

Plant Community Dynamics, Nutrient Cycling, and Alternative Stable Equilibria in Peatlands

John Pastor,^{1,*} Bruce Peckham,^{2,†} Scott Bridgham,^{3,‡} Jake Weltzin,^{4,§} and Jiquan Chen^{5,||}

1. Department of Biology and Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota 55812;

2. Department of Mathematics and Statistics, University of Minnesota, Duluth, Minnesota 55812;

3. Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556;

4. Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996;

5. Department of Earth, Ecological, and Environmental Sciences, University of Toledo, Toledo, Ohio 43606-3390

Submitted February 26, 2001; Accepted May 15, 2002

ABSTRACT: Although observational data and experiments suggest that carbon flux and storage in peatlands are controlled by hydrology and/or nutrient availability, we lack a rigorous theory to account for the roles that different plant species or life-forms, particularly mosses, play in carbon and nutrient flux and storage and how they interact with different hydrologic sources of nutrients. We construct and analyze a model of peatlands that sheds some light on this problem. The model is a set of six coupled differential equations that define the flow of nutrients from moss and vascular plants to their litters, then to peat, and finally to an inorganic nutrient resource pool. We first analyze a simple version of this model (model 1) in which all nutrient input is from precipitation and enters the moss compartment directly, mimicking the dynamics of ombrotrophic bogs. There is a transcritical bifurcation that results in a switch of stability between two equilibrium bog communities: a moss monoculture and a community where mosses and vascular plants coexist. The bifurcation depends on the magnitudes of the input/output budget of the peatland and the life-history traits of the plants. We generalize model 1 to model 2 by dividing nutrient inputs between precipitation and groundwater, thus also allowing the development of minerotrophic fens that receive nutrient subsidies from both groundwater and precipitation and adding intraspecific competition (self-limitation)

terms for both moss and vascular plants. Partitioning precipitation inputs between moss and the nutrient pool resulted in the greatest changes in model behavior, including the appearance of a lake and a vascular plant monoculture as well as the moss monoculture and coexistence equilibrium. As with model 1, these solutions are separated by transcritical bifurcations depending on critical combinations of parameters determining the input-output budget of the peatland as well as the life-history characteristics of the plant species. Model 2 also allowed for an early transient spike in vascular plant dominance followed by approach to near moss monoculture and then eventual approach to coexistence equilibrium. This generalized model mimics the broad features of successional development of peatlands from fens to bogs often found in the paleorecords of peat cores.

Keywords: alternative stable equilibria, nutrients, peatlands, transcritical bifurcation.

Northern peatlands occupy less than 2% of the world's land surface (Post et al. 1982; Bridgham et al. 2001) yet contain one-third of the world's soil carbon and nitrogen pools (Post et al. 1982, 1985; Gorham 1991) and provide 6%–9% of global methane emissions (Mathews and Fung 1987; Aselmann and Crutzen 1989; Bartlett and Harriss 1993). Thus, the contributions of peatlands to the global carbon and nitrogen cycles are far out of proportion to their land areas. An understanding of the processes that control carbon flux and storage in peatlands is crucial because peatlands are located in the latitudes expected to experience the greatest changes in temperature and precipitation within the next 2–5 decades (Houghton et al. 1995) and because they may switch from being net sink for atmospheric carbon dioxide to net sources (Gorham 1991; Bridgham et al. 1995).

Recent research suggests that the accumulation of carbon in peat, the flow of nutrients and water, and the fluxes of temperature and energy depend to a large degree on how these material and energy fluxes interact with the plant community (Updegraff et al. 1995, 2001; Bridgham et al. 1996, 1999; Aerts et al. 1999; Bedford et al. 1999; Hilbert et al. 2000; Weltzin et al. 2000, 2001). Broadly speaking, two different communities (bogs and fens) can be found in peatlands; these in turn appear to be related

* E-mail: jpastor@nrri.umn.edu.

† E-mail: bpeckham@d.umn.edu.

‡ E-mail: scott.d.bridgham.1@nd.edu.

§ E-mail: jweltzin@utk.edu.

|| E-mail: jiquan.chen@utoledo.edu.

to hydrologic sources of nutrient inputs (Wright et al. 1992). In bogs, peat accumulation has raised the local water table above the regional water table; bogs, therefore, receive their exogenous nutrient inputs solely from precipitation. Fens are in lower topographic positions or on the margins of peatlands and are not isolated from the regional groundwater table; they receive nutrient inputs from both precipitation and groundwater. *Sphagnum* mosses, ericaceous shrubs, and black spruce (*Picea mariana*) dominate the vegetation of bogs, while sedges and other graminoids dominate fens.

Previous theoretical treatments of peatlands have focused solely on carbon stores and fluxes and have assumed linear (first-order) kinetics of peat decay (e.g., Clymo 1992; Almquist-Jacobson and Foster 1995; Wieder 2001) or simple input-output budgets of the entire peatland (Rivers et al. 1998). In such an approach, production of litter is assumed to be a constant input to the peat profile. Competition between plant species and feedbacks between producers and decomposers are absent in these models. Furthermore, these models do not consider the cycling of limiting nutrients and how they affect carbon stores and community composition of peatlands.

While such simple approaches are necessary and valuable first steps, they are limited in their ability to capture the richness of behavior of peatland ecosystems. In particular, they do not capture complex transient dynamics such as succession from one species to another or the long-term transition from fen to bog communities (Glaser 1992; Janssens et al. 1992; Wright et al. 1992). They also do not show how different species affect productivity and the cycling of nutrients in peatlands (Bridgham et al. 1995, 1998; Weltzin et al. 2000, 2001).

Of these two types of peatland plant communities, bogs are most unlike any other ecosystem and, therefore, most problematic theoretically. First, all exogenous nutrient inputs to bogs are through precipitation rather than through a combination of precipitation with ground and surface waters. Second, *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; Aerts et al. 1999). Mosses take up the bulk of their nutrients from atmospheric input rather than from nutrient pools lower in the peat profile (Urban et al. 1988; C. Kellogg and S. Bridgham, unpublished data). Mosses also 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 bogs. Insofar as the flux of nutrients at least partially limits net primary production (Bridgham et al. 1996; Chapin 1998; Bedford et al. 1999),

such delays can strongly affect carbon flux and accumulation in peatlands.

To understand why a peatland is a bog or a fen and (if it is a bog) under what conditions mosses coexist with vascular plants, we need to understand more completely the theoretical underpinnings of the relationships between the plant community and the cycling of limiting nutrients. To address these problems, we present two simple models of nutrient flow through a peatland made up of mosses and vascular plants.

We begin by analyzing model 1 for a bog, in which all exogenous nutrient inputs are taken up by mosses and enter the inorganic nutrient pool only after being processed through live moss, moss litter, and peat. We begin with a bog model for two reasons: since bogs are unique among ecosystems, a theory of peatlands must account for their existence and properties, and since there is only one nutrient input (precipitation), the mathematics are simpler than if there are two inputs (precipitation and groundwater). This bog model has some relatively tractable analytical solutions for equilibria that shed some light on the relationship of plant life-history traits and community dynamics to the input-output budget of the bog. In particular, we will show that there are two equilibria and that the stabilities of each equilibrium community depend on the nutrient input and export rates and various life-history traits of mosses and vascular plants.

Model 1 requires three simplifying assumptions to achieve tractable analytical equilibrium solutions: first, there is no self-limitation of the mosses or vascular plants, and their compartment sizes are entirely determined by their input-output budgets; second, there is no nutrient input from groundwater; and, finally, mosses capture all nutrient inputs before they enter the inorganic resource pool. We generalize to model 2 by relaxing these assumptions to include self-limitation terms, add groundwater inputs, and partition precipitation inputs between moss and inorganic nutrient pools. This generalized model therefore includes fens as well as bogs along gradients of hydrologic sources of nutrient inputs.

Model 1: Plant Community Nutrient Cycling Feedbacks in Bogs

We begin by examining plant community nutrient cycling feedbacks in bogs using a simple differential equation model (fig. 1) that consists of six state variables or compartments: moss (M), vascular plants (V), moss litter (L_M), vascular plant litter (L_V), peat (P), and an inorganic nutrient resource pool (R). All units of each state variable are as mass of nutrient. Although mosses and vascular plants are “functional groups” of taxonomic species, for

simplicity we will refer to them as “species” in a generic rather than a taxonomic sense.

The model is a set of six coupled differential equations that are the sums of inputs and outputs for each state variable as shown in figure 1:

$$\begin{aligned}
 \frac{dM}{dt} &= Q - k_1M - \alpha_{MV}VM, \\
 \frac{dV}{dt} &= \mu VR - k_2V - \alpha_{VM}VM, \\
 \frac{dL_M}{dt} &= k_1M - k_3L_M, \\
 \frac{dL_V}{dt} &= k_2V - k_4L_V, \\
 \frac{dP}{dt} &= k_3L_M + k_4L_V - k_5P, \\
 \frac{dR}{dt} &= k_5P - \mu VR - eR.
 \end{aligned} \tag{1}$$

The mass balance of inputs and outputs on each state variable are determined by the following assumptions. Mosses, whose growth is often limited by incoming nitrogen and phosphorus (Austin and Wieder 1987; Bayley et al. 1987; Aerts et al. 1992), effectively absorb all incoming nutrients (Urban et al. 1988) from precipitation (Q) and transfer them to peat through moss litter. In contrast to mosses, the growth of the vascular plant nutrient pool is partly limited by the size of the vascular plant nutrient capital itself (V), by an intrinsic uptake rate μ (uptake per unit R and per unit V), and also by R , which reflects a nearly ubiquitous nutrient limitation to vascular plant growth in peatlands and heathlands (Aerts and Heil 1993; Bridgham et al. 1995; Bedford et al. 1999; Aerts and Chapin 2000). Live moss and vascular plant nutrient capitals are transferred to litter at specific rates k_1 and k_2 , respectively. Litter decays at rates intrinsic to each species (k_3 and k_4 for moss and vascular plant litters, respectively) and eventually becomes peat. We assume that nutrients are conserved in the litter during this period to satisfy microbial demands during initial stages of decay. The peat, in turn, decays and releases nutrients into the inorganic nutrient pool at rate k_5 . Nutrients leave the system from the inorganic nutrient pool at a proportional rate e .

