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Improved simulation of poorly drained forests using Biome-BGC

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Summary Forested wetlands and peatlands are important in boreal and terrestrial biogeochemical cycling, but most general-purpose forest process models are designed and parameterized for upland systems. We describe changes made to Biome-BGC, an ecophysiological process model, that improve its ability to simulate poorly drained forests. Model changes allowed for: (1) lateral water inflow from a surrounding watershed, and variable surface and subsurface drainage; (2) adverse effects of anoxic soil on decomposition and nutrient mineralization; (3) closure of leaf stomata in flooded soils; and (4) growth of nonvascular plants (i.e., bryophytes). Bryophytes were treated as ectohydric broadleaf evergreen plants with zero stomatal conductance, whose cuticular conductance to CO_2 was dependent on plant water content. Individual model changes were parameterized with published data, and ecosystem-level model performance was assessed by comparing simulated output to field data from the northern BOREAS site in Manitoba, Canada. The simulation of the poorly drained forest model exhibited reduced decomposition and vascular plant growth (–90%) compared with that of the well-drained forest model; the integrated bryophyte photosynthetic response accorded well with published data. Simulated net primary production, biomass and soil carbon accumulation broadly agreed with field measurements, although simulated net primary production was higher than observed data in well-drained stands. Simulated net primary production in the poorly drained forest was most sensitive to oxygen restriction on soil processes, and secondarily to stomatal closure in flooded conditions. The modified Biome-BGC remains unable to simulate true wetlands that are subject to prolonged flooding, because it does not track organic soil formation, water table changes, soil redox potential or anaerobic processes.

Keywords: boreal forest, decomposition, moss growth, peatland modeling, soil flooding.

Introduction

Forested wetlands and peatlands cover at least 2.5×10^8 ha globally and are influential in global biogeochemical cycles (Matthews and Fung 1987, Lugo et al. 1990, Gorham 1991). In particular, much of the boreal forest is poorly drained, ranging from black spruce/sphagnum peatlands to true wetlands. Frequently saturated, these areas have high organic matter storage but their carbon sequestration dynamics are poorly understood (Zoltai and Martikainen 1996). Poorly drained areas often exhibit high and variable rates of primary production (Harden et al. 1997, Camill et al. 2001, Vitt et al. 2001), low decomposition rates and different successional pathways, with bryophytes frequently dominant (O'Neill 2000, Turetsky 2003).

Most general process-based models used to simulate forest biogeochemical cycles do not deal adequately with the unique characteristics of forested wetlands and other poorly drained ecosystems (Trettin et al. 2001). These characteristics include a high and fluctuating water table, high-clay or histosol soils, methane production and consumption, anoxic soil and low soil redox potentials and the presence of productive bryophyte communities. Dedicated wetland models (Frolking et al. 2001, Yu et al. 2001) incorporate many of the hydrological and biogeochemical complexities characteristic of wetlands but are of limited applicability in well-drained systems. General purpose biogeochemical process models frequently lack mechanisms to simulate biotic and abiotic processes in poorly drained soils (Peng and Apps 1999, Yarie and Billings 2002, Zhuang et al. 2003, Thornley and Cannell 2004), although efforts have been made to modify such models for application to poorly drained soils and even to continually inundated wetlands (e.g., Potter et al. 2001, Zhang et al. 2002, Grant 2003, Pietsch et al. 2003).

Biome-BGC is a biogeochemical and ecophysiological model that uses general stand information and daily meteorological data to simulate energy, carbon, water and nitrogen cycling (Running and Hunt 1993, Thornton 1998, White et al. 2000, Bond-Lamberty et al. 2005). Leaf area index controls radiation absorption in a Farquhar photosynthesis model for a homogeneous canopy separated into sunlit and shaded leaves (Kimball et al. 1997). Respiration components (heterotrophic, autotrophic growth and autotrophic maintenance) are treated separately and governed by temperature and water limitations. Net primary production is partitioned into biomass compartments following dynamic allocation patterns that reflect nitrogen limitations (Running and Gower 1991). Many of the assumptions and algorithms built into Biome-BGC reflect its origins in simulating well-drained temperate forests, although it has been applied at regional, continental and global scales (Churkina and Running 1998, Keyser et al. 2000, Kimball et

al. 2000). Several of these assumptions, as they relate to simulating forested wetlands, are outlined below.

