

BIOCOMPLEXITY IN PEATLANDS

Northern peatlands occupy less than 2% of the world's land surface, yet provide 10-15% of global methane emissions, contain 1/3 of the world's soil carbon pool, and are located at latitudes where climate change models predict the greatest changes in temperature and precipitation will occur (Mathews and Fung 1987, Aselmann and Crutzen 1989, Gorham 1991, Bartlett and Harriss 1993, Bridgham et al. 1995). Thus the contributions of peatlands to the global carbon cycle are far out of proportion to their land area. Despite theoretical reasons and empirical data that suggest complex behavior in peatlands (discussed below), current models of carbon accumulation are linear functions of net primary productivity (Clymo 1992, Almquist-Jacobson and Foster 1995) which can only exhibit simple asymptotic behavior.

Northern peatlands exhibit surprisingly complicated spatial patterns and pathways of development (Wright et al. 1992). Large boreal and subarctic peatlands are complex landscapes in which the accumulation of peat is determined by, and in turn controls, the flow patterns of water. Bogs are domed portions of peatlands where peat accumulation has raised the surface above the water table; they receive their water from rain or from higher portions of the raised dome and deliver it to fens in lower topographic positions in the same peatland. *Sphagnum* mosses and ericaceous shrubs dominate the vegetation of bogs, whereas sedges and other graminoids dominate fens. Recent research indicates strong feedbacks between plant community dynamics, fluxes of carbon, nutrients, and energy, soil temperature, and hydrology in peatlands (Bridgham et al. 1995, 1999, Hilbert et al., in press, Weltzin et al., in press).

Such feedbacks may be responsible for the large variability in peatland soil properties that are important to carbon flux, such as bulk density, carbon quality, and nutrient availability. Measurements of these properties range over orders of magnitude among different kinds of peatlands (Bridgham et al. 1998), which is far greater variability than found in many upland systems (Reichle 1981). Despite this, many global carbon models have treated peatlands as homogeneous ecosystems with relatively simple behavior, if they consider them at all.

We propose that northern peatlands are not simple, homogeneous systems but instead exhibit complex behavior both spatially and temporally because of at least two feedbacks that are unique to these ecosystems: (1) Organic matter accumulation is controlled by hydrology, but as thick organic deposits accumulate, they in turn control the hydrology and the resultant biogeochemical environment (Glaser 1992). Recently, Hilbert et al. (in press) showed that coupling organic matter accumulation with water table elevation leads to a cusp-catastrophe in peatland development which corresponds to the sharp boundaries between bog and fen communities often seen in peat profiles. (2) *Sphagnum* mosses dominate productivity in peatlands, especially in bogs, but influence nutrient and carbon fluxes unlike any other vegetation type (Malmer 1993, Bridgham et al. 1996, Chapin 1998, Aerts et al. 1999, Weltzin et al., in press). First, mosses acquire all of their nutrient inputs from the atmosphere or the first several cm of surface peat (Rydin and Clymo 1989). Second, mosses decay at extremely slow rates and have very low nutrient concentrations (Aerts et al. 1999). Thus, mosses act as a strong filter for nutrient fluxes to other plant life forms, and thereby introduce a delay in the flux of nutrients through peatlands. Insofar as the flux of nutrients at least partially limits net primary production (Bridgham et al. 1996, Chapin 1998), such delays can cause complex behaviors in carbon flux and accumulation in peatlands. Recent theoretical work by us (Pastor and Bridgham, unpublished) shows that such delays could also cause bifurcations in plant communities and complex temporal and spatial behaviors similar to those shown by Hilbert et al. (in press) for the organic matter-hydrology coupling.

There is a strong need for a detailed simulation model of the structure and function of peatlands in order to project their response to global change. Because of the unique characteristics of peatlands previously discussed, current terrestrial ecosystem models are inadequate for this purpose. Before constructing such a model, we need to understand more completely how complex peatland behavior and spatial patterns arise from the hydrology-organic matter and plant community-nutrient cycling feedbacks.