Because mosses and vascular plants do not draw nutrients from a common pool, they do not directly compete for nutrients (although mosses delay the availability of incoming nutrients to vascular plants). However, mosses and vascular plants reduce the growth of each other’s nutrient capital in a Lotka-Volterra manner through com-

petition coefficients (α_{VM} = effect of mosses on vascular plants and α_{MV} = effect of vascular plants on mosses). These competition coefficients reduce nutrient uptake rates through a variety of other limiting processes, most likely the shading of mosses by vascular plants or the engulfing of meristemic tissues of vascular plants by vertical growth of the moss carpet (Crum 1992), but also possibly by interspecific effects such as differential susceptibility to herbivores, pathogens, or fire and other unspecified processes. When uptake rates by mosses and vascular plants are reduced by interspecific competition, the nutrients that would otherwise be incorporated into these pools are not retained in the ecosystem. Reduction in uptake rates through interspecific competition, therefore, represents implicit exports of nutrients from the ecosystem, analogous to the export term eR from R .

In order to achieve analytical solutions that are not unwieldy, we had to make several simplifying assumptions to the model: we do not add self-limitation or carrying capacity terms to either mosses or vascular plants; all incoming nutrients are absorbed first by moss before being

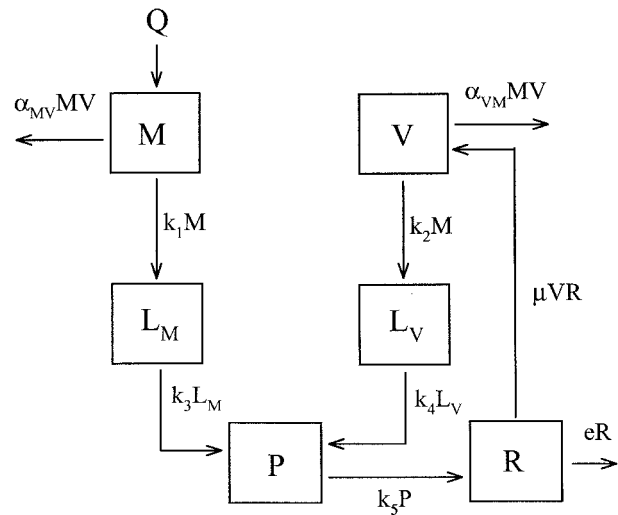


Figure 1: Compartments and flows of nutrients in a bog model (eqq. [1]). M is live moss; V is live vascular plant; L_M and L_V are moss and vascular plant litters, respectively; P is peat; R is inorganic nutrient pool; Q is nutrient input; k_1, \dots, k_5 are linear transfers between compartments; e is a fractional loss rate through leaching or, in the case of nitrogen, gaseous losses via denitrification; μ is the instantaneous uptake rate of inorganic nutrients by vascular plants; and α_{VM} and α_{MV} are Lotka-Volterra competition coefficients that determine how moss and vascular plants reduce the growth of each other’s nutrient capital through interference competition for other resources (e.g., shading of mosses by vascular plants and engulfing of vascular plant meristems by upward growth of the moss carpet).

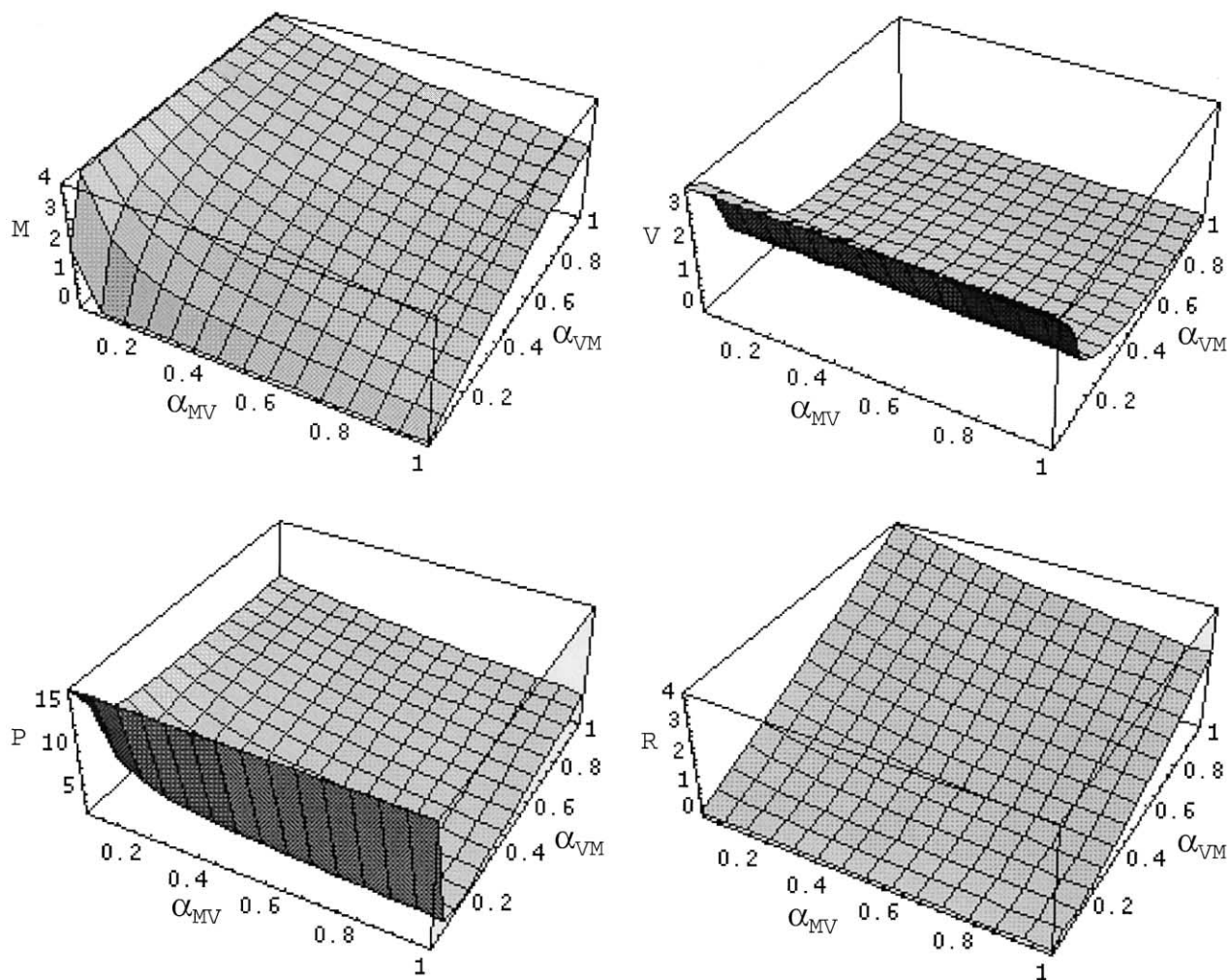


Figure 2: Sensitivity of coexistence equilibrium values of selected state variables to competition coefficients α_{VM} and α_{MV} (eqq. [3]). Symbols as in figure 1. Parameter values are $k_1 = 0.25$ and $k_2 = 0.1$ (Eckstein and Karlsson 1997); $k_3 = 0.002$ and $k_4 = 0.015$ (Hobbie 1996); $k_5 = 0.1$ (Updegraff et al. 1995; Bridgham et al. 1998). We set $\mu = 1.0$ to reflect rapid uptake of nutrients by vascular plants from R (Aerts and Chapin 2000). These parameter values were kept the same for figures 2 through 6. For this figure, we also set $e = 0.1$ (J. Pastor, B. Dewey, and S. Bridgham, unpublished data from the experiment described by Bridgham et al. 1999; Weltzin et al. 2000) and $Q = 1.0$.

passed through litter and peat to the inorganic resource pool that is available to vascular plants; and there are no groundwater inputs to the inorganic nutrient pool.

As we will later show, adding self-limitation terms to these pools does not qualitatively change our conclusions about the existence of alternative monoculture or coexistence stable states. Having mosses absorb all incoming nutrients from precipitation is a reasonable first approximation in a bog (Urban et al. 1988), where precipitation is the sole source of incoming nutrients, because the height of the peat surface effectively decouples the rooting zone from groundwater inputs (Glaser 1992). We will relax each of these assumptions later, in model 2. Although model 1

lacks much realistic detail, we believe it is the simplest possible model that captures the essential features of nutrient flow through bog ecosystems.