Decomposition

Soil decomposition and mineralization dynamics change with soil drainage status. Aerobic microbial processes increase with increasing soil water content, until the displacement of air by water restricts oxygen diffusion and availability (Skopp et al. 1990). Thus, both high and low soil water contents limit microbial activity. Laboratory studies indicate that maximum microbial activity occurs at ~60% of the soil's total water-holding capacity for a wide range of soil types (Linn and Doran 1984, Doran et al. 1988, Skopp et al. 1990, Howard and Howard 1993). Field studies showing low water restrictions on decomposition are common, but studies showing high water restrictions are not (Kučera and Kirkham 1971, Schlentner and Van Cleve 1985, Silvola et al. 1996, O'Neill et al. 2002). Decomposition of detritus on the soil surface and in the upper soil horizons is similarly affected by water content (Landsberg and Gower 1997, Vogt et al. 1986, Wang et al. 2002). Decomposition in Biome-BGC is currently limited only by water, and not oxygen, availability.

Plant responses to soil flooding

In most woody plants, soil inundation results in suppressed leaf formation and leaf senescence, shoot dieback, inhibited root formation and root decay, and an overall reduction in tree growth or death (Kozlowski 1984, Armstrong et al. 1994, Pezeshki 2001, Kreuzwieser et al. 2004). The low soil redox potential of many flooded soils means greater oxygen demand within the soil and thus greater root stress (Pezeshki 2001). In response, leaf stomata close and photosynthesis is reduced (Pezeshki 2001), and there is a shift to anaerobic metabolism, which results in the production of a variety of phytotoxic compounds (Kreuzwieser et al. 2004), although the formation of hypertrophied lenticels, aerenchyma tissue and adventitious roots may help mitigate the effects of soil anoxia (Armstrong et al. 1994). Biome-BGC currently has no provision for the deleterious effects of soil flooding on plant growth.

Bryophytes

Bryophytes have an important role in carbon and nitrogen cycling in poorly drained areas (Turetsky 2003, Vitt et al. 2001), particularly in the boreal region but on a global scale as well (O'Neill 2000). The photosynthetic tissue of bryophytes lacks stomata, and molecular diffusion of CO_2 through water is about 10^4 times slower than through air; thus CO_2 leaf conductance is mediated by tissue water content (Silvola 1990, Williams and Flanagan 1998, Proctor 2000). In addition, because of their poikilohydric nature, bryophytes are limited in their capacity to use light and CO_2 at low water contents because the lack of water constrains or damages the photosynthetic apparatus (Green and Lange 1994). Finally, evaporation of externally conducted capillary water from ectohydric bryophytes often dominates water vapor flux in poorly drained systems (Dilks and Proctor 1979, Kim and Verma 1996, Proctor 2000). Thus, although the bryophyte photosynthetic apparatus is similar to that of a C_3 vascular plant (Green and Lange 1994), the stomatal-constrained assimilation model used by Biome-BGC cannot accurately model bryophyte photosynthesis.

Study goals

The goals of this study were to develop and apply relatively simple logic changes to Biome-BGC to improve its ability to model biogeochemical cycling of forested peatlands. Specifically, we examined the model's processes relating to soil drainage, aerobic soil respiration, the effects of soil anoxia on vascular plant growth and the unique role of bryophytes in many poorly drained systems. Changes to the model were tested individually and in concert at the stand level against published data from a variety of laboratory- and field-based studies. We focused particularly on the BOREAS NSA research sites in the central Canadian boreal forest, where soil drainage has been shown to have large effects on ecosystem structure, function and productivity (Harden et al. 1997).

Methods

The Biome-BGC model was modified in the areas of soil water inflow, aerobic soil processes, stomatal response to soil flooding and bryophyte assimilation and water relations to better simulate forested wetlands. For each of these areas, Biome-BGC's current algorithm or treatment is described along with a detailed description of the changes made.