We propose to build a theoretical basis for uniting these two sets of feedbacks by fostering collaboration between a group focusing on the organic matter-hydrology feedback (Nigel Roulet, McGill University and Steve Frolking, University of New Hampshire) and a group focusing on the plant community-nutrient cycling feedback (Scott Bridgham, University of Notre Dame, John Pastor, University of Minnesota, Jiquan Chen, Michigan Technological University, and Jake Weltzin, University of

Tennessee). The immediate objective of this work is a mathematically rigorous and ecologically sound elucidation of the theoretical basis of complex behavior in peatlands. The ultimate objective, which would be the focus of a larger follow-up proposal to the Biocomplexity Initiative in two years, is the development, parameterization, and testing of a detailed and accurate simulation model of peatlands that will be used to (1) model their initiation, development, and complex landscape patterns over a time-frame of thousands of years, and (2) project their responses to global warming over the temporal scale of decades.

Sources of Complex Behavior in Peatlands—(1) Organic Matter-Hydrology Feedbacks

Hilbert et al. (in press) present a coupled model of peatland hydrology-organic matter accumulation with interesting complex behaviors. Specifically, the depth to the water table (W) and the thickness of the peat layer (H) affect each other according to the following coupled differential equations:

$$\begin{cases} \frac{dW}{dt} = G - k_1 H - (k_1 + k_2)W + \frac{\epsilon}{\theta(1 + cW)} \\ \frac{dH}{dt} = G - (k_1 - k_2)W - k_2 H \end{cases}$$

and

$$G = g(W - W_{\min})(W_{\max} - W)$$

$$\frac{d\theta}{dt} = P - E - d$$

where k_1 and k_2 are the decay rates in the upper, aerobic layer of peat down to the water table and below the water table, respectively, ϵ is potential evapotranspiration, c controls the rate by which evapotranspiration declines with increasing depth to water table, E is actual evapotranspiration, P is total water input in precipitation and groundwater, d is drainage, and θ is the moisture content of the peat at saturation. G is annual height growth of the peat, which varies quadratically between a minimum (W_{\min}) and maximum (W_{\max}) water table depth and grows at an intrinsic rate g . Thus, the first two terms of the differential equation for water table depth relate to carbon accumulation while the second two terms relate to the water budget. Similarly, the first term of the peat thickness equation relates to carbon inputs (quadratic functions of W) while the second two terms relate to carbon output due to decomposition.

Due to the non-linearity of these equations, there are three sets of equilibria for W and H , two of which are stable separated by a third unstable equilibrium point. These sets of equilibria form a cusp-catastrophe (Fig. 1) with respect to total water input (P). This complex behavior suggests several features of peatland formation in relation

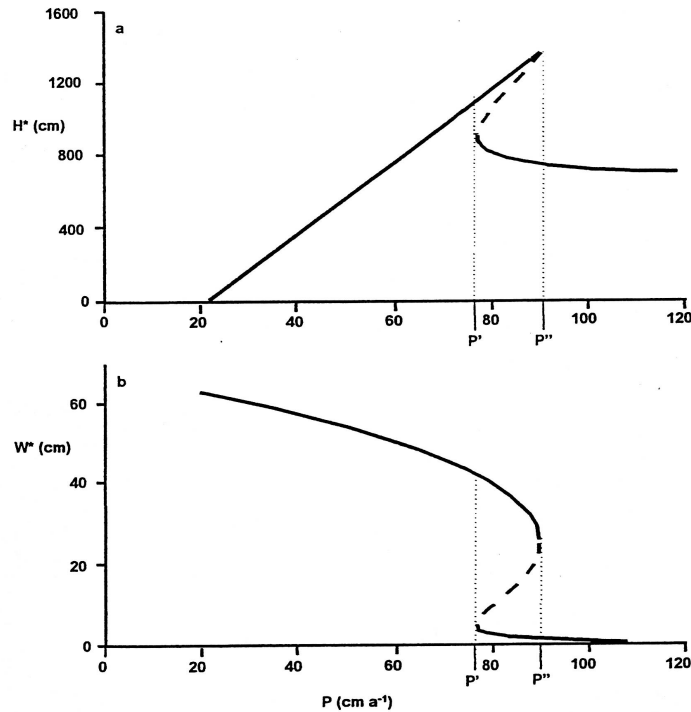


Fig. 1. Change in peat depth (H) and water table depth (W) as a function of total water input (P) during the successional development of a peatland (Hilbert et al. in press).

to carbon and water balance: (1) there is a minimum water input below which peat does not accumulate; (2) as water input increases, peat accumulates and the water table depth is near the surface; (3) at P' , there are two possible stable peatland types, a thinner but wetter peatland or a thicker but drier peatland. Beyond a higher water input (P''), only the thinner, wetter peatland is stable.