Equilibrium Solutions

The model has two sets of equilibrium solutions that are obtained by setting all the right-hand sides of equations (1) to 0 and solving simultaneously for each compartment. The first set is a monoculture of mosses without vascular plants:

$$\begin{aligned}
M^* &= \frac{Q}{k_1}, L_M^* = \frac{Q}{k_3}, V^* = 0, L_V^* = 0, \\
P^* &= \frac{Q}{k_5}, R^* = \frac{Q}{e}.
\end{aligned} \tag{2}$$

In this set of equilibria, the sizes of the nonzero pools are simply the ratios of inputs to the ecosystem (Q) to the output from each pool. There is also a more complex set of equilibria in which vascular plants and mosses coexist:

$$\begin{aligned}
M^* &= \frac{\alpha_{MV}ek_2 + \alpha_{VM}Q\mu}{(\alpha_{MV} + \alpha_{VM})k_1\mu - \alpha_{MV}\alpha_{VM}e}, \\
L_M^* &= \frac{k_1(\alpha_{MV}ek_2 + \alpha_{VM}Q\mu)}{k_3[(\alpha_{MV} + \alpha_{VM})k_1\mu - \alpha_{MV}\alpha_{VM}e]} = \frac{k_1}{k_3}M^*, \\
V^* &= \frac{(k_1\mu - \alpha_{VM}e)Q - ek_1k_2}{\alpha_{MV}ek_2 + \alpha_{VM}Q\mu}, \\
L_V^* &= \frac{k_2[(k_1\mu - \alpha_{VM}e)Q - ek_1k_2]}{k_4(\alpha_{MV}ek_2 + \alpha_{VM}Q\mu)} = \frac{k_2}{k_4}V^*, \\
P^* &= \left\{ \frac{k_1(\alpha_{MV}ek_2 + \alpha_{VM}Q\mu)}{(\alpha_{MV} + \alpha_{VM})k_1\mu - \alpha_{MV}\alpha_{VM}e} \right. \\
&\quad \left. + \frac{k_2[(k_1\mu - \alpha_{VM}e)Q - ek_1k_2]}{\alpha_{MV}ek_2 + \alpha_{VM}Q\mu} \right\} / k_5 \\
&= \frac{k_3L_M^* + k_4L_V^*}{k_5}, \\
R^* &= \frac{(\alpha_{VM} + \alpha_{MV})k_1k_2 + \alpha_{VM}^2Q}{(\alpha_{MV} + \alpha_{VM})k_1\mu - \alpha_{MV}\alpha_{VM}e}.
\end{aligned} \tag{3}$$

The moss monoculture is not unlike the extensive areas of *Sphagnum* lawns observed in many bogs (Crum 1992; Wright et al. 1992), and patches of mosses coexisting with vascular plants are also observed in many bogs (Crum 1992; Wright et al. 1992).

Dependence of Coexistence Equilibrium Values on Parameters

At first glance the set of coexistence equilibrium solutions may appear daunting. However, they contain many common terms that suggest some interesting correlations, both positive and negative, between the equilibrium values of the compartments. For example, M^* , L_M^* , P^* , and R^* all contain the term $(\alpha_{MV} + \alpha_{VM})k_1\mu - \alpha_{MV}\alpha_{VM}e$ in their denominators, thereby suggesting positive correlations between these state variables. Furthermore, the term

$\alpha_{MV}ek_2 + \alpha_{VM}Q\mu$ appears in the denominators of both V^* and L_V^* but in the numerators of both M^* and L_M^* . This suggests that the equilibrium nutrient capitals of vascular plant and vascular plant litter vary inversely with those of moss and moss litter. Finally, the two large terms added together in the solution for P^* are the solutions for L_M^* and L_V^* multiplied by their respective turnover rates. This reduces P^* to $(k_3L_M^* + k_4L_V^*)/k_5$, or the inputs to P^* divided by its turnover rate. Later, we will show numerical solutions in which the trajectories of growth of these compartments also reflect these correlations.

The coexistence equilibrium value for each state variable in equations (3) includes the competition coefficients between vascular plants and mosses. Therefore, competitive interactions between mosses and vascular plants for resources other than nutrients affect not only their relative nutrient capitals but also the sizes of the peat and inorganic nutrient pools.

Unlike the other parameters in the model, the quantitative strengths of competition between mosses and vascular plants are not well characterized in the literature. Later, we shall make suggestions for some experiments to determine them. For now, we can examine the sensitivity of each state variable to the competition coefficients by fixing all other parameters to realistic values and plotting response surfaces of each equilibrium state variable to each competition coefficient. We assume, on average, that turnover fraction for moss nutrient capital (k_1) = 0.25 and that of vascular plant nutrient capital (k_2) = 0.1 (a slow turnover rate typical of evergreen shrubs; Eckstein and Karlsson 1997). Based on the decomposition experiment of Hobbie (1996), we set k_3 = 0.002 and k_4 = 0.015 to reflect the slower decay of mosses compared with vascular plants. We assume that decay and N and P mineralization from peat (k_5) = 0.1 (Updegraff et al. 1995; Bridgman et al. 1998). We set μ = 1.0 to reflect rapid uptake of nutrients by vascular plants from R (Aerts and Chapin 2000). We also set e = 0.1 (J. Pastor, B. Dewey, and S. Bridgman, unpublished data from the experiment described by Bridgman et al. 1999; Weltzin et al. 2000). For simplicity, we also set Q = 1.0.

The sensitivities of the coexistence equilibrium values for moss, vascular plant, peat, and inorganic nutrient resource pools (eqq. [3]) within a range of [0.01, 1.0] for the competition coefficients are shown in figure 2. As competition from mosses increases (i.e., as α_{VM} becomes large), vascular plant nutrient capital declines and moss nutrient capital approaches its moss monoculture equilibrium value of 4.0, given these values of Q and k_1 . Moss nutrient capital declines with increased interference competition from vascular plants, but vascular plant nutrient capital is less sensitive to changes in α_{MV} . Equilibrium peat nutrient capital declines with increased strength of competition of either

species toward the other, but it is more sensitive to increased interference competition of mosses on vascular plants than vice versa. This is surprising because *Sphagnum* moss is the major source of peat, owing to its slow decay rate (Janssens et al. 1992), and so one might infer that the peat pool should be more sensitive to reductions in moss nutrient capital than in vascular plant nutrient capital. Instead, these results suggest that variation in peat accumulation is due more to variations in proportions of vascular plant litter inputs even when moss litter remains the dominant source of peat. Finally, increased interference competition of mosses on vascular plants increases equilibrium inorganic resource pool because vascular plant uptake from this pool is reduced.

Stabilities of the Equilibria: Existence of a Transcritical Bifurcation

Since the model admits two equilibrium solutions, the stabilities of these solutions are of particular interest. At the moss monoculture equilibrium, the eigenvalues of the Jacobian are easily computed to be $[-e, -k_1, -k_3, -k_4, -k_5, \text{ and } C/(k_1e)]$, where C is defined by

$$C = (k_1\mu - \alpha_{\text{VM}}e)Q - ek_1k_2. \quad (4)$$

Stability of the moss monoculture solution thus depends on this critical combination of parameters: it is stable for $C < 0$ and unstable for $C > 0$. When $C < 0$, the moss monoculture also appears to be globally stable (attracting) for all nonnegative initial conditions of the six components.

Note that the same critical combination of parameters appears as a factor in V^* and L_V^* for the coexistence equilibrium (eqq. [3]). If $C < 0$, then vascular plant coexistence equilibrium nutrient capital (V^*) is negative, and it is therefore physically unattainable, but when $C > 0$, both V^* and M^* are positive, and we then have the coexistence equilibrium solution. If $C = 0$, the two equilibria coincide.

Thus, the change in stability of the moss monoculture is accompanied by a "crossing" of the moss monoculture to the coexistence equilibrium. The sign of C determines whether the system tends toward a moss monoculture or a moss-vascular plant coexistence.

The parameter $C = 0$ thus can be used to locate a transition in which the locations and the stabilities of the two solutions cross. This standard transition in dynamical system theory is termed a "transcritical bifurcation" (Guckenheimer and Holmes 1983; Strogatz 1994). Although computation of the eigenvalues at the coexistence equilibrium is intractable (in terms of all the parameters), we claim that the coexistence solution is locally stable, with

all eigenvalues negative, for $C > 0$, and unstable, with at least one positive eigenvalue, for $C < 0$. This claim of local stability for the coexistence equilibrium solution when $C > 0$ is justified by the existence of the transcritical bifurcation, in which the two solutions cross and exchange stabilities. We expect that the coexistence equilibrium is globally stable for all $C > 0$ as well, although we have not analytically eliminated the possibility that parameter values resulting in $C \gg 0$ might spawn other more complicated attractors, such as a periodic orbit. In summary, as various combinations of parameter values cause C to cross through 0, the plant community switches between a moss monoculture to moss coexisting with vascular plants.

There are many ways of passing through $C = 0$ that depend on various values and combinations of the parameters on the right-hand side of equation (4). We will examine the relationship between e and Q and the species life-history characteristics (k_1, k_2, μ , and α_{VM}) that result in $C = 0$.

