrients in the sediment/soil aerobic zone are vertically stratified processes. However, the model assumption of equilibrium within this zone appears reasonable when most of the dynamic processes occur within the shallow, upper zone of the profile.

Adsorption and desorption of phosphorus to soil particles in the sediment also assumes equilibrium conditions over daily periods. This process is modeled by:

$$PO4\_sorbtion = PO4\_K \bullet \left(PO4\_sed\_wt\_conc^{0.8} \right)$$
$$\bullet DEPOS\_ORG\_MAT - PO4\_SORB,$$

(16)

where *PO4_sorbtion* is the daily net mass flux of PO^4 among the PO4_SED_WT (kg PO^4) and the mass of phosphorus sorbed to sediments PO4_SORB (kg PO^4), *PO4_K* is the phosphorus sorption coefficient ($m^3 \bullet kg^{-1}$) for the DEPOS_ORG_MAT, *PO4_sed_wt_conc* is the concentration of PO^4 in the sediment/soil water ($kg \bullet m^{-3}$), and DEPOS_ORG_MAT is the mass (kg) of deposited organic matter (Deposited Organic Matter Sector).

Dissolved Nitrogen Sector

The other potentially limiting nutrient is nitrogen. Dissolved inorganic nitrogen is stored in surface water (DIN_SF_WT, kg) and sediment water (DIN_SED_WT, kg).

NO_2^-, NO_3^- and NH_4^+ are aggregated into one value of nitrogen to represent all forms of nitrogen that are directly available for plant uptake. There are a number of redox reactions that determine the species of nitrogen present in a given type of environment, and thus the extent to which the inorganic nitrogen is available for plant uptake. We assume that the proportion of the available inorganic nitrogen is a function of particular environmental conditions that are typical for different habitats (e.g., anaerobic sediments, aerobic water column, and shallow aerobic sediments). It is also assumed that the daily concentrations of NO_3-N in the surface water and NH_4-N in the sediment water are in equilibrium.

The primary functional difference between the simulated dynamics of phosphorus and nitrogen is the addition of denitrification losses from the sediment water storage. Gaseous denitrification losses occur in the anaerobic portion of the sediment profile, the depth of which is determined in the Deposited Organic Matter Sector. Denitrification is determined by:

$$din\_sed\_wt\_denitrific = sed\_anaerob\_vol \bullet DIN\_sed\_wt\_conc \bullet rc\_DIN\_denit$$
$$\bullet 1.2^{(\mathbf{min}(wat\_temp - T_C, 0.0))}, \tag{17}$$

where *sed_anaerob_vol* is the volume (m^3) of the water in the anaerobic layer in the sediments, DIN_sed_wt_conc the concentration ($kg \bullet m^{-3}$) of DIN in the sediment water, *rc_DIN_denit* is the specific rate ($1 \bullet d^{-1}$) of denitrification, *wat_temp* is the water temperature, and T_C is the critical temperature, at which denitrification is at its maximum rate.

Algae Sector

This sector contains one state variable which may be used to represent either phytoplankton or periphyton/algae. If both types of communities are to be included, then the sector as described here for phytoplankton is duplicated and modified to remove flows with surface water runoff and depth of residence of the community (benthic vs. within the water column). Carbon fixation in primary production increases the aggregate value for organic carbon in algal biomass (ALGAE).

Growth of the standing stock of algae is described by a maximum growth rate multiplied by the standing stock, a density-dependent feedback, and a control function involving several environmental parameters:

$$Alg\_gross\_PP = rc\_alg\_prod \bullet ALGAE \bullet \left(1 - \frac{ALGAE}{alg\_max}\right) \bullet alg\_prod\_cf, \tag{18}$$

where *Alg_gross_PP* is the flux of carbon fixed by algae ($kg \cdot d^{-1}$), *rc_alg_prod* is the specific rate of carbon fixation (1/d), *alg_max* is the maximum biomass of algae (kg), and

alg_prod_fb is the (dimensionless) control function incorporating environmental factors. This combined function is a multiplicative expression that has 3 control functions of light intensity, temperature, and nutrient availability.

The dimensionless control function due to light intensity in the water column is based on Steele's (Steele, 1965) photoinhibition formulation integrated over depth (Bowie et al., 1985):

$$alg\_light\_cf = 2.718 \ \frac{\dfrac{daylength}{24}}{midepth \bullet light\_extinct}$$

$$\bullet \quad \begin{array}{c} \exp \dfrac{-incident\_light}{alg\_sat\_light} \bullet \exp\left(-light\_extinct \bullet midepth\right) \\ \\ -\exp \dfrac{-incident\_light}{alg\_sat\_light} \end{array} \tag{19}$$

where *midepth* is the midpoint of the surface water depth (m),. The *light_extinct* variable is the light extinction (1/m) resulting from concentrations of algae and suspended organic and inorganic matter, and is determined by multiplying the concentrations by the appropriate extinction coefficient. The *incident _light* (kcal•cm^{-2}•d^{-1}) is light reaching the water surface, and is determined by solar radiation at ground surface level (*SolRadGrd*), corrected for shading by macrophytes. The *alg_sat_light* is the saturating light intensity for algae (kcal•cm^{-2}•d^{-1}).

The temperature control function, based on Lassiter (Lassiter, 1975), describes the biological responses to temperature in the other living biotic sectors, with an example shown here for algae:

$$Alg\_temp\_cf = \exp\left[C\left(H2O\_temp - T_{op}\right)\right] \left(\frac{T_{mx} - H2O\_temp}{T_{mx} - T_{op}}\right)^{C\,T_{mx} - T_{op}}, \tag{20}$$

where C is a curvature parameter, $H2O\_temp$ the water temperature, T_{mx} the maximum temperature (˚C), and T_{op} the optimal temperature (˚C). This constraint rises to 1 at the optimal temperature at an exponential rate which depends on a curvature parameter. The interval width between the optimal temperature (response=1) and maximum temperature (response=0) determines the rate at which the function decreases to 0.

Nutrient limitation is based on the standard Michaelis-Menten relations for nitrogen and for phosphorus. The formulation assumes that one nutrient is most limiting:

$$Algal\_nut\_cf = \textbf{min} \left[\frac{DIN\_sf\_wt\_conc}{DIN\_sf\_wt\_conc + DIN\_half} , \frac{PO4\_sf\_wt\_conc}{PO4\_sf\_wt\_conc + PO4\_half} \right],$$

(21)

where *DIN_sf_wt_conc* and *PO4_sf_wt_conc* are the surface-water concentrations (g•l^{-1}= kg•m^{-3}) of inorganic nitrogen and phosphorus, respectively, and *DIN_half* and *PO4_half* are the half-saturation constants for the respective nutrients.