These bifurcations in stable equilibria bear a striking resemblance to the two major types of peatland ecosystems, namely fens (thin and wet) and bogs (thicker and drier). Whether or not the model accurately simulates the bifurcation between these two peatland types depends of course on the parameter values, especially on carbon input, G . However, in this model, G is a dynamic function only of water table depth, whereas the intrinsic growth rate of fen and bog communities (g) must be inserted by hand. But we know that bogs and fens differ greatly in productivity (Chapin 1998, Frohling et al. 1998, Weltzin et al., in press). Such differences in productivity are also related to nutrient availability (Bridgham et al. 1996, Chapin 1998), which is in turn a function of the nutrient content and intrinsic decay rate of the litter from the different plant communities (Bridgham et al. 1998). Therefore, the Hilbert et al. model needs to be expanded to include plant community-nutrient cycling feedbacks.

Sources of Complex Behavior in Peatlands—(2) Plant Community-Nutrient Cycling Feedbacks

We (Pastor and Bridgham unpublished) have begun to examine plant community-nutrient cycling feedbacks in bogs using a differential equation model, which for mathematical tractability is the simplest model that we believe captures the essential dynamics causing complex behavior due to the plant community-nutrient feedback in peatlands (Fig. 2). This model consists of moss (M), vascular plants (S), moss litter (ML), vascular plant litter (SL), peat (P), and an inorganic nutrient pool (R). Mosses intercept incoming nutrients from the atmosphere (Q), which provides their entire nutrient requirement, and transfer them to peat through moss litter. The peat decays and releases nutrients into the nutrient pool. Nutrients leave the system from the inorganic nutrient pool at a rate e . Vascular plants take up nutrients (intrinsic uptake rate μ) from R in a Lotka-Volterra manner (i.e., uptake depends on both vascular plant biomass and the size of R) and also return them to peat via vascular plant litter. All transfers to litter or to the nutrient pool through decay are done by simple decay coefficients ($k_1 \dots k_5$). Mosses and vascular plants reduce each other's biomass through competition coefficients (α_{sm} = effect of mosses on vascular plants and α_{ms} = effect of vascular plants on mosses) and Lotka-Volterra mechanisms. Competition is presumably by means of vascular plants shading mosses or by the mosses growing vertically and engulfing the meristemic tissues of the vascular plants. Competition for nutrients is spatially segregated: mosses acquire nutrients solely from the atmosphere, whereas vascular plants acquire nutrients from deeper soil layers. Thus, mosses introduce a strong delay in the transfer of atmospheric nutrient inputs to other members of the plant community. The model is a set of 6 coupled differential equations which are the sums of inputs and outputs for each state variable as shown in Fig. 2.

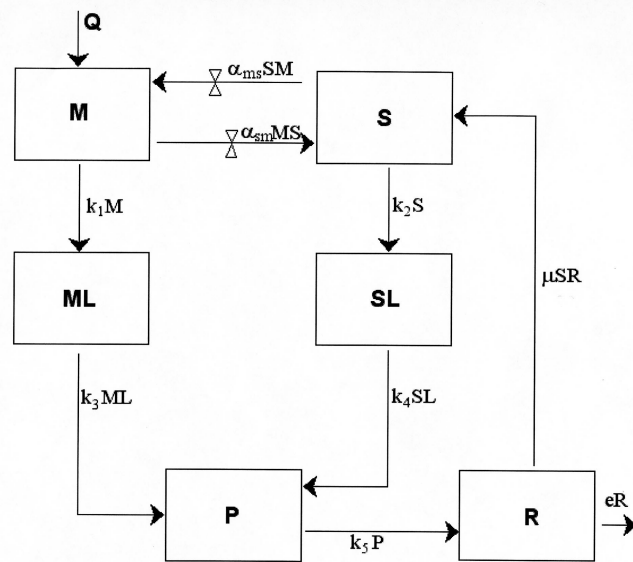


Fig. 2. A model of plant community-nutrient cycling feedbacks in peatlands.