We call the export rate at the transcritical bifurcation between the moss monoculture and coexistence solution e_{crit} . Surprisingly, solving equation (4) for e_{crit} yields a Michaelis-Menten equation with the limit of $e_{\text{crit}} = k_1\mu/\alpha_{\text{VM}}$ as Q increases; the approach to the limit is determined by the half-saturation constant $k_1k_2/\alpha_{\text{VM}}$:

$$e_{\text{crit}} = \frac{k_1\mu}{\alpha_{\text{VM}}} Q \left/ Q + \frac{k_1k_2}{\alpha_{\text{VM}}} \right. \quad (5)$$

Equation (5) describes a link between ecosystem input-output budgets (e and Q), species traits ($k_1, k_2, \alpha_{\text{VM}}$, and μ), and the stabilities of the two equilibrium communities. The bifurcation from a stable moss monoculture to a stable moss-vascular plant coexistence therefore arises from interactions between the input/output budget with the life-history traits of the species in the communities. When $e > e_{\text{crit}}$, then moss monoculture is stable, but if $e < e_{\text{crit}}$, then coexistence is (locally) stable. This is biologically reasonable, since when e is small, nutrients stay in the system and are available for vascular plant uptake. An illustration is given in figure 3 given the above parameter values for the internal transfer coefficients ($k_1 \dots k_5$ and μ) from the literature (Updegraff et al. 1995; Hobbie 1996; Eckstein and Karlsson 1997; Bridgham et al. 1998; Aerts et al. 1999) that we used in the above sensitivity analysis for the competition coefficients (fig. 2) and setting $\alpha_{\text{VM}} = 0.1$.

This interaction of ecosystem nutrient budgets with life-history characteristics has some interesting consequences. For example, it implies that fertilizing a bog (increasing Q) should shift the ecosystem to the right of e_{crit} in figure 3, thereby allowing vascular plants to invade and increase at the expense of mosses. Such shifts in species composition from moss to vascular plant dominance have been

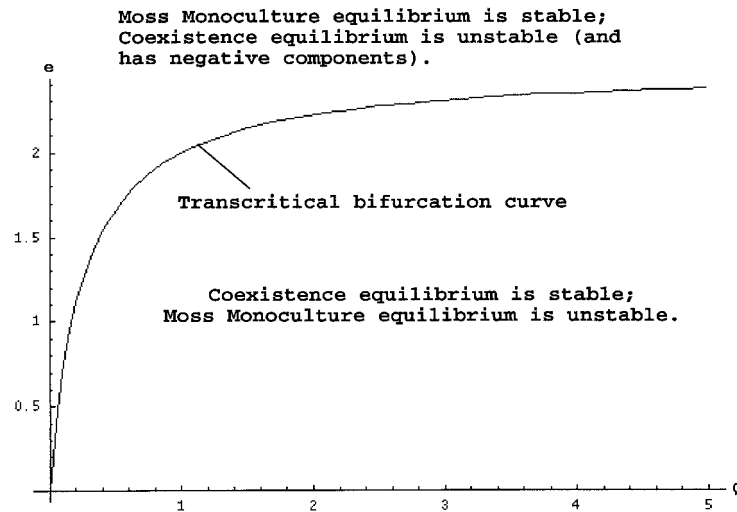


Figure 3: Bifurcation diagram for model 1 (eq. [1]) that shows how the combination of nutrient input rate Q and export coefficient e determines whether the moss monoculture or coexistence equilibrium is stable (see eq. [5]). $\alpha_{MV} = \alpha_{VM} = 0.10$. The transfer coefficients ($k_1 \dots k_5, \mu$) used in figure 2 were kept the same for comparison. Note that figure 4 can be thought of as following a “one-parameter cut” through this diagram along the vertical line at $Q = 1$ and crossing the transcritical bifurcation curve at $e = 2$.

experimentally observed in fertilized bogs and heathlands (Aerts and Heil 1993; Chapin 1998), although these studies have not related them to the input-output budget and specific life-history traits as suggested here.

As a second way to view the transcritical bifurcation occurring by passing through $C = 0$, we now examine how the system switches from a stable coexistence to a stable moss monoculture by increasing e (fig. 4). In contrast to figure 3, here we fix Q at 1 but add the state space equilibrium values for the six compartments. As e increases, coexistence equilibrium moss nutrient capital increases monotonically (fig. 4a), and coexistence equilibrium vascular plant nutrient capital declines to 0 (fig. 4b). The bifurcation between the two stable states occurs at the value of e_{crit} where equilibrium vascular plant nutrient capital becomes 0 and a moss monoculture ensues. For these parameter values, $C = 0$ when $e_{crit} = 2$. Note that the magnitude of e also determines whether nutrient capital is dominated by mosses or vascular plants: moss dominates when e is large and vascular plants dominate when e is small, although they do not drive mosses extinct because mosses still receive nutrient subsidies from precipitation.

Behavior of Time-Dependent Numerical Solutions

To examine the model further, we found a time-dependent numerical solution given the above parameter values for the internal transfer coefficients ($k_1 \dots k_5, \mu$, and e) from

the literature (Updegraff et al. 1995; Hobbie 1996; Eckstein and Karlsson 1997; Bridgham et al. 1998; Aerts et al. 1999) with $Q = 1$. For illustration, we assume $\alpha_{MV} = 0.5$ and $\alpha_{VM} = 0.1$. Initial conditions for each of the state variables were arbitrarily set to 0.01, which is very small compared with their final equilibrium values.

These parameter values yield a coexistence equilibrium (fig. 5) because $C > 0$. That this equilibrium is locally stable is confirmed by the fact that the eigenvalues of the Jacobian matrix evaluated at the coexistence equilibrium for these parameter values all have negative real parts, and so perturbations near equilibrium will decay. However, four eigenvalues are complex, and so perturbations decay with oscillations.

The time-dependent solutions (fig. 5) mimic successional dynamics of mosses and vascular plants during bog development. For these parameter values, the model predicts that early dominance of living biomass by mosses should eventually succeed to later dominance by vascular plants, although the mosses do not go extinct. In the initial stages of bog development, moss nutrient capital rises to almost the equilibrium value for a moss monoculture. The mosses continue to dominate living biomass until the nutrients retained in live moss and litter pass through the peat pool and enter the inorganic nutrient pool. Vascular plant nutrient capital rises only after the nutrient pool becomes large enough to support vascular plant nutrient uptake.

These successional dynamics from initial dominance by

moss to later invasion by vascular plants are not unlike the later invasion of *Sphagnum* lawns by shrubs and spruce often seen during bog development once the peatland community is uncoupled from regional groundwater inputs by the accumulation of peat (Crum 1992; Janssen 1992; Janssens et al. 1992; Kuhry et al. 1993). Thus, given reasonable parameter values, many of which are experimentally determined, the model mimics the observed moss and vascular plant coexistence during bog development, with mosses dominating before vascular plants invade.

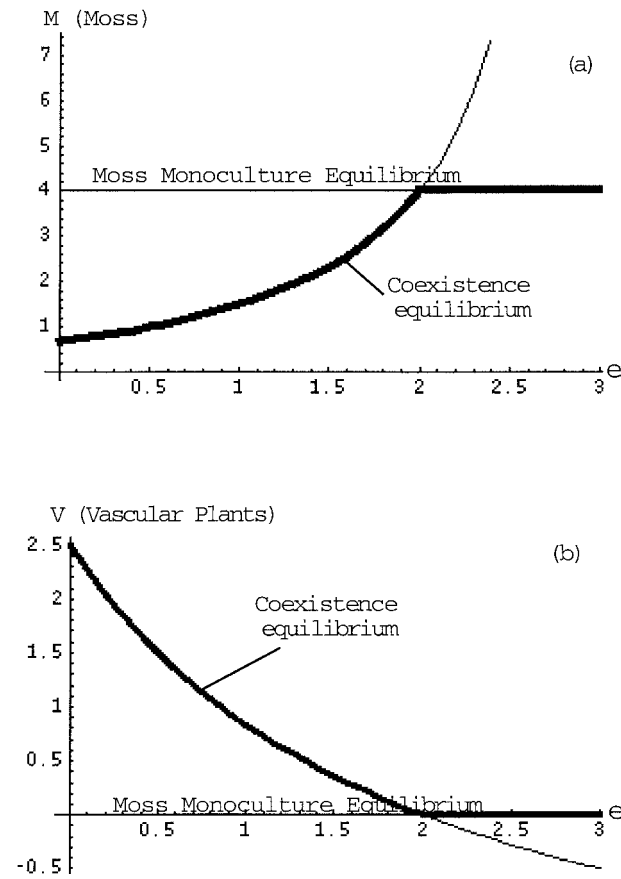


Figure 4: Bifurcation diagram for model 1 (eqq. [1]) that shows projections to (a) the (e, M) plane and (b) the (e, V) plane of the crossing and coincident exchanges of stabilities between the moss monoculture equilibrium and the coexistence equilibrium as the export coefficient e passes through $e = 2$. Q was fixed at 1.0 and all other parameter values are fixed as for figure 3. The thick lines indicate the stable solution: the coexistence equilibrium is conjectured to be stable when $e < 2$, while the moss monoculture equilibrium is stable when $e > 2$. Similar bifurcation diagrams exist for the other four variables L_M, L_V, P , and R , all having equilibrium values crossing at the transcritical bifurcation value of $e = 2$ for these parameter values (see the explicit formula for equilibria in eqq. [2] and [3]).

Model 2: A General Model for Bogs and Fens

Generalizing model 1 to include fens as well as to provide a more realistic model of moss vascular plant interactions requires relaxing the three assumptions discussed for model 1, namely, adding self-limitation terms to the moss and vascular plant compartments, adding groundwater inputs, and partitioning precipitation inputs between moss and the nutrient pools. We wish to determine whether and how relaxing these assumptions alters the equilibria, stability, and transient behaviors of the model.