Export and import of phytoplankton biomass depends on the direction and magnitude of the associated water flux and ingestion by consumers. The rate of algal mortality is constant when water is present, but increases to a high value near 1.0 when the algae are exposed to desiccation. The standard respiratory losses for biotic components in the GEM has the form:

$$Alg\_resp = rc\_alg\_resp \bullet alg\_temp\_cf \bullet \text{ALGAE},$$

(22)

where *rc_alg_resp* is the maximum specific rate of respiration, and (1•d^{-1}), *alg_temp_fb* is the dimensionless temperature control function analogous to Equation 20.

Macrophytes Sector

Macrophytes are modelled using two state variables, photosynthetic (MAC_PH_BIOMAS) and non-photosynthetic carbon biomass (MAC_NOPH_BIOMAS). This partition is used to represent variations in plant carbon storage and the concomitant carbon:nutrient ratios in subsequent detrital dynamics from the two stocks. As in the Algae Sector, this sector aggregates all macrophyte species into one stock using weighted averages for the parameter values.

Biomass is added to the sector through the photosynthetic pathway that determines net production of MAC_PH_BIOMAS, with the maximum rate of net production limited by a multiplicative environmental control function that includes light, nutrients, temperature, and water. Using a form similar to Equation 18 for algal gross production, the rate is further constrained by maximum density considerations . The light control function is based on the Steele (Steele, 1965) formula representing the effects of photoinhibition, without self-shading:

$$Mac\_light\_cf = \frac{SolRadGrd}{mac\_sat\_light} \textbf{exp} \left[1 - \frac{SolRadGrd}{mac\_sat\_light} \right],$$

(23)

where *mac_sat_light* is the saturating light intensity (kcal•cm^{-2}•d^{-1}), and *SolRadGrd* is solar radiation (kcal•cm^{-2}•d^{-1}) received at ground level (see the Global Inputs Sector).

The nutrient control function is similar to Equation 21 for algae, but uses nutrients in the surface water instead of in the sediment water. The temperature control function also

uses the form of that in the Algae Sector, but replaces water temperature with air temperature.

Water availability to plants is a dimensionless (0-1) function of the soil moisture, the depth of the unsaturated zone and the root depth:

$water\_avail\_cf =$

$$\min \begin{array}{l} 1.0, unsat\_moist\_prp \\ +\exp(-10 \bullet \max(unsat\_depth - NPhBio\_root\_depth, 0)) \end{array}, \tag{24}$$

where *unsat_moist_prp* is the (dimensionless) moisture proportion in the unsaturated zone of the sediment/soil, *unsat_depth* the depth (m) of the unsaturated zone, and *NPhBio_root_depth* the root depth (m) of the macrophytes. Water is not limiting at all (returning 1.0) if the roots reach the saturated zone. When the unsaturated water table is shallower than the root zone depth, the value returned is the *unsat_avail_water* proportion plus an exponentially decreasing amount from the saturated zone. Thus water may be available to the root system when the roots do not reach the saturated zone due to the capillary draw of water from a nearby saturated layer.

Shoot growth is related to simulated net production, but is used in determining the extent of translocation between the photosynthetic and nonphotosynthetic stocks.

$PhBio\_shoot\_grow = rc\_PhBio\_NPP \bullet MAC\_PH\_BIOMAS$

$$\bullet PhBio\_shoot\_seas \bullet \left(1 - \frac{MAC\_PH\_BIOMAS}{PhBio\_max} \right), \tag{25}$$

where *PhBio_shoot_grow* is the biomass increase (kg•d^{-1}) in the MAC_PH_BIOMAS (kg), *rc_PhBio_NPP* is the maximum specific rate (d^{-1}) of net production (used in the photosynthetic pathway above), *PhBio_shoot_seas* is an empirically derived (0-1) function that operates primarily during peak periods of new-shoot development, and *PhBio_max* is the maximum photosynthetic biomass (kg). If shoot growth (*PhBio_shoot_grow*) requires more carbon than is fixed in the photosynthetic pathway simulated above, that carbon is translocated from the available nonphotosynthetic pool. That available reserve of labile carbon is calculated by *NPhBio_avail* (using the form of Equation 31) multiplied by the proportion of labile carbon in plant biomass for the habitat. If carbon fixed by the photosynthetic pathway is in excess of that needed for net growth of shoot and leaf biomass, that carbon is translocated to the nonphotosynthetic stock, thus assuming a homeostatic mechanism between roots and shoots.

Mortality within the photosynthetic stock is determined from seasonal cues and current water stress. The maximum specific rate of mortality is limited by the unweighted average of seasonal litterfall (from empirical data) and water stress limitations (both range

0,1). Mortality of the nonphotosynthetic module is assumed to occur at a constant rate. The effects of salinity and other factors simulated in the model could be incorporated into a control function depending on the model requirements.

The carbon:nitrogen:phosphorus (C:N:P) ratios of MAC_NOPH_BIOMAS and MAC_PH_BIOMAS are different, but do not change for a given habitat (plant) type. The significance of these ratios lies principally in their influence on the rate of decomposition (described below). Consumers ingest both types of biomass depending on their relative availability. Fire (described below) may also burn both types of biomass depending on their fuel quality and content, as determined in the Fire Sector.