This model has two stable equilibria: (1) a monoculture in which mosses win completely and vascular plants go extinct. The equilibrium sizes of the remaining pools are determined simply by the ratios of inputs to the ecosystem (Q) to the output from each pool. Therefore, this simple linear behavior is not complex. (2) A more complex equilibrium solutions exists where vascular plants and mosses

coexist. The equilibrium size of the inorganic nutrient pool (R) is non-linearly related to the competitive effect of mosses on vascular plants (α_{sm}^2). This suggests that in any competition experiments between mosses and vascular plants, the nutrient pool will respond in a non-linear fashion to the relative ratio of moss to vascular plant biomass.

There are no solutions where vascular plants win and mosses go extinct (although adding in a dynamic water table which responds to soil organic matter accumulation may change this result). Therefore, at equilibrium, a bog could be patches of moss where the time-dependent behavior is simple, interspersed with patches of moss and vascular plants where the time-dependent behavior is complex. In fact, many bogs have this appearance with small patches of pure moss interspersed with patches of both moss and vascular plants.

To examine the model behavior further, we found numerical solutions (Fig. 3) for the time-dependent trajectories of bog development given parameter values for the transfer coefficients from the literature (Updegraff et al. 1995, Hobbie 1996, Bridgman et al. 1998). Note the complex behavior of moss and vascular plant biomass and the inorganic nutrient pool. These follow directly from the second equilibrium solution. Apparently, the size of the inorganic nutrient pool (an ecosystem property) depends in a complex and non-linear way on the competition between moss and vascular plants (community properties).

Interestingly, the model also predicts that early dominance by mosses should eventually succeed to later dominance by vascular plants, although the mosses do not go locally extinct. Thus, succession is a natural dynamic of the model; the paleorecord shows dominance by *Sphagnum* mosses often precedes dominance by ericaceous shrubs during bog development (Janssen 1992, Janssens 1992). Thus, given reasonable experimentally determined parameter values, the model suggests that mosses and shrubs can coexist, with mosses dominating before shrubs.

To extend this model further, we need to make water table depth a function of carbon accumulation in peat, and then relate competition between plants and nutrient mineralization to water table depth. The Hilbert et al. model provides this linkage. Conversely, the Pastor-Bridgman approach provides dynamically variable growth and decay rates as functions of the plant community composition, which must be specified in the Hilbert et al. approach. To do this in a realistic and dynamic manner, it is clear that the Pastor-Bridgman model must be coupled with the Hilbert et al. model.

Workplan

We propose to use these two models as starting points for developing and analyzing a theoretically sound model of multiple feedbacks in peatland complexes. To begin, the peat layer in the Pastor-Bridgman model must be divided into two layers, one above and the other below the water table to correspond to the two layers in the Hilbert et al. model. Second, the inorganic nutrient pool must also be divided into two layers, each receiving inputs from the corresponding peat layer. Vascular plants will take up nutrients from both layers; we will also allow mosses to take up nutrients from the uppermost (aerobic) layer above the water table. Evapotranspiration will be a function of moss and vascular plant biomass and water table level. We have previously shown that evapotranspiration is a complex function of plant community, water table level, and temperature (Bridgman et al. 1999).

These revisions of the Pastor-Bridgman model will enable us to couple it with the Hilbert et al.

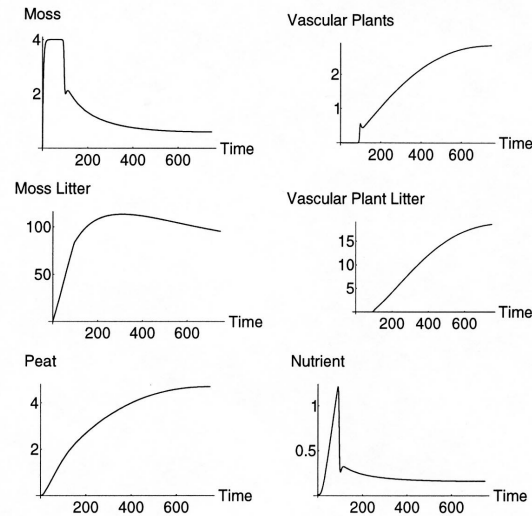


Fig. 3. Trajectory over approximately 800 years from the model of plant community-nutrient feedbacks in Figure 2.

model in two ways: (1) the intrinsic growth rate of vegetation in the Hilbert et al. model (g) will now be a function of species composition and nutrient feedbacks as well as water table; (2) evapotranspiration in the Hilbert et al. model will be a dynamic function of plant biomass. Once these two models are coupled, then the contributions of precipitation and groundwater (which now are combined in the Hilbert et al. model) will change in a natural way during peatland development. This in turn will feedback and alter competitive relations between mosses and vascular plants.