The full version of model 2 with all three assumptions relaxed now becomes

$$\begin{aligned} \frac{dM}{dt} &= Q_1(1 - \delta e^{-\beta_1 M}) - k_1 M - \alpha_{MV} VM - \alpha_{MM} M^2, \\ \frac{dV}{dt} &= \mu VR - k_2 V - \alpha_{VM} VM - \alpha_{VV} V^2, \\ \frac{dL_M}{dt} &= k_1 M - k_3 L_M, \\ \frac{dL_V}{dt} &= k_2 V - k_4 L_V, \\ \frac{dP}{dt} &= k_3 L_M + k_4 L_V - k_5 P, \\ \frac{dR}{dt} &= Q_1 \delta e^{-\beta_1 M} + Q_2 e^{-\beta_2 P} + k_5 P - \mu VR - eR, \end{aligned} \tag{6}$$

where Q_1 and Q_2 are precipitation and groundwater nutrient inputs whose destinations depend on moss nutrient capital (M) and peat nutrient capital (P), respectively; β_1 are per capita rates by which moss and peat control the entry of Q_1 and Q_2 , respectively, into M and R ; δ is a partition coefficient between 0 and 1 that controls the split of precipitation between M and R ; and α_{MM} and α_{VV} are intraspecific competition coefficients (self-limitation terms) for M and V , respectively. When $\delta = 0$ and $\alpha_{MM} = \alpha_{VV} = 0, Q_2 = 0$, and $Q_1 = Q$, then model 2 reduces to model 1. We first add the self-limitation terms and later adjust the two input terms.

Adding Self-Limitation Terms to Mosses and Vascular Plants

We first subtracted the self-limitation terms $\alpha_{MM} M^2$ and $\alpha_{VV} V^2$ from the dynamical equations for moss and vascular plants, respectively. The forms of these intraspecific competition terms parallel those for intraspecific competition, $\alpha_{MV} MV$ and $\alpha_{VM} MV$ in model 1. At this step, all inputs (Q) entered moss directly, as in model 1.

Analytical solutions for equilibrium values of all com-

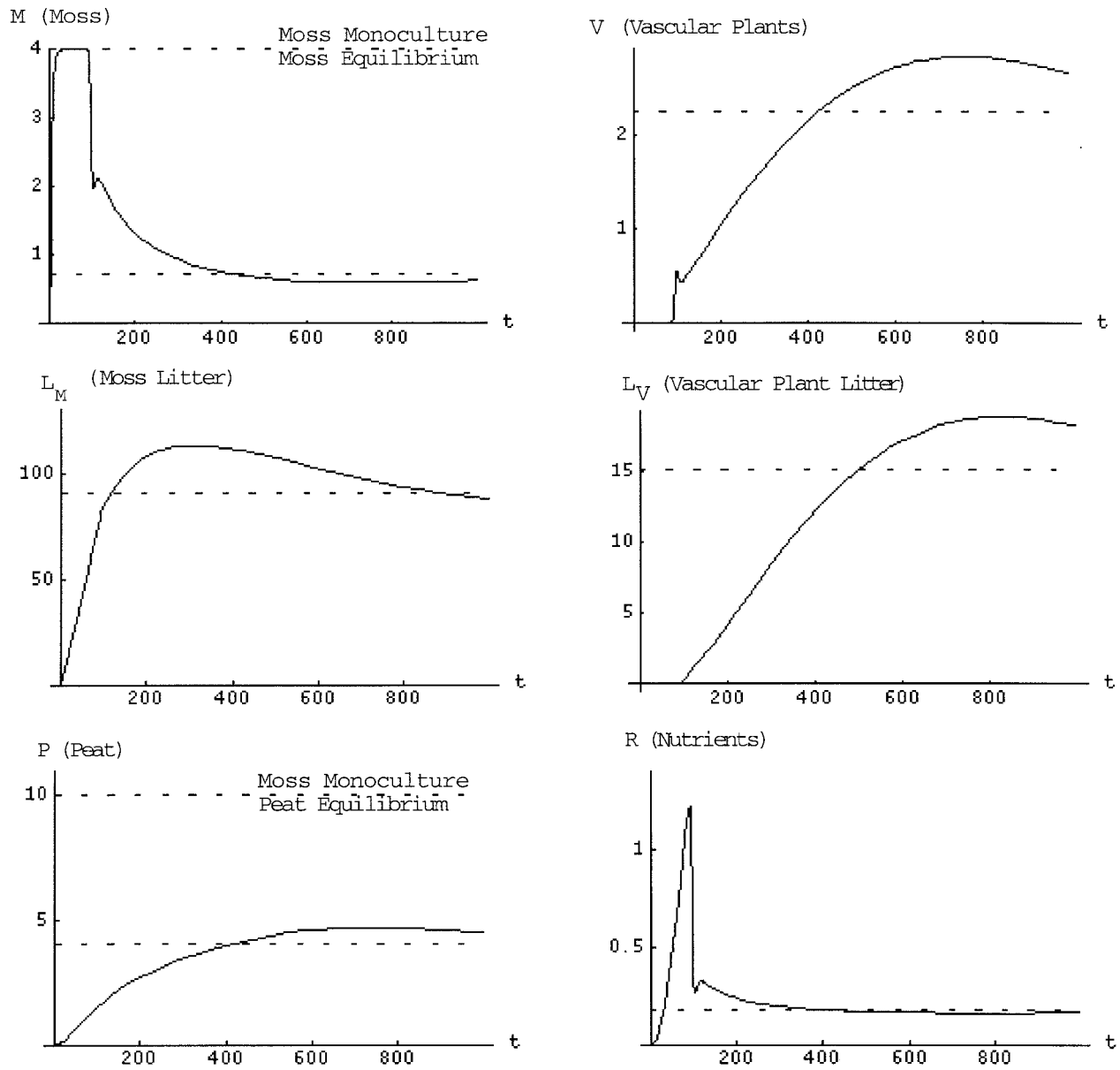


Figure 5: Numerical solutions for the time trajectories for model 1 (eq. [1]) using initial conditions of 0.01 for all six variables. The transfer coefficients ($k_1 \dots k_5, \mu$) used in figures 2–4 were kept the same for comparison. For this figure, we set $\alpha_{MV} = \alpha_{VM} = 0.10$ as in figures 3 and 4 and $e = 0.1$ as in figure 2. The unlabeled dashed lines indicate the equilibrium values that each variable approaches under the coexistence solution. For comparison, the equilibrium values for moss and peat under the moss monoculture solution are also indicated and labeled. The values for vascular plants and their litter are 0 for the moss monoculture equilibrium and are too high to depict for moss litter (500) and nutrients (100). Note the succession between what initially is essentially a moss monoculture (between $t = 10$ and $t = 100$) to the eventual coexistence equilibrium being approached when $t > 800$.

partments are now unwieldy. Nonetheless, the analytical solutions still only allow either moss monoculture or moss–vascular plant coexistence although equilibrium values are decreased, as would be expected. We still have the same qualitative conclusions as before for model 1. The

stabilities of the two solutions are still determined by a critical combination of parameters analogous to, but more complicated than, equation (4). Crossing this critical set of parameters still results in a transcritical bifurcation. Numerical solutions for this modified model (with

$\alpha_{MM}M^2 = \alpha_{VV}V^2 = 0.10$) are qualitatively similar to those for model 1 shown previously in figure 5, except that equilibrium values for all state variables are now smaller. Therefore, self-limitation or intraspecific competition within species do not qualitatively change our conclusions and cannot account for the dominance of vascular plants early in fen development with almost complete exclusion of mosses. In the following modifications to model 2, we keep the self-limitation terms in the dynamical equations for M and V .

*Adding Groundwater Inputs but Not
Partitioning Precipitation Inputs*

To simulate groundwater inputs, we allow the peat pool (P) to dynamically control the level of nutrients transferred directly from groundwater (Q_2) to the resource pool: without peat, the maximum level of nutrient input from groundwater (Q_2) is available to vascular plants, but as peat grows, the resource pool becomes decoupled from the groundwater, and fewer and fewer of the groundwater inputs enter R . Inputs to R then become dominated by the decay of peat (k_3P), and Q_1 becomes the only input to the system. This modification allows the model to mimic the hydrologic changes that happen as the peat accumulates and causes fens, which receive nutrient inputs from both precipitation and groundwater, to succeed to bogs, which receive nutrient inputs only from precipitation.

Adding groundwater inputs alone to R did not qualitatively change long-term equilibrium behavior. The only equilibria are still the moss monoculture and the coexistence solutions. When both equilibria occur with “large” values of peat (P), the new contribution of Q_2 is negligible at equilibrium because as P increases, the contribution of Q_2 to R is eliminated. Thus, the stabilities of the equilibria are essentially the same as for adding the two self-limitation terms to model 1 discussed above.

*Partitioning Precipitation Inputs between Moss and the
Inorganic Nutrient Pool, without Groundwater Inputs*

To simulate partitioning of precipitation inputs, we change δ from 0 to 1 in equations (6). This allows the split of precipitation input (Q_1) to be dynamically controlled by the growth of moss: all precipitation input of nutrients go directly to the inorganic resource pool (R) in the absence of moss, but as the moss increases, it is able to capture an increasing fraction of the precipitation inputs. The coefficient β_1 is the per capita uptake rate by moss biomass.

Partitioning of precipitation between M and R resulted in two additional sets of equilibrium solutions. Besides the moss monoculture and moss–vascular plant coexistence equilibria, this modification also allows for a vascular plant

monoculture ($M = L_M = 0$) and a solution where there is only a nutrient pool with precipitation inputs (with or without groundwater) and no mosses, vascular plants, or peat ($M = L_M = V = L_V = P = 0$). The vascular plant monoculture represents such wetland types as cattail marshes or sedge fens without moss. The solution consisting of the resource pool alone represents a lake. We discuss the stabilities of these four equilibrium solutions in the context of the full model 2 (with all above modifications) below. Differences in transient solutions are also discussed for the full model 2 below.