Macrophytes have direct feedbacks on the physical environment that are important to overall model dynamics. The areal density of stems and trunks is calculated based on data for the plant type such as those shown in Figure 6 based on Steward (Steward and Ornes, 1975) for a subtropical sedge .   These data and the plant height are used in determining a Manning's roughness coefficient (see the Hydrology Sector) for the system's (cell's) community type.
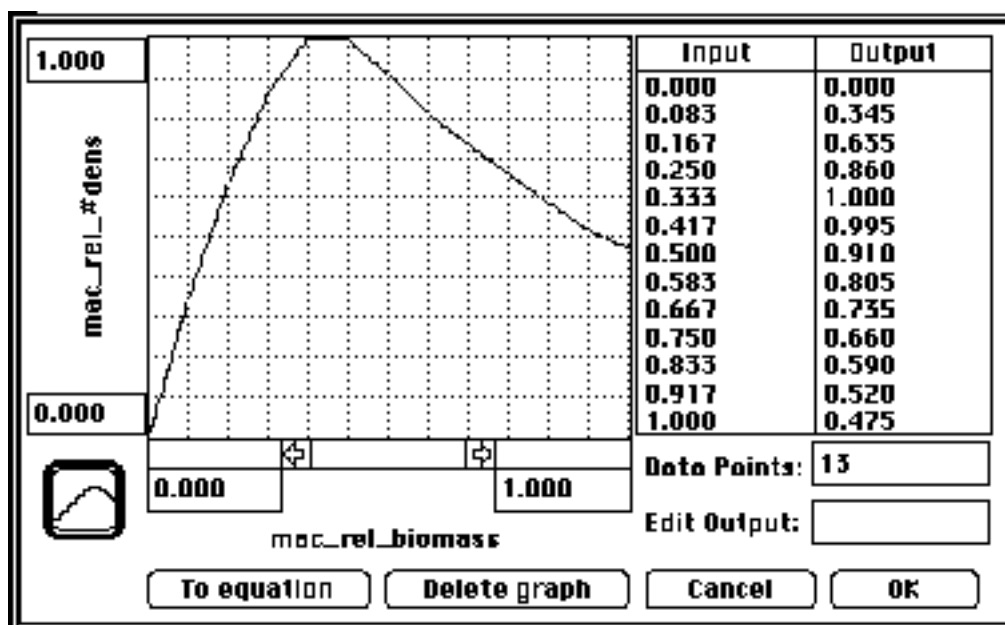
Figure 6. The STELLA dialog box containing the relationship between the ratio of the current macrophyte biomass to its maximum (*mac_rel_biomass*) and the ratio of the number of stems or trunks to its maximum (*mac_rel_#dens*).

Suspended Organic Matter Sector

The stock of suspended organic matter (SUS_ORG_MAT) in this sector includes an aggregate mass of live and dead organic matter suspended in surface water.   As

indicated in the Inorganic Sediments Sector above, the GEM is designed to be able to simulate the dynamics of suspension and deposition of both organic and inorganic material. Thus, for the purposes of tracking such changes in the sediment/soil depth via suspension and deposition, the units for the suspended (and deposited) organic material stocks are in mass of total organic matter, as opposed to only organic carbon. The GEM assumes that the stock of suspended organic matter is homogeneously distributed throughout the water column, and that organic material of all size fractions have the same characteristics.

Mortality of algae, macrophytes, and consumers, along with consumer egestion, are inputs to the Suspended Organic Matter Sector. The ratios of carbon to organic matter for these living carbon stocks determine the mass of total organic material associated with each input. Depending on the habitat and thus the type of living plants and organisms, specific proportions of the organic mortality pool are then allocated to either suspended, deposited, or (in the case of macrophytes), standing dead detritus.   For example, suspended organic matter input to this stock from consumers (kg•OM•d^{-1}) is given by:

$$SOM\_fr\_consum = Cons\_prop\_to\_SOM \bullet \frac{(cons\_mort\_biom + cons\_egest)}{Cons\_C\_to\_OM} \; , \tag{26}$$

where *Cons_prop_to_SOM* is the dimensionless proportion of consumer losses that is directly allocated to the suspended stock, *cons_mort_biom* is consumer mortality (kg•C•d^{-1}), *cons_egest* is the egestion by consumers (kg•C•d^{-1}), and *Cons_C_to_OM* is the ratio of carbon to total organic matter of consumers (kgC•kgOM^{-1}).   The complement of *Cons_prop_to_SOM* is the proportion that is allocated to the deposited organic matter stock (described below). A similar relationship is used for the flux of carbon due to mortality of macrophytes and algae and due to degradation of standing dead detritus. Inputs to this stock from suspension of organic matter from the sediments is described in the Deposited Organic Matter Sector.

Outflows from this stock include decomposition, deposition, consumer ingestion, and export with surface water. Decomposition is implicitly driven by the microbial community, with no internal feedback mechanism or recycling within the sector.   This mineralization of organic material is assumed to be an aerobic process in the water column, and thus there are two control functions in the decomposition equation:

$$SOM\_decomp = rc\_decomp \bullet SUS\_ORG\_MAT$$

$$\bullet decomp\_temp\_cf \bullet \mathbf{min} \left(\frac{SOM\_NC}{SOM\_NC_{opt}}, 1 \right) \; , \tag{27}$$

where *rc_decomp* is the maximum specific rate of decomposition in aerobic conditions (d^{-1}), SUS_ORG_MAT the biomass of organic matter (kg OM), *decomp_temp_cf* a

temperature control function (Equation 20), and *SOM_NC* and *SOM_NC$_{opt}$* the current and the optimal nitrogen:carbon substrate ratios, respectively·

Suspended material can flow into and out of the system with surface water flux determined in the Hydrology Sector. Ingestion of suspended organic matter is controlled by the consumption rate determined in the Consumer Sector, assuming complete availability of this resource to the consumers. Deposition of organic matter is controlled by the shear stress calculated in the Hydrodynamics Sector. If the shear stress is below a threshold value, then all of the suspended organic material is deposited in one time step. Above the threshold, a constant proportion of the organic material is deposited in each time step.

Deposited Organic Matter Sector

The organic matter (DEPOS_ORG_MAT) stock in this sector includes the mass of non-living organic matter and of living microscopic decomposers that are deposited into the sediment/soil complex. All non-living organic material is included within this sector, from particulates to dead plant roots. Thus, changes in sediment organic biomass are part of the sediment elevation that is calculated in the Inorganic Sediments Sector. Inputs to this stock are from deposition of suspended organic matter, mortality of macrophyte non-photosynthetic biomass, and from consumer mortality and egestion. Outputs occur via suspension, fire, decomposition, and ingestion by consumers.

Suspension and deposition are driven by the shear stress calculated in the Hydrodynamics Sector; deposition was described in the Suspended Organic Matter Sector, and erosion was described in the Inorganic Sediments Sector. However, decomposition in sediments differs from that in the water column due to the extent of the aerobic/anaerobic zonation of the sediments. Decomposition in the sediments takes the same basic functional form as decomposition in the water column, but with fluxes described separately for the aerobic and the anaerobic zones. For the aerobic sediment/soil zone, an analogous form of Equation 27 was further constrained by:

$$\frac{sed\_aerob\_depth}{sed\_elev} \bullet unsat\_moist\_prp \; , \tag{28}$$

where *sed_aerob_depth* is the depth (m) of the aerobic layer and *unsat_moist_prp* is the (dimensionless) moisture proportion in the zone of unsaturated water of the sediments. The depth of the aerobic layer is taken to be the depth of the unsaturated zone of the sediment plus a constant depth of a (habitat-specific) thin aerobic zone at the surface. Thus, in situations where the sediment is entirely saturated, a thin aerobic zone will be present. The same form is used for the anaerobic decomposition, replacing aerobic depth

with the depth of the anaerobic zone of the sediments, and a dimensionless factor that reduces the maximum anaerobic decomposition rate from the maximum aerobic rate. Total decomposition in the sediment/soil is the addition of the aerobic plus the anaerobic fluxes.