Soil water inflow and outflow

Currently in Biome-BGC, soil water outflow always occurs if soil water exceeds field capacity. The algorithm that calculates each day's soil water outflow is:

$$w_{\text{out}} = \begin{cases} w - w_{\text{sat}} & : \quad w > w_{\text{sat}} \\ 0.5\left(w - w_{\text{fc}}\right) & : \quad w_{\text{fc}} < w \le w_{\text{sat}} \\ 0 & : \quad w \le w_{\text{fc}} \end{cases} \tag{1}$$

where outflow (w_{out}, kg H_2O m^{-2}) is a function of soil water content (w), saturation point (w_{sat}), and field capacity (w_{fc}; the latter two parameters are determined from soil structure): soil water above saturation runs off immediately, whereas half of soil water above field capacity drains away each day. There is no provision for soil water inflow; all water is directly from precipitation. A new algorithm was implemented:

$$w_{\text{in}} = \alpha_0 P \tag{2}$$

$$w_{\text{out}} = \begin{cases} \alpha_1\left(w - w_{\text{sat}}\right) & : \quad w > w_{\text{sat}} \\ \alpha_2\left(w - w_{\text{fc}}\right) & : \quad w_{\text{fc}} < w \le w_{\text{sat}} \\ 0 & : \quad w \le w_{\text{fc}} \end{cases} \tag{3}$$

where soil water inflow (w_{in}) is a function of daily precipitation (P). The site-specific parameter α_0 (a unitless fraction) is

determined from information about the area of the watershed relative to the area of the simulated forest and its hydrological response (Mitsch and Gosselink 1993, Zhang et al. 2002). Thus, α_0 determines how much additional water will arrive via lateral inflow for every unit of rain or snowmelt. The site-specific parameters α_1 and α_2 modulate the daily quantity of surface and ground water outflow, respectively. The range of soil water contents produced in several soil types and precipitation patterns were examined by running a bare-soil simulation in Biome-BGC with this new algorithm. (See Table A1 of the Appendix for details on Biome-BGC code changes.)

Aerobic soil processes

To simulate the effects of soil water on decomposition and mineralization, Biome-BGC uses daily soil water conditions to calculate a scalar (E_Ψ) between 0 and 1; this value is multiplied by the potential decomposition rate to calculate the actual (scaled) rate. A log-linear equation (Orchard and Cook 1983, Andrén and Paustian 1987) is used to calculate E_Ψ:

$$E_\Psi = \begin{cases} 0 & : \Psi < \Psi_{\min E} \\ \dfrac{\log(\Psi_{\min E}/\Psi)}{\log(\Psi_{\min E}/\Psi_{\max E})} & : \Psi_{\min E} \le \Psi \le \Psi_{\max E} \\ 1 & : \Psi > \Psi_{\max E} \end{cases} \tag{4}$$

where Ψ is the total soil water potential and $\Psi_{\min E}$ and $\Psi_{\max E}$ are boundary values; in the current version of Biome-BGC, $\Psi_{\min E} = -10.0$ MPa and $\Psi_{\max E}$ = soil saturation. This resulted in a smoothly increasing E_Ψ curve from dry to saturated soil, with $E_\Psi = 1$ only at saturation and above (i.e., ponding on the soil surface). The soil studied by Andrén and Paustian (1987) was light-textured and well drained, and a negative effect of extreme soil water on decomposition was neither found nor subsequently implemented in Biome-BGC.

A new algorithm was implemented to allow restriction of decomposition processes by both low and high soil water contents. Below a water content of $\theta_{\max E}$ (here all θ variables are relative, i.e., volumetric water content divided by total pore space; θ_v/ε), soil organic matter decomposition is log-linear and limited by water availability. Above this value, it is also limited, in a negative log-linear manner, by oxygen availability. No limitation occurs at $\theta = \theta_{\max E}$ (where also $\Psi_{\max E}$), and thus the new scalar $E_{\Psi,\theta} = 1$. This scalar is defined as:

$$E_{\Psi,\theta} = \begin{cases} 0 & : \Psi < \Psi_{\min E} \\ \dfrac{\log\left(\frac{\Psi_{\min E}}{\Psi}\right)}{\log\left(\frac{\Psi_{\min E}}{\Psi_{\max E}}\right)} & : \Psi_{\min E} \le \Psi < \Psi_{\max E} \\ \max\left(0.1, \dfrac{\log\left(\frac{\theta_{\max E}}{\theta_{\min E}+\theta_{\max E}-\theta}\right)}{\log\left(\frac{\theta_{\max E}}{\theta_{\min E}}\right)}\right) & : \theta_{\max E} < \theta \le \theta_{\min E} \\ 0.1 & : \theta > \theta_{\min E} \end{cases} \tag{5}$$

These four cases correspond, respectively, to no decomposition because of dryness; decomposition limited by water availability; decomposition limited by oxygen availability; and extremely limited decomposition owing to anoxia. The value of 0.1 in the last case reflects the results of Trumbore and Harden (1997). The parameters delineating these cases were set as: $\Psi_{\min E} = -20$ MPa; $\Psi_{\max E} = \Psi$ at $\theta_{\max E}$ ($\Psi_{\max E}$ is thus dependent on soil texture); $\theta_{\max E} = 60\%$; and $\theta_{\min E} = 100\%$.

Equation 5 is consistent with several published studies (Figure 1). Peak $E_{\Psi,\theta}$ values, at 55–65% relative volumetric water content, match published laboratory incubations (Linn and Doran 1984, Skopp et al. 1990). Changing $\Psi_{\min E}$ from –10 (used in the original model) to –20 MPa provided a better match to these data; numerous studies have documented microbial activity at such extremely low soil water potentials (Swift et al. 1979).

Stomatal response to soil flooding

In the current version of Biome-BGC, there is no recognition that soil flooding has complex and generally deleterious effects on plant growth. As a first step to improve the model in this area, an exponential-decay algorithm controlling stomatal closure in flooded conditions was implemented:

$$E_{\text{dsf}} = E_{\min} + (1 - E_{\min})e^{-\frac{5}{D}T_f} \tag{6}$$

where E_{dsf} is a scalar value, 0 to 1, that is multiplied by maximum stomatal conductance (g_s) to produce a scaled conductance. Three parameters are used to control stomatal closure in flooded conditions: two ($E_{\min}$ and D) are vegetation-specific ecophysiological constants (and thus specified by the user) describing the minimum value $E_{\min}$ to which E_{dsf} will decline after D days. The third parameter, the time in days that the soil has been flooded (T_f), is calculated by the model. The constant value (5) in Equation 6 ensures that E_{dsf} will drop to within 1% of $E_{\min}$ by day D after flooding; larger constants will produce faster declines in E_{dsf}. According to Equation 6, $E_{\text{dsf}} = 1$ (i.e., no effect) when $T_f = 0$.

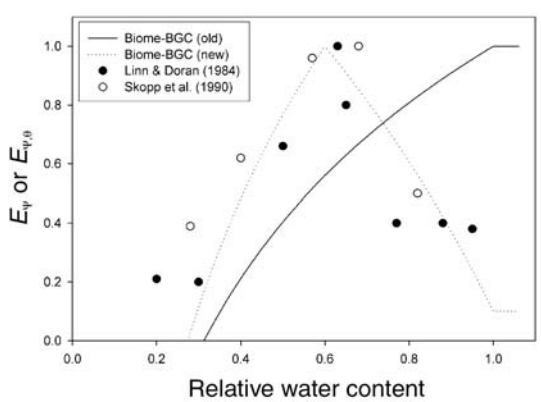

Figure 1. Simulated and observed decomposition versus relative soil water content (θ_V/ε, where θ_V is volumetric water content, and ε is total pore volume). Decomposition is expressed as a scalar (E_Ψ in the old algorithm and $E_{\Psi,\theta}$ in the new algorithm) that indicates the restriction of soil water and oxygen on the maximum potential decomposition rate. Simulated curves are based on a 12:54:34 (v/v) sand:silt:clay soil mix, similar to those studied by Linn and Doran (1984) and Skopp et al. (1990); values are redrawn from those studies.