*Adding Self-Limitation Terms, Groundwater Inputs, and
Partitioning Precipitation Inputs between Moss and the
Inorganic Nutrient Pool: Equilibria of the
Full Version of Model 2*

As for the previous case of partitioning precipitation without groundwater (above), the full model 2 has four equilibria: a lake, two monocultures, and a coexistence equilibrium. Since only the lake equilibrium has a closed form of analytical expression, we begin our analysis with it. The only nonzero equilibrium of the lake solution is $R = (Q_1 + Q_2)/e$. The eigenvalues of the Jacobian evaluated at this lake equilibrium solution are easily computed to be

$$(\lambda_1 \dots \lambda_6) = [-e, -k_3, -k_4, -k_5, (Q_1 + Q_2)\mu - k_2e, Q_1\beta_1\delta - k_1]. \quad (7)$$

Clearly, the first four eigenvalues are negative, which would impart stability, but the last two are negative only with certain restrictions on parameter values. Specifically, the lake equilibrium is stable only if λ_5 and λ_6 are both negative. Recall that δ must equal 1 to allow for the split of precipitation between M and R .

We claim that as parameters are varied to make λ_6 positive (assuming λ_5 remains negative), the system undergoes the same type of transcritical bifurcation discussed in the context of model 1. Across this new transcritical bifurcation, the lake equilibrium and the moss monoculture equilibrium cross and exchange stabilities.

Although the exponential terms in the differential equations (eqq. [6]) prevent us from computing closed-form expressions for the moss monoculture equilibrium, we can show that there are two equilibrium solutions that have $V^* = 0$. This is best seen by examining the dynamic equations for moss growth when $V = 0$:

$$\frac{dM}{dt} = Q(1 - \delta e^{-\beta_1 M}) - \alpha_{MM}M^2 - k_1M. \quad (8)$$

This equation has two roots: the trivial solution $M_1^* =$

0 and a nonzero root M_M^* . The subscript L is for the lake equilibrium and the subscript M is for the moss monoculture equilibrium. It can be shown through calculus that M_M^* is negative if $\lambda_6 < 0$, zero if $\lambda_6 = 0$, and positive if $\lambda_6 > 0$. This corroborates our claim of a transcritical bifurcation between the lake and moss monoculture equilibria solutions. It can also be shown that the dynamical equation for moss growth in the absence of V (eq. [8]) is positive if and only if $Q_1 > k_1/\beta_1$, which are sufficient for $\lambda_6 > 0$ from above and the lake becoming unstable. There is, therefore, a minimum $Q_1 > k_1/\beta_1$ required for the existence of a moss monoculture.

Similarly, if we choose parameter values so that λ_6 stays negative but λ_5 passes through zero, there is a similar transcritical bifurcation between the lake equilibrium and the vascular plant equilibrium. For $\lambda_5 < 0$, the lake equilibrium is stable and $V_V^* < 0$ (where the subscript V refers to the vascular plant monoculture). If $\lambda_5 = 0$, the two equilibria coincide. For $\lambda_5 > 0$, the lake equilibrium is now unstable, and the vascular plant monoculture equilibrium is now positive and stable. This behavior is justified in a manner similar to the justification of the transcritical bifurcation discussed above as λ_6 passes through 0, separating the lake from the moss monoculture. As with the moss monoculture, the dynamical equation for V is positive if and only if there is a minimum total input of nutrients $(Q_1 + Q_2) > (k_2 e/\mu)$. These are also the conditions for which $\lambda_5 > 0$. Both of these minimum nutrient inputs required by moss and vascular plant monocultures imply that very oligotrophic (nutrient poor) lakes with low nutrient inputs per unit volume would not succeed to peatlands. In fact, peatlands typically form in large shallow basins formerly filled by glacial lakes, basins that would have had a large nutrient input rate per unit volume by virtue of being shallow (Wright et al. 1992).

Since we do not have closed-form expressions for each monoculture, we cannot compute explicitly the Jacobian at either equilibrium, nor can we compute corresponding eigenvalues. However, we can do a more subtle sensitivity analysis in order to determine whether the two monoculture equilibria are stable. For example, if the dynamic equations for M are negative for values of V_V^* when M is small, then the vascular plant equilibrium is stable (i.e., a small introduction of moss into the vascular plant monoculture equilibrium will decay to zero). If positive, then the vascular plant equilibrium is unstable, moss can invade, and we get a coexistence solution. Thus, there is yet another critical combination of parameters defining another transcritical bifurcation between vascular plant monoculture and the coexistence solution. Similarly, and finally, there is fourth transcritical bifurcation defined by a final critical set of parameter values that separate the

moss monoculture equilibrium from the coexistence equilibrium.

We now have four transcritical bifurcations, each depending on a critical combination of parameters, C_i , analogous to equation (4) for model 1, separating a lake, and three potentially stable plant communities, two monocultures and one coexistence community of moss and vascular plants:

$$\begin{aligned} C_1 &= Q_1\beta_1 - k_1 \quad (\text{moss/lake}), \\ C_2 &= (Q_1 + Q_2)\mu - k_2e \quad (\text{vascular plant/lake}), \\ C_3 &= Q_1\beta_1 - k_1 - \alpha_{MV}V_V^* \\ &\quad (\text{coexistence/vascular plant}), \\ C_4 &= Q_1e^{-\beta_1 M_M^*} + Q_2e^{-\beta_2(k_3/k_5)M_M^*} + k_3\mu M_M^* \\ &\quad - \alpha_{VM}eM_M^* - k_2e \quad (\text{coexistence/moss}), \end{aligned} \tag{9}$$

where M_M^* and V_V^* are the moss and vascular plant equilibria in their respective monoculture solutions (denoted by the subscript). These, of course, are also dependent on parameter values, and so C_3 and C_4 , as presented here, are not closed-form solutions.

As for model 1, there are many ways to change parameters to change the signs of the four critical parameter combinations. One way to do this, analogous to equation (4) and figure 3 for model 1, is to fix all parameters except for the inputs (Q_1 and Q_2) and leaching loss (e) parameters. We now have a three-dimensional space ($e - Q_1 - Q_2$) in which there are four surfaces representing transcritical bifurcations. Each of these surfaces depends on one or more of the four critical combinations of parameters in equations (9). These surfaces separate regions in the $e - Q_1 - Q_2$ space that denote the different stable solutions. For example, when all four $C_i < 0$, then the solution is a stable lake; when $C_1 > 0$ but $C_4 < 0$, then the solution is stable moss monoculture; when $C_2 > 0$ but $C_3 < 0$, then the solution is stable vascular plant monoculture; when all four $C_i < 0$, then the solution is stable coexistence between moss and vascular plants. Therefore, different plant communities emerge from interactions of plant nutrient uptake rates (β_1, μ), death rates (k_1, k_2), decay rates (k_3, k_4, k_5), and competition for other resources (α_{VM}, α_{MV}), with the parameters controlling the input/output budget of the ecosystem (e, Q_1, Q_2). Further elaborations of the shapes of these bifurcations and the regions they separate is beyond the scope of this article.

Time-Dependent Behaviors of the Full Version of Model 2

Further analysis of changes in time-dependent behavior due to these successive modifications to model 2 requires