Not all of the deposited organic material is available to consumer and fire consumption. The mass of organic material that is available is:

$$DepOM\_avail = \textbf{min} \begin{cases} \text{DEPOS\_ORG\_MAT} \bullet \dfrac{DepOM\_max\_avail}{sed\_elev}, \\[2mm] \text{DEPOS\_ORG\_MAT} \bullet \dfrac{sed\_aerob\_depth}{sed\_elev} \end{cases}, \qquad (29)$$

where *DepOM_max_avail* is the depth of sediment that is accessible by fire and consumers of a particular habitat. The mass of carbon available to consumer ingestion is determined by the carbon to organic matter ratio for the sediment type. As with the inorganic sediments, there is downwarping of organic sediments past the base datum of measurement.

Standing Detritus Sector

Dead organic matter attached to plants or earth, and which can not be moved under normal hydrologic flows, is defined as standing detritus (STAND_DETRITUS). This stock includes dead standing grass and marsh grass leaves, snags, dead brush, matted leaf litter, and fallen stems and trunks. The stock is increased by plant mortality and decreased by fire, consumer ingestion, and fragmentation to the suspended or deposited organic matter stock.

Mortality of macrophytes is the only input to this stock, with the rate determined in the Macrophytes Sector. The flux from nonphotosynthetic biomass is partitioned between deposited organic material and standing detritus, whereas the flux of dead photosynthetic biomass is partitioned between suspended organic matter and standing detritus.

Wind and animal consumers contribute to the fragmentation and shredding of standing detritus, whereby the standing detritus becomes part of the suspended or deposited organic material. The rate of loss to suspended organic matter is calculated as:

$St\_det\_to\_SOM = cons\_ingest\_std\_detr \bullet StDet\_shred\_to\_ingest$

$$+\text{STAND\_DETRITUS} \bullet 0.9 \bullet \textbf{max} \left[1 - \frac{\textbf{max}(wind\_storm - Wind\_speed, 0)}{wind\_storm - wind\_thresh}, 0 \right], \qquad (30)$$

where *cons_ingest_std_detr* is the flux of standing detritus to consumer ingestion (kg•C•d^{-1}), *StDet_shred_to_ingest* is the ratio of mass shredded to mass ingested, 0.9 is a calibrated rate constant (1•d^{-1}), *wind_storm* is the wind speed (m•sec^{-1}) at which maximal damage to

standing detritus occurs, and *wind_thresh* is the threshold wind speed (m•sec^{-1}) below which wind does not affect the standing dead detritus.

Consumer Sector

The consumer module represents an aggregate carbon mass of all consumers (CONS). At this level of aggregation it is used primarily as a processor of organic matter, producing a time lag in the mineralization of nutrients. The consumer is omnivorous, ingesting all carbon stocks in the model with equal preference and has a maximum rate of ingestion which is applied to all equations of ingestion of resources. For each carbon food source, the realized ingestion rate is limited by functions of temperature, the availability of that resource, and density dependent regulation of the consumer.

The control function for the availability of a particular resource X (kg organic carbon) to ingestion by consumers follows the general form of Wiegert (Wiegert and Wetzel, 1979):

$$X\_avail = \mathbf{max}\left[\left(1 - \frac{(X_s - X)}{(X_s - X_r)}\right), 0\right] \cdot X\_biomass , \tag{31}$$

where X_S is the saturation density of resource X at which ingestion by consumers is maximal, X is the current density of the food resource, X_r is the density of the resource at which consumption does not occur, and X_*biomass* the standing stock of the resource X. This availability function is used for all living and dead food carbon resources.

Total ingestion of combined carbon resources is:

$$Cons\_ingest = \mathbf{min}\left[\begin{array}{c} Cons\_temp\_cf \cdot \text{CONS} \cdot rc\_cons\_ingest \cdot \left(1 - \dfrac{\text{CONS}}{cons\_max}\right), \\ OM\_tot\_C\_avail \end{array}\right] \tag{32}$$

where *Cons_temp_cf* the is the dimensionless temperature control function analogous to Equation 20, *rc_cons_ingest* is the maximum specific rate of ingestion (d^{-1}), *cons_max* the maximum biomass of consumers for the modeled habitat, and *OM_tot_C_avail* the sum of all available carbon resources for ingestion (kg). Ingestion of each resource is then partitioned among the resources in accordance with availability.

Losses within the consumer stock include respiration and mortality (including emigration), using maximum specific rates that are constrained by the same form of temperature control function used in the Algae and Macrophyte Sectors. Egestion is a proportion of the material ingested, or the complement of an average (carbon) assimilation efficiency.

Fire Sector

Fire can burn living and non-living plant biomass in GEM, whether the material is emergent vegetation, peat or other organic material in the soil. The probability of a lightning strike is a random function of time, using a pseudo random number generator in STELLA. However, the threshold probability of a strike occurrence varies seasonally, allowing for varying probability distributions of fire source. The distribution of threshold values for a lightning strike is:

$$lightn\_strike\_thresh = 0.02 \bullet \cos\left(\frac{DayJul}{365} \bullet 2 \bullet PI\right) + 0.98 \; , \tag{33}$$

which ranges from 1.0 in January and December (Julian dates 1 and 365) to 0.96 in July. If the random number generator returns a value larger than the threshold, a lightning strike is generated.

Ignition from a fire source and the rate of fire propagation within the system are calculated using a formulation similar to Kessell's (Kessell, 1977) fire model. A state variable is used to store the attribute of a new lightning strike or a continued fire presence. If this FIRE_ORIG value is non-zero, then the fire spread rate across the horizontal area of the system (m•d^{-1}) is described by:

$$fire\_spread\_rate =$$
$$\frac{fuel\_heat\_content \bullet fuel\_loading \bullet fire\_rx\_veloc \bullet fuel\_moist \bullet fuel\_ash\_free}{fuel\_bulk\_dens \bullet fire\_heat\_for\_ignit} \; , \tag{34}$$

where *fuel_heat_content* is the potential heat content of the fuel type (kcal•g^{-1}), *fuel_loading* is the biomass of available fuel (g•m^2), *fire_rx_veloc* is the consumption rate of the fire (d^{-1}), *fuel_moist* is a dimensionless function of the moisture of the fuel, *fuel_ash_free* is the dimensionless proportion of the fuel that is organic material, *fuel_bulk_dens* is the effective bulk density of the fuel (kg•m^{-3}), and *fire_heat_for_ignit* is the threshold heat required to ignite the given fuel (kcal•g^{-1}).