Tractable, analytical solutions of such a complex model may be difficult to find. If so, we can simplify the model further. For example, we could remove the moss and vascular plant litter state variables and add moss and vascular plant litter directly to the peat pools, adjusting transfer coefficients to reflect both litterfall and decay rates. Recent work by Frolking et al. (submitted) indicate that it may be possible to represent the litter/peat continuum as a single decomposing carbon pool with a linearly decreasing rate of decomposition. The stability of the equilibrium solutions will then be determined by examining the eigenvalues of the Jacobian matrix. We expect multiple equilibria, some of which are stable, and some of which most likely have complex eigenvalues with negative real parts. The sensitivity of each of the state variables to uncertainty in parameter values will be determined by the partial derivatives.

If tractable, analytical solutions cannot be found, then we will add numerical values for the parameters from the literature as above or from our own experiments (Frolking et al. 1996, Bridgman et al. 1999, Updegraff et al., in press, Weltzin et al., in press), and find numerical solutions. These will be analyzed for cusp-catastrophe behavior as above as well as other forms of complex behavior (i.e., oscillating solutions). Sensitivity analyses with respect to parameter values will be determined by varying pairs of parameter values simultaneously, calculating the numerical solutions at equilibrium, and examining the response surfaces of the state variables of interest.

We will hire a postdoctoral associate to work with the two modeling groups to develop an integrated approach that incorporates feedbacks between plant community composition, nutrients, carbon accumulation, and hydrology. Additionally, we will hold two meetings where all members of the research groups will work to develop an integrated model of peatlands. These meetings are essential for the free exchange of ideas, the melding of the two research groups into a coherent team, and for planning the experiments and theoretical work that will be part of our full Biocomplexity proposal in two years. Thus, construction and analysis of this model will provide the focus for building a collaboration between our two research groups.

These exercises will be of great interest in themselves and will lead to new insights into biocomplexity in peatlands, but by the end of the second year we will have developed at least the outlines of a comprehensive simulation model of peatlands that will yield accurate predictions of their initiation, development, and landscape characteristics and their response to climate change. For example, we already have outlined an extended version of the Pastor-Bridgman model (Fig. 2) that incorporates additional peat layers, woody litter, and additional vascular plant life forms. We plan to add components that include biophysical feedbacks (e.g., temperature and energy flux) and methane flux. Our previous research has indicate complex behaviors of both biophysical variables and methane flux to plant community composition and productivity, hydrology, nutrient fluxes, and carbon quality (Bridgman et al. 1998, 1999, Updegraff et al. 1998, in press). S. Frolking has previously published a model of methane fluxes that can be incorporated into our larger ecosystem simulation model (Frolking and Crill 1994). The final development and experiments to parameterize and test the comprehensive simulation model will be the topic of a larger proposal to be submitted to the Biocomplexity Special Competition in two years. We have a wealth of experimental data from which to begin, and we plan to test the working version of our model against a variety of ongoing experiments which manipulate climate, nutrient availability, and pH in peatlands (Bridgman et al. 1998, 1999, Chapin 1998, Updegraff et al., in press, Weltzin et al., in press). Furthermore, we will see if the model can at least qualitatively reproduce the landscape patterns of the well-studied Red Lake Peatland Complex of northwestern Minnesota (Heinselman 1970, Wright et al. 1992, Glaser et al. 1996, 1997). Another important benefit of the proposed model is that it has the potential to link two relatively temporally disparate sets of measurements: (1) long-term peat accumulation (peat cores, palynology, radiocarbon dating) and (2) contemporary carbon fluxes (net primary production, flow-through chambers, eddy-flux towers).