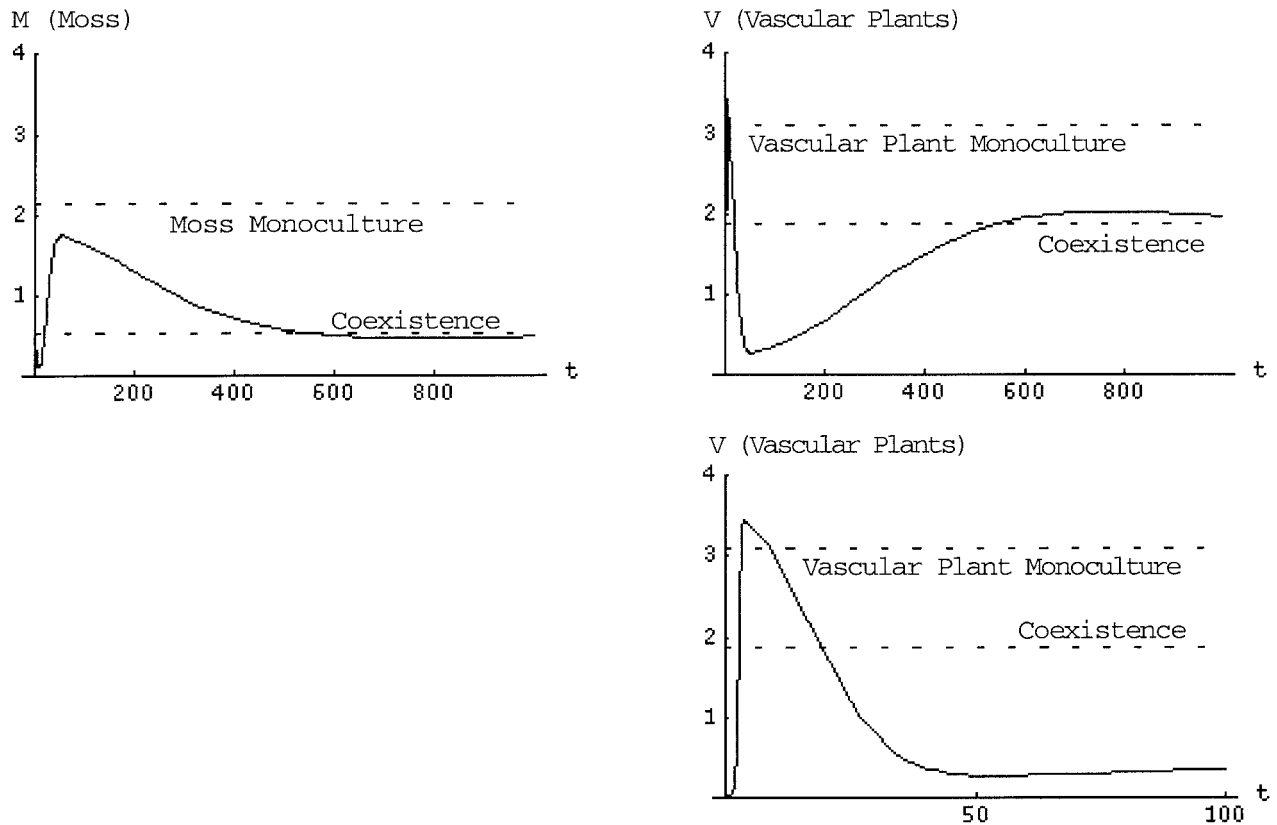


Figure 6: Numerical solutions for a time trajectory of model 2 modifications to model 1 given by equations (6) with two input sources of nutrients (Q_1 and Q_2) and self-limitation terms α_{MM} and α_{VV} . The parameters ($k_1 \dots k_5, \mu, e, \alpha_{MV}, \alpha_{VM}$) common to model 1 (eqq. [1]) used in figure 5 were kept the same for comparison. Values for new parameters in the generalized model: $Q_1 = Q_2 = 1.0; \beta_1 = 2, \beta_2 = 5$, and $\alpha_{MM} = \alpha_{VV} = 0.10$. Initial values of 0.01 were given to all six state variables. Of the six state variables, only the moss and vascular plants are displayed, with an enlargement of the initial spike in the vascular plant nutrient capital shown in the lower right. The dashed lines indicate the coexistence equilibria values that the solution approaches and, for comparison, the vascular plant and monoculture equilibria values for their respective compartments. Note the succession from an initial vascular plant dominance between $t = 5$ and $t = 25$ to what is nearly a moss monoculture between $t = 100$ and $t = 150$, followed by the eventual coexistence equilibrium (after about $t = 500$).

numerical solutions, which we found using the parameter values and initial conditions for the numerical solutions to model 1 previously shown in figure 5 and assuming, for illustration, that $Q_1 = Q_2 = 1.0, \beta_1 = 2, \beta_2 = 5$, and $\alpha_{ii} = 0.10$. We always chose parameter values corresponding to a stable coexistence solution (all four $C_i > 0$ in eqq. [9]).

Although we indicated earlier that adding groundwater inputs (Q_2) alone to R without partitioning precipitation inputs ($\delta = 0$) did not alter the equilibria of the model or their stabilities, it did alter the transient behavior of the model from that of model 1 in the early stages. Initially, the peatland was dominated by a spike in vascular plant biomass subsidized by the groundwater inputs to R . This subsidy allowed vascular plants initially to grow faster than

mosses and to suppress their growth through the interspecific competition term. However, as the peat accumulated, groundwater inputs to R declined, causing this early dominance in vascular plant biomass to decline as mosses became dominant. As with model 1, as nutrients from precipitation were transferred through moss, moss litter, and peat to R , the vascular plant biomass recovered, resulting in a stable coexistence equilibrium similar to model 1. Partitioning precipitation inputs between moss and the resource pool ($\delta = 1$) but without groundwater inputs ($Q_2 = 0$) also resulted in this early transient spike in vascular plant biomass even without adding groundwater inputs, for the same reason as above.

Numerical solutions to the full model 2 with the above parameter values for $Q, \beta,$ and α_{ii} are shown in figure 6.

Again, a transient spike in vascular plant nutrient capital occurs, but the magnitude of this spike is now larger than when some of Q_1 and Q_2 were added alone because it is now being subsidized simultaneously by Q_1 and Q_2 when both M and P are initially small. For the full model with these parameter values, only the coexistence equilibrium is stable (three pairs of complex eigenvalues all with negative real parts). Both monocultures have one positive eigenvalue, and the lake equilibrium has two positive eigenvalues; they are therefore unstable for these parameter values.

The time-dependent behavior of this final model mimics the development of peatlands from glacial lakes through fens to bogs. The instability of shallow lakes in these numerical solutions mimics the disappearance of large shallow glacial lakes as they have become filled in with peatlands (Wright et al. 1992). In the paleorecord, vascular plants such as deciduous shrubs and graminoids dominate during the early stages of peatland development, when the peatland is occupied by a fen plant community in which mosses are a minor component or are even absent (Janssen 1992; Janssens et al. 1992; Kuhry et al. 1993; Swinehart and Parker 2000). At some point during peatland development there is often (although not always) an abrupt transition to a transient near-monoculture of mosses followed by reinvasion of vascular plants such as ericaceous shrubs and black spruce (Janssen 1992; Janssens et al. 1992; Kuhry et al. 1993; Swinehart and Parker 2000), not unlike the transition simulated here.

In our current model, we do not distinguish between these different types of vascular plants in fens and bogs. We also do not claim numerical accuracy given these parameter values and, indeed, given this relatively crude modification to sources of nutrient inputs and the factors that control them. Nevertheless, it is encouraging that a relatively simple modification to the input/export balance of our model results in a qualitative pattern of succession not unlike that seen during 10,000 yr of peatland development after deglaciation (Janssen 1992; Janssens et al. 1992; Kuhry et al. 1993; Swinehart and Parker 2000).

In conclusion, allowing some input to R other than from decay of peat (either from groundwater or from precipitation) allows for a transient early spike in vascular plant dominance over mosses, which characterizes the early dominance of peatlands by fens. The effect of groundwater inputs in this model are ephemeral, as they are in real peatlands, because eventually the accumulation of peat effectively decouples the plant community from groundwater inputs of nutrients. Partitioning of precipitation inputs between moss and the resource pool and having this partitioning dynamically dependent on moss biomass cause the greatest changes in model behavior, allowing a potentially stable vascular plant biomass when precipita-

tion inputs are below a threshold value to support moss growth.

Discussion

The models account for a variety of peatland behaviors (such as peat accumulation and successional dynamics between mosses and vascular plants) within the constraint of mass balance of nutrients. More generally, we have shown how alternative stable states in peatlands, other wetlands, and lakes can arise from their input-output budgets and the life-history characteristics of species within them. All major types of wetlands, as well as lakes, are represented by these solutions. These solutions or stable states are separated by transcritical bifurcations that depend on critical combinations of input-output parameters of the whole system as well as life-history characteristics of the species within them that determine nutrient flows. Succession emerges from the interactions between competing species as they affect the entry of nutrients into the inorganic nutrient pool. Apparently, the life-history traits of mosses and vascular plants (species properties), the competitive dynamics between these species (community properties), and the inorganic nutrient pool and the input/output budget (ecosystem properties) mutually affect one another in a nonlinear manner. Although we have lumped all moss and vascular plant species into two functional groups, it is possible to expand the model by subdividing these functional groups into taxonomic species that differ in the values of the life-history traits that determine nutrient flows. In fact, the values of these traits describe the fundamental niche of each species with respect to nutrient cycling.

The strengths of the competition coefficients between mosses and vascular plants strongly determine the equilibrium sizes of each of the ecosystem compartments (fig. 2). While we and others (Verhoeven et al. 1990; Walbridge 1991; Updegraff et al. 1995, 2001; Hobbie 1996; Bridgman et al. 1998; Aerts et al. 1999) have determined nutrient dynamics of decaying litter from peatland species and from peat in mechanistic detail, we have very sparse data on the mechanisms and strengths of competitive interactions among different peatland species and how such competition influences nutrient pools and fluxes. This suggests the need for competition experiments between mosses and vascular plants (e.g., in a DeWitt replacement series design) with concurrent measurements of the nutrient resource pool in these experiments. We predict that the inorganic nutrient pool will respond to the relative ratio of moss to vascular plant nutrient capital because of the presence of α_{VM} and α_{MV} in the equilibrium solution of R (eqq. [3]).

The input/output budget of the ecosystem (determined

by Q and e in model 1 and Q_1 , Q_2 , and e in model 2) sets constraints on life-history traits required by vascular plants and mosses for monocultures and coexistence communities. This can be experimentally tested by documenting changes in species composition and the life-history traits of these species following fertilizer additions (increasing Q). If transcritical bifurcations separate real plant communities in peatlands and if these bifurcations represent critical relationships between inputs and outputs (e.g., eqq. [6] and eqq. [9]; fig. 3), then it should be possible to predictably drive a peatland from one stable state to another by adding a specified amount of nutrients.

A feature of peatland communities only crudely captured by model 2 is that the accumulation of peat is controlled by, and in turn controls, the peatland's hydrology. This hydrology–organic matter feedback is another source of complex behaviors. In this regard, we note that Hilbert et al. (2000) present a coupled model of peatland hydrology–organic matter accumulation that has some interesting complex behaviors that may bear some similarity to those depicted here. Specifically, in the Hilbert et al. model, the depth to the water table and the thickness of the peat layer affect each other through coupled differential equations. In the Hilbert et al. model, there are three sets of equilibria for water table and peat thickness, two of which are stable but are separated by a third unstable equilibrium point. The two equilibria represent either a peatland that is wet and has a thin peat layer or one that is drier and has a thick peat layer. These two sets of equilibria bear a striking resemblance to fens (thin peat and high water table with high water input) and bogs (thicker peat and lower water table with lower water input).