Vegetation height and root depth modify the bulk density, with the effective bulk density being equal to the biomass of the fuel divided by the mean height and depth of the vegetation; higher densities slow down the spreading rate of fire. The algorithm for determining the moisture conditions includes current rainfall, soil moisture, and surface ponding; moisture can either prevent fire ignition, modify the rate of fire spread, or extinguish a present fire.

Model Dynamics

We are in the process of parameterizing and calibrating the GEM for a range of ecosystem types in regions in Maryland and Florida, US. Prior to, and during this process

we have been testing its submodels and determining which parameters should be most closely scrutinized. The basic sensitivity analyses that we present are a representative subset of those model analyses for the Florida Everglades.

These simulations were parameterized to represent two ecosystem types from the Everglades/Big Cypress region. The fresh marsh system is dominated by sawgrass (*Cladium jamaicense*), a perennial sedge that historically covered on the order of 70% of the Everglades (Loveless, 1959). Sawgrass does well in an oligotrophic environment with variable surface water depths that are characteristic of much of the Everglades (Steward and Ornes, 1975; Herndon et al., 1991). However, phosphorus appears to be a limiting nutrient for these marsh communities, and cattail (*Typha sp.*) is replacing sawgrass in some areas that are undergoing apparent eutrophication (Davis, 1991; Davis, 1994) . The relative nutrient requirements of these plants may be a factor in determining their relative proportions in the marsh ecosystem. In the first set of sensitivity examples we compared the model response to variations in plant nutrient requirements..

The second major ecosystem type considered in these simulation examples is that of a forested ecosystem dominated by cypress (*Taxodinum sp.*). Various forms of cypress communities exist in areas with hydroperiods (time of inundation) around 0.25-0.75 year, and plant production may decrease by an order of magnitude if the soil is drained (Carter et al., 1973). Both the marsh and the forest ecosystem types may exist in proximity to each other depending on a variety of controls due to hydroperiod, fire and other environmental attributes (Duever et al., 1986). In the second set of sensitivity analysis examples, differences in canopy morphology and their link to biological and physical controls on transpiration were compared between model ecosystems.

Although both are wetland systems, we used them to indicate the ability of the GEM to simulate ecosystems with variable water tables whose range may include the lower water tables characteristic of upland communities. The full set of sensitivity analyses and calibration for a large number of systems is beyond the scope of this paper, and will be the topic of future manuscripts. Our objective here was to indicate the range of dynamics of the model and its response to specific parameter changes. These simulations were not designed to incorporate finely calibrated responses, but rather to demonstrate the modeled system behaviors.
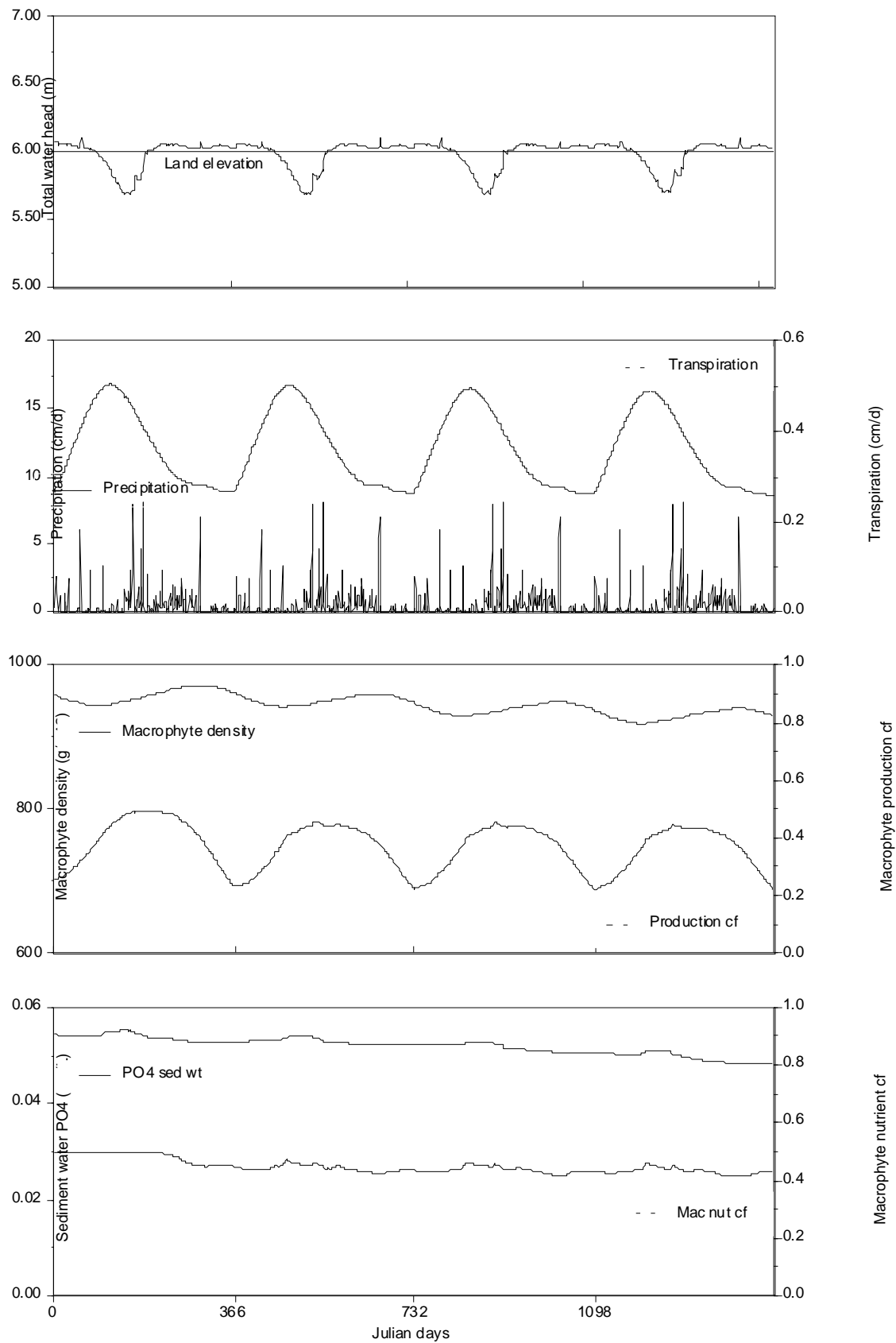
Figure 7.   A 4 yr run of GEM in a fresh marsh habitat, with selected hydrologic, macrophyte, and nutrient dynamics. The top graph shows the total water head relative to a constant (6 m) land elevation. The next graph contains (repeated, one-year) daily rainfall input and simulated transpiration. The third graph shows changes in macrophyte biomass density and the overall production control function (0-1 multiplier). The bottom panel shows the concentration of PO4 dissolved in the sediment water and the resulting control function that is part of the macrophyte production control.