While this is different from the transcritical bifurcations of our models, it is significant that both models predict bifurcations from one stable state to another as inputs of either nutrients or water increase. The Hilbert et al. (2000) model and our model 2 are complementary. In contrast to the Hilbert et al. model, where the position of the water table is dynamically modeled, we do not explicitly consider the position of the water table in the peat profile. In addition, while the potential growth rate of the plant compartment(s) in the Hilbert et al. model is constant, in reality it must vary with the dynamics of plant species composition. This latter dynamic is simulated explicitly by our model. A coupling of the two models may contain even more interesting complex dynamics.

In conclusion, the dynamics of peatland ecosystems and their ability to store or release carbon and nutrients appear to be governed at least in part by interactions between nutrient input/output budgets, the hydrologic sources of nutrients, and the life-history characteristics of their constituent species. Central to these dynamics is the unique and sometimes dominant role of mosses in controlling the

transfer of incoming nutrients into the rest of the ecosystem. Many observed patterns of peatland development and dynamics, as well as their role in the global carbon cycle, may emerge from these unique characteristics.

Acknowledgments

This research was supported by a grant from the National Science Foundation's Ecosystem Ecology Program. We are grateful for the continuing support of this program. The development of this model began when B. Peckham invited J. Pastor to present early results of model 1 to his dynamical systems class; we thank the students for their thoughtful comments and questions. H. Stech also raised several questions that helped us clarify the models, as did P. Camill and an anonymous reviewer. We thank them all.

Literature Cited

- Aerts, R., and F. S. Chapin III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of patterns and processes. *Advances in Ecological Research* 30:1–67.
- Aerts, R., and G. W. Heil, eds. 1993. *Heathlands: patterns and processes in a changing environment*. Kluwer Academic, Dordrecht.
- Aerts, R., B. Wallén, and N. Malmer. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology* 80:131–140.
- Aerts, R., J. T. A. Verhoeven, and D. Whigham. 1999. Plant mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* 80:2170–2181.
- Almqvist-Jacobson, H., and D. R. Foster. 1995. Toward an integrated model for raised-bog development: theory and field evidence. *Ecology* 76:2503–2516.
- Aselmann, I., and P. J. Crutzen. 1989. Global distribution of natural freshwater wetlands, their net primary productivity, seasonality, and possible methane emissions. *Journal of Atmospheric Chemistry* 8:307–359.
- Austin, K. A., and R. K. Wieder. 1987. Effects of elevated H^+ , SO_4^{2-} , NO_3^- , and NH_4^+ in simulated acid rain precipitation on the growth and chlorophyll content of three North American *Sphagnum* species. *Bryologist* 90: 221–229.
- Bartlett, K. B., and R. C. Harriss. 1993. Review and assessment of methane emissions from wetlands. *Chemosphere* 26:261–320.
- Bayley, S. E., D. H. Vitt, R. W. Newbury, K. G. Beatty, R. Behr, and C. Miller. 1987. Experimental acidification of a *Sphagnum*-dominated peatland: first year results. *Canadian Journal of Fisheries and Aquatic Science* 44 (suppl.):194–205.

- Bedford, B. L., M. A. Walbridge, and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North America wetlands. *Ecology* 80: 2151–2169.
- Bridgham, S. D., C. A. Johnston, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. *BioScience* 45:262–274.
- Bridgham, S. D., J. Pastor, J. A. Janssens, C. Chapin, and T. J. Malterer. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands* 16:45–65.
- Bridgham, S. D., K. Updegraff, and J. Pastor. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79:1545–1561.
- Bridgham, S. D., J. Pastor, K. Updegraff, T. J. Malterer, K. Johnson, C. Harth, and J. Chen. 1999. Ecosystem control over temperature and energy flux in northern peatlands. *Ecological Applications* 9:1345–1358.
- Bridgham, S. D., C.-L. Ping, J. L. Richardson, and K. Updegraff. 2001. Soils of northern peatlands: histosols and gelisols. Pages 343–370 in J. L. Richardson and M. J. Vepraskas, eds. *Wetland soils: genesis, hydrology, landscapes, and classification*. CRC, Boca Raton, Fla.
- Chapin, C. 1998. Plant community response and nutrient dynamics as a result of manipulations of pH and nutrients in a bog and fen in northeastern Minnesota. Ph.D. diss. University of Notre Dame, Notre Dame, Ind.
- Clymo, R. S. 1992. Models of peat growth. *Suo* 43:127–136.
- Crum, H. 1992. A focus on peatlands and peat mosses. University of Michigan Press, Ann Arbor.
- Eckstein, R. L., and P. S. Karlsson. 1997. Above-ground growth and nutrient use by plants in a subarctic environment: effects of habitat, life-form and species. *Oikos* 79:311–324.
- Glaser, P. 1992. Ecological development of patterned peatlands. Pages 27–42 in H. E. Wright, B. A. Coffin, and N. E. Aaseng, eds. *Patterned peatlands of Minnesota*. University of Minnesota Press, Minneapolis.
- Gorham, E. 1991. Northern peatlands: role in the global carbon cycle and possible responses to climatic warming. *Ecological Applications* 1:182–195.
- Guckenheimer, J., and P. Holmes. 1983. *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*. Springer, New York.
- Hilbert, D. W., N. Roulet, and T. Moore. 2000. Modelling and analysis of peatlands as dynamic systems. *Journal of Ecology* 88:230–242.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* 66:503–522.
- Houghton, J. T., L. G. M. Filho, B. A. Callender, N. Harris, A. Kattenberg, and K. Marshall, eds. 1995. *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge.
- Janssen, C. R. 1992. The Myrtle Lake peatland. Pages 223–238 in H. E. Wright, B. A. Coffin, and N. E. Aaseng, eds. *Patterned peatlands of Minnesota*. University of Minnesota Press, Minneapolis.
- Janssens, J. A., B. C. S. Hansen, P. H. Glaser, and C. Whitlock. 1992. Development of a raised bog complex. Pages 189–222 in H. E. Wright, B. A. Coffin, and N. E. Aaseng, eds. *Patterned peatlands of Minnesota*. University of Minnesota Press, Minneapolis.
- Kuhry, P., B. J. Nicholson, L. D. Gignac, D. H. Vitt, and S. E. Bayley. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10–22.
- Malmer, N. 1993. Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. *Advances in Bryology* 5:223–248.
- Mathews, E., and I. Fung. 1987. Methane emissions from natural wetlands: global distribution, area, and environmental characteristics of sources. *Global Biogeochemical Cycles* 1:61–86.
- Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. *Nature* 298:156–159.
- Post, W. M., J. Pastor, P. Zinke, and A. Stangenberger. 1985. Global patterns of soil nitrogen storage. *Nature* 317:613–616.
- Rivers, J. S., D. I. Siegel, L. S. Chaser, J. P. Chanton, P. H. Glaser, N. T. Roulet, and J. M. McKenzie. 1998. A stochastic appraisal of the annual carbon budget of a large circumboreal peatland, Rapid River Watershed, northern Minnesota. *Global Biogeochemical Cycles* 12: 715–727.
- Strogatz, S. H. 1994. *Nonlinear dynamics and chaos*. Perseus Books, Reading, Mass.
- Swinehart, A. L., and G. R. Parker. 2000. Palaeoecology and development of peatlands in Indiana. *American Midland Naturalist* 143:267–297.
- Updegraff, K., J. Pastor, S. D. Bridgham, and C. A. Johnston. 1995. Environmental and substrate quality controls over carbon and nitrogen mineralization in a beaver meadow and a bog. *Ecological Applications* 5: 151–163.
- Updegraff, K., S. D. Bridgham, J. Pastor, P. Weishampel, and C. Harth. 2001. Ecosystem respiration response to warming and water-table manipulations in peatland mesocosms. *Ecological Applications* 11:311–326.
- Urban, N. R., S. J. Eisenreich, and S. E. Bayley. 1988. The relative importance of denitrification and nitrate assimilation in midcontinental bogs. *Limnology and Oceanography* 33:1611–1617.
- Verhoeven, J. T. A., E. Maltby, and M. B. Schmitz. 1990. Nitrogen and phosphorus mineralization in fens and bogs. *Journal of Ecology* 78:713–726.

- Walbridge, M. T. 1991. Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. *Ecology* 72:2083–2109.
- Weltzin, J. F., J. Pastor, C. Harth, S. D. Bridgham, K. Updegraff, and C. T. Chapin. 2000. Response of bog and fen plant communities to warming and water-table manipulations. *Ecology* 81:3464–3478.
- Weltzin, J. F., C. Harth, S. D. Bridgham, J. Pastor, and M. Vonderharr. 2001. Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia* (Berlin) 128:557–565.
- Wieder, R. K. 2001. Recent past, present, and future peatland carbon balance: an empirical model based on ²¹⁰Pb-dated peat cores. *Ecological Applications* 11:327–342.
- Wright, H. E., B. A. Coffin, and N. E. Aaseng, eds. 1992. *Patterned peatlands of Minnesota*. University of Minnesota Press, Minneapolis.

Associate Editor: Thomas E. Miller