All simulation runs were based on daily rate parameters using a 0.5 d time step. One (repeating) year of rainfall, humidity and temperature data was used to drive the model. Figure 7 shows some of the results from a four year run for a marsh habitat. The total water (Hydrology Sector) head dropped below the land elevation in the spring dry period, then increased to flooded conditions through the rest of each year in response to precipitation and varying amounts of transpiration (and runoff, etc.). Seasonal changes in macrophyte biomass density were small, but showed a slight interannual decrease in response to changing nutrient levels during the period of this example.

Nutrient limitation

As described above, macrophytes are controlled by several functions, one of which is that involving plant nutrient requirements. Laboratory experiments indicated that cattails appeared to take up PO_4 at a faster rate than sawgrass, with a lower saturation coefficient for maximum uptake rate (Reddy, *pers. comm.*). Cattails appear to have better competitive ability than sawgrass under enriched nutrient conditions (Davis, 1994), and may have higher transpiration rates (Koch and Rawlik, 1993).   Under different ambient nutrient concentrations, the varying plant growth response may alter the biomass of plants in a mixed sawgrass/cattail marsh, with associated changes in the water losses via transpiration and overland flow. For this first model exercise, we varied the Michaelis Menton half-saturation coefficients (K_S) near the appropriate ranges reported for these plant species. In addition, we modified the coefficient significantly above and below the experimental values in order to explore the extremes that would mimic a) relatively low ambient nutrients and high plant requirements, limiting growth, and b) relatively high ambient nutrient concentrations with low plant requirements.

Four runs were made using half-saturation coefficients for the Michaelis Menten kinetics of nutrient limitation on net production (K_S = 0.001, 0.045, 0.055, and 0.5 mg $PO_4 \cdot l^{-1}$). The nutrient concentration in incoming surface water was set equal to that currently in the system cell. There were no other changes in input or parameters for the simulations, whose results are summarized in Figure 8. At the lowest K_S value (0.001 mg/l), nutrients had some constraint on the growth away from its maximum rate, indicated by the curve of the production control function which includes controls from
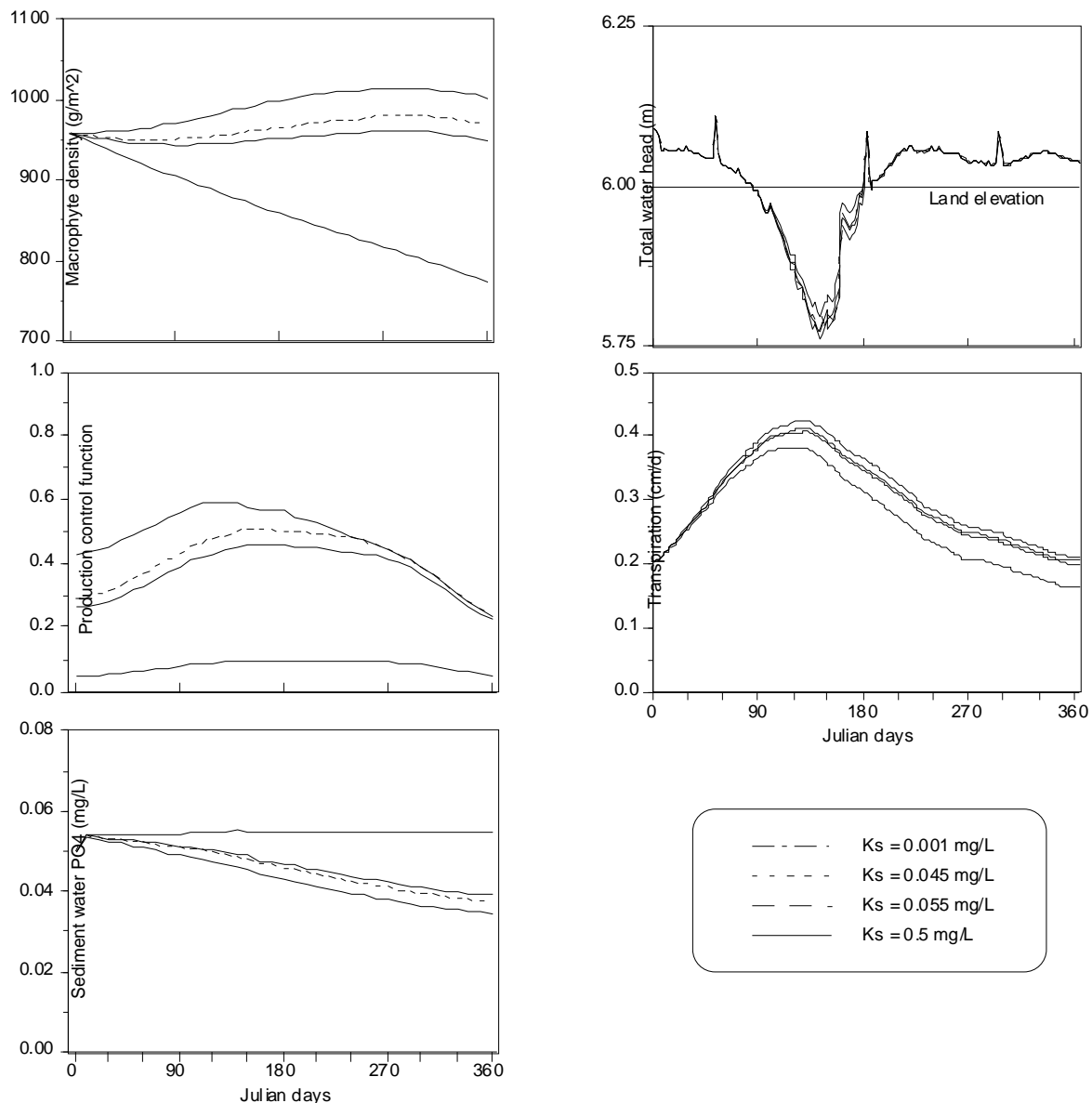
Figure 8. A series of one year model runs showing the sensitivity of hydrologic, macrophyte and nutrient variables to changes in the half-saturation coefficients of PO4 for the Michaelis Menten uptake kinetics. Values close to 0.05 mg/L are in the range appropriate for the natural system. Higher and lower values show the model behavior to extreme nutrient limitation and low levels of limitation.

temperature, light, water and nutrients. Macrophyte biomass increased during the year-long simulation, with nutrients lowering in concentration due to the relative uptake and mineralization imbalance. After significantly increasing the plant requirements to a K_S value of 0.045 mg/l, the macrophyte production was more limited than the prior run for most of the year. Macrophyte biomass was less than that of the first run, and nutrient concentrations concomitantly decreased to a lesser extent. Very little change was observed

in the water levels in the cell between runs, but transpiration losses were very slightly decreased with lowered plant biomass. An approximately 20% further increase in the K_S value (to 0.055 mg/l) resulted in a further observable decrease in plant biomass, but large differences were not apparent in the production control function, biomass, or nutrient concentrations between the two runs (using K_S values that are near those for the marsh community). Using a high K_S value of 0.5 mg/l, plant production was severely limited by nutrient levels, and plant biomass dropped rapidly, with nutrient levels remaining approximately level. Total water levels were higher during the dry season, with a significant decrease in transpiration losses.

Transpiration

Evaporation and transpiration are known to be critical "loss" components within the hydrologic cycle, particularly in areas such as wetlands where water is generally stored at or near the land surface (Duever, 1988; Ewel and Smith, 1992). Evaporation occurs from water in contact with the atmosphere, whereas transpiration is the similar process of evaporation from plant tissues. While there is a critical difference in that the latter evaporative flux can be controlled by plant physiology, the fluxes are often combined into one term, evapotranspiration (ET), for ease of measuring or modeling. Depending on the scale of measurement, researchers have come to widely varying views on what controls the transpiration part of this flux. As summarized by Jarvis and McNaughton (Jarvis and McNaughton, 1986) , meteorologists concerned with large scale fluxes of water (over hundreds to thousands of meters distance) emphasize the evaporative energy and thus the heat and radiative flux involved, whereas the stomata of plants may control transpiration at some level in response to differences in its internal and external environments. At the moment, a single "best" approach does not exist, and we agree with Jarvis and McNaughton's (Jarvis and McNaughton, 1986) suggestion that quantifying the controls on transpiration depends on the scale with which one is addressing the objectives.

We analyzed the total atmospheric water loss for a GEM parameterized for a cypress- dominated community and for a sawgrass dominated freshwater marsh. The sensitivity exercise indicates the range of relative losses in the two different canopy types with changes in transpiration- related parameters which include the decoupling factor related to canopy morphology and the maximum rate of canopy conductance. For simplification, we parameterized the model to represent situations where the maximum Leaf Area Indices (LAI) and other pertinent parameters were equivalent among the two communities (such as a may be the situation in sparse cypress scrub habitat). Thus, the transpiration sensitivity analyses only incorporate differences as a result of the identified parameter changes.

With the canopy conductance held at a reference rate of 0.1 mol•m^{-2}•sec^{-1}, varying
the decoupling factor (Hydrology Sector) from that characteristic of a marsh (0.2) to an
intermediate (0.5) value resulted in a decreased transpiration loss in the colder months, and
similar losses during the dry season when the water table dropped near or below the root
zone (Figure 9). This lowered water availability decreased the plant production control
function, a growth constraint that decreased plant biomass during that

Figure 9. A series of one year model runs showing the sensitivity of hydrologic and
macrophyte variables to changes in the parameter representing the degree of decoupling of
the canopy from the atmospheric saturation deficit. A decouple factor (range=0-1) of 0.2
is typical of a forested canopy, whereas 0.8 is representative of a grassland type canopy.

simulation run compared to the prior run. A further increase in the decoupling factor to that
approximating a forested canopy further reduced the transpiration losses in this particular
analysis, resulting in a water table that did not reach much below the (0.3 m) root depth and
no negative influence on the plant growth. In all three runs, transpiration was linked to the
saturation deficit and could be potentially the same for the different canopy decoupling
factors (such as shown for the fall period). However, differences in canopy morphology

altered the extent to which transpiration was controlled by plant water stress and canopy conductance, significantly modifying the transpiration water losses in the GEM.

DISCUSSION

The GEM was used to model ecosystem level dynamics for different ecosystems. The simulation examples indicated the linkages and feedbacks among the biotic and abiotic components of the model, which are the more critical features of the model structure. Hydrology, plant production dynamics, and nutrient cycling are the focus of the model, which may operate for a single ecosystem or a cell in a spatial landscape model with distributed ecosystem types. The range of scales and ecosystems for which the model is suitable depends upon the questions being addressed, but this version is being applied to wetland and upland terrestrial sites to evaluate basic system dynamics. The GEM requires a large number (~100) of parameters that may change with ecosystem (habitat) type, and ongoing sensitivity analyses indicate which parameters are most important to quantify for application to particular systems. The biological thresholds built into the model make the model robust to changes in parameter sets and constrain stocks to levels that are realistic, while control functions affect the biological and physical dynamics in accordance with their basic underlying mechanisms.

Using this model formalism, we are implementing the GEM in a range of ecosystems and incorporating refinements where the need is indicated. Changes to the model structure are easily accomplished by duplicating or modifying the different sector modules. For example, explicit trophic dynamics would be incorporated into the model by replicating the Consumer Sector and varying feeding preferences to represent different trophic levels. Phytoplankton may replace algae by making such changes as the depth at which light is considered to control production in its control function, and incorporating fluxes into and out of the system with surface water. Fire disturbances or hydrodynamic control of suspension of sediments may be unimportant to certain model objectives and either made inoperative within the model (by software commands), or the sector modules may be easily deleted altogether. Control functions may be modified for sites that have different control mechanisms from the basic set included in this version. Whereas salinity is currently used only as a tracer for spatial model application, an hypothesis of salinity effects on plant production could be introduced into its control function as needed. Different versions, and new sector modules, may be maintained within the version control software component of this general modeling system.

Comparative research

Two aspects of ecosystem comparison are most readily evaluated using this general model: across ecosystems and across scales. We are using the GEM framework to evaluate our understanding of different ecosystems in the Everglades and other sites. Using field data from different ecosystems in a region, the model can be used as a tool for synthesis and focusing research on the more important processes for each system. Whereas eutrophication appears to be a control in the development of an Everglades sawgrass/cattail system, salinity changes may be more critical to the development of an ecotone between mangrove and marsh communities in south Florida. Using available data, we can evaluate the extent to which these processes are affecting the ecosystems under different scenarios of nutrient inputs or water flows, comparing such processes as the relative transpiration losses in marsh and mangrove communities.

As part of a new Multiscale Experimental Ecosystem Research Center (at the University of Maryland), we are using a GEM to evaluate various aspects of scale- effects on ecosystem behavior. Using experimental ecosystems ranging from microcosm to mesocosms to small watersheds (macrocosms), we can calibrate the GEM at each scale and see how parameters change with scale. This may allow us to develop scaling rules to extrapolate results to the landscape and global scales. The hypotheses to be tested involve the extent to which model algorithms and their parameterization may effectively capture the cross- scale behavior observed in the experimental ecosystems. Whereas many of the components of GEM are derived from calibration and partitioning methods (Rastetter et al., 1992), the experimental outcomes of this exercise is intended to facilitate the use of literature and experimental data in models of varying scales.

Ecosystem dynamics

A model is never completely finished, as its use may indicate where knowledge of the ecosystem is incomplete or the aspects of the model that do not fully characterize the system dynamics. Field, laboratory, and model experiments can be usefully integrated into a comprehensive program of ecosystem ecological research. In order to facilitate such integration, the GEM is a generalized model with an easily perceived, modular format and a graphical "map" of flows of matter and their mathematical controls. Within this modeling environment, the model structure, requirements, assumptions, and flaws-to-be-corrected are readily communicated to the research community. We are using this framework to develop some level of consensus among the research participants on the level of effort needed to study different parts of an ecosystem. In one instance, we are structuring significant components of an Everglades research program (at the South Florida Water Management District) using information outlined by the GEM and its incorporation into a

spatial modeling system. Moreover, because of its designed generality and focus on ease-of-use, the basic structure may be used at a variety of sites. Ultimately, the model may be used to continually develop hypotheses concerning the key variables in the structure and function of the system of study. In this context, a coupled modeling and field/lab research program may provide a better understanding of the ecology of the ecosystem.

Such integration may be one of the greatest strengths of modeling in ecosystem research. Wiegert et al. (Wiegert et al., 1975) initiated a salt marsh ecosystem model that continued to be developed over a decade (Wiegert and Wetzel, 1979; Wiegert, 1986) as different hypotheses were incorporated in modelling experiments and evaluated or further parameterized from new field research. The US National Science Foundation's Long-Term Ecological Research Program (LTER) of the 1980's and 1990's has a commitment to develop long term ecological research in different ecosystems across North America. The LTER sites have a basic set of core research topics (Callahan, 1984) aimed at understanding ecosystem level processes, including: 1) pattern and control of primary production, 2) spatial and temporal distribution of populations selected to represent trophic structure, 3) pattern and control of organic matter accumulation in surface layers and sediments, 4) patterns of inorganic inputs and movements of nutrients through soils, groundwater and surface waters, and 5) patterns and frequency of site disturbances. The GEM incorporates most of these dynamics in its current structure at a scale that may be useful for synthesizing site-specific knowledge, yet general enough to be used for across-site comparisons. The use of general models such as the GEM for a range of applications should be considered an important component of developing a holistic understanding of ecological processes, and their controls, in different ecosystems.

Landscape dynamics

A model (such as the GEM) that assumes homogeneity within set boundaries may be useful if the system boundaries are appropriately chosen for the stated objectives. However, the heterogeneity of large natural systems may significantly alter system dynamics as a result of interactions among the varying classes of objects in the system. Partitioning parameter values in accordance with some attribute class such as habitat or ecosystem reduces the aggregation problems inherent in large scale, lumped parameter models (Rastetter et al., 1992). Thus, spatial models for heterogeneous landscapes hold promise to better understand the interactions of the landscape pattern and associated ecological processes within the landscape components. We have developed a Spatial Modeling Package (SMP), [Costanza, 1991 #34; Maxwell, in press #51] for the development, implementation, and testing of spatially explicit ecosystem models in a distributed computational environment. The landscape is divided into square grid cells of

an appropriate scale, and the GEM (tested for each ecosystem and translated into C source code) is replicated as a unit model within each cell of the landscape. The unit model is differently parameterized for each cell's ecosystem type in the landscape, and a configuration step allows the user to link the unit model with spatial data from a GIS. This generates a dynamic spatial model with fluxes of water and associated dissolved and suspended matter across cells in the landscape. Thus, the landscape mosaic affects the dynamics within the modeled region, and changing ecological processes may alter that landscape pattern via rule-based transition algorithms.

Various versions of the GEM are now being applied using the SMP at three different sites in the United States: Sawmill Creek, Maryland (22 km^2 of a largely urbanized and degraded watershed in inland Maryland), the Patuxent River watershed, Maryland (2400 km^2 of mixed forest and agricultural uplands draining to wetlands and open estuary), and the Everglades/Big Cypress region, Florida (10,000 km^2 of mainly wetland habitats). The combined sites offer the opportunity to test and develop the GEM in sub-tropical and temperate climate zones of open-water, wetland and terrestrial ecosystems.

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TABLE 1

The number of parameters needed for 13 sectors (submodels), classified into seven categories: Stoichiometry (C:N:P of organic matter, e
nutrient requirements, coefficients of nutrient adsorption to sediments, etc.); Rate Parameters (hydraulic conductivity, specific rates of growth
Conditions (initial mass or concentration for each state variable); Physical Structure (related to height of macrophytes, hydraulic roughn
(related to response to temperature, solar radiation, etc.); Other parameters, such as allocation of dead organic material to particular detritus po

	Stoich	NutFlux	RateParm	InitCond	PhysStruct	Environ	Other	Sum
Hydrology			4	3	3			10
Hydrodynamics								0
Macrophytes	6	2	5	2	9	6		30
Algae	3	2	4	1		2		12
Consumer	3		3	1		1	1	9
St_Detritus	3			1		1	2	7
InOrgSeds				1				1
SOM	3			1			2	6
DOM	3		2	1	1	1	3	11
DIN		3		3			1	7
PO4		3		3				6
Salt				2				2
Fire			1				1	2
Sum	21	10	19	19	13	11	10	103