In the model, soil flooding occurs whenever w is above w_{sat}. Because stomata generally open slowly after the cessation of soil flooding (Kozlowski 1984), the T_f value is initialized to 0 and calculated on a daily basis as:

$$T_f = \begin{cases} \max(T_f - 1, 0): & w \le w_{sat} \\ \min(T_f + 1, 15): & w > w_{sat} \end{cases} \quad (7)$$

Thus when w drops below w_{sat}, the T_f value "counts back" to 0, and the stomata slowly reopen. The maximum T_f value of 15 is arbitrary, but similar to the observed time required for stomatal conductance to recover from short-term flooding (e.g., Davies and Flore 1986). Equations 6 and 7 adequately reproduced stomatal behavior in the studied flood-tolerant and non-flood-tolerant tree species (Figure 2). Although this algorithm ignores the complexity of plant responses to soil flooding, particularly at long time scales (Kozlowski 1984, Armstrong et al. 1994, Pezeshki 2001), it introduces into Biome-BGC the phenomenon of reduced plant growth in poorly drained systems.

Bryophytes: assimilation

The photosynthetic apparatus of nonvascular bryophytes is similar in most respects to that of any shade plant (Green and Lange 1994), and the existing photosynthetic routines of Biome-BGC were employed to model bryophyte assimilation (A). The effects of low water content on A must be considered (Proctor 2000), because many studies have documented the effects of tissue desiccation on A (Skre and Oechel 1981, Titus et al. 1983, Williams and Flanagan 1996, Maseyk et al. 1999). A sigmoidal curve that is a function of relative water content (w_{rel}, plant water content divided by water content at full turgor) (Proctor 2000) was used to describe this effect:

$$E_A = \frac{1}{1 + e^{-(w_{rel} - 0.5)/b}} \quad (8)$$

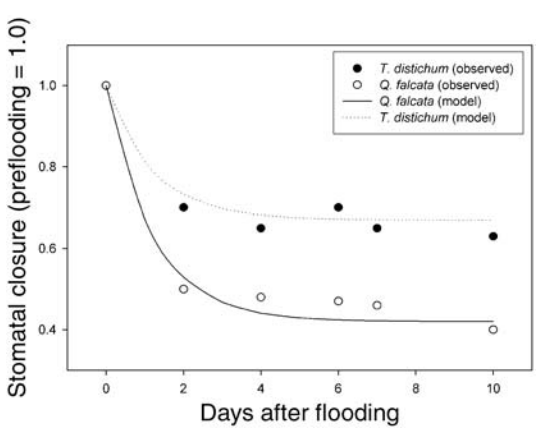

Figure 2. Stomatal closure as a function of number of days that the soil has been flooded. Data for *Taxodium distichum* and *Quercus falcata* are redrawn from Pezeshki et al. (1996). Curves were fit with Equation 6 (E_{min} = 0.67and D = 6 for *T. distichum*, E_{min} = 0.42 and D = 6 for *Q. falcata*).

where E_A is a scalar, 0 to 1, that is multiplied by the potential A, in the same manner that Biome-BGC models stomatal regulation of A in vascular plants. Equation 8 generally matched published data (Slavik 1965, Titus et al. 1983, Tuba et al. 1996, Williams and Flanagan 1998, Maseyk et al. 1999) (Figure 3a).

In supraoptimal water conditions, CO_2 diffusion to the photosynthetic apparatus is restricted, and thus total leaf conductance to CO_2 (g_c) must be computed as a function of leaf water content, and not stomatal conductance. We are aware of only one study examining this relationship: Williams and Flanagan (1998) used $^{13}CO_2$ data (Williams and Flanagan 1996) to calculate g_c and fit a fifth-order polynomial describing the relationship between water content and g_c. But the polynomial parameters have no easily understood meaning, and the equation takes on physiologically impossible values outside of the fitted data range. For these reasons we fit an inverse-sigmoidal model to the data of Williams and Flanagan (1998), modeling a 0–1 scalar E_{gc} as a function of w_{rel}:

$$E_{gc} = E_{gc\,min} + \frac{1 - E_{gc\,min}}{1 + e^{-(0.5 w_{rel=gcmin} - w_{rel} + 0.5)/b}} \quad (9)$$

where E_{gc} declines from (w_{rel} = 1, E_{gc} = 1) to ($w_{rel} = w_{rel=gcmin}$, $E_{gc} = E_{gcmin}$). If for simplicity we treat b, which describes the shapes of the sigmoid curve, as fixed, then this model requires only two parameters: E_{gcmin}, the minimum value to which E_{gc} declines, and $w_{rel=gcmin}$, the relative water content at which E_{gcmin} is attained. Equation 9 provided a good fit to the polynomial model used by Williams and Flanagan (1998) (Fig-

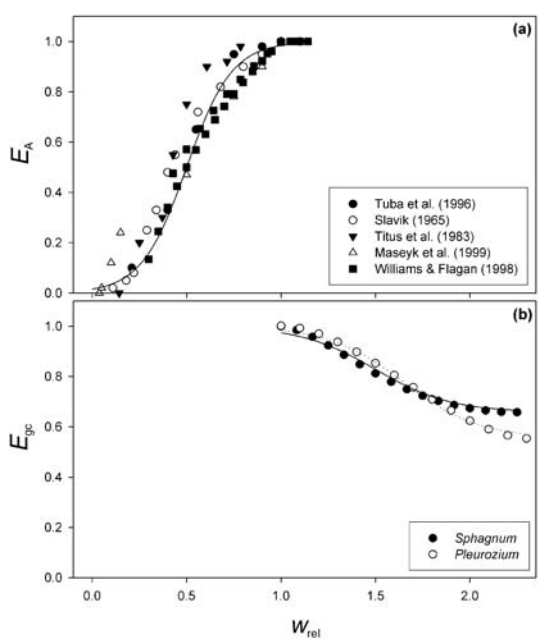

Figure 3. (a) Scalar effect of relative water content (w_{rel}) on assimilation capacity (E_A) for a variety of bryophyte studies. (b) Scalar effect of w_{rel} on total leaf conductance to CO_2 (E_{gc}) for *Sphagnum* and *Pleurozium*, from the data of Williams and Flanagan (1998). In both panels, the solid line shows the model described in the text.

ure 3b). Equation 9 is a "lower-level" approach, manipulating an input (g_c) into Biome-BGC's photosynthesis routine, whereas Equation 8 mechanistically down-regulates A, the output of this routine. We are unaware of studies giving a tractable approach to modeling the adverse effects of desiccation on the photosynthetic apparatus.

Bryophytes: water relations

Bryophytes are poikilohydric, which means that the water vapor partial pressure of the plant body is in equilibrium with ambient humidity (Green and Lange 1994). Water status of bryophytes is a function of factors such as cell turgidity and osmotic potential, local hydrology, distance from the water table and thallus water content (Dilks and Proctor 1979, Hayward and Clymo 1982, Proctor et al. 1998, Proctor 2000). A process-based model of bryophyte water potential (or water content) would require a complete rewriting of the Biome-BGC hydrological model, which was beyond the scope of this study. Instead, w_{rel}, which was used to regulate A and evapotranspiration (ET), was treated as a simple function of bryophyte water potential Ψ_{bry}, which in turn was a function of Ψ_{soil}.

The relationship between Ψ_{bry} and w_{rel} is distinguished by multiple phases as cell turgor pressure falls (Hayward and Clymo 1982, Proctor et al. 1998), but in general the two are inversely related, with a break point at the turgor-loss point (Ψ_{tloss}) (Proctor 2000). The relationship was treated as linear above Ψ_{tloss} and hyperbolic below it:

$$w_{rel} = \begin{cases} w_{rel\,=\,tloss}\dfrac{\Psi_{tloss}}{\Psi_{bry}} & : \Psi_{bry} \le \Psi_{tloss} \\ m\Psi_{bry} + b & : \Psi_{bry} > \Psi_{tloss} \end{cases} \tag{10}$$

where m and b denote the slope and intercept, respectively, of the line connecting the points (Ψ_{tloss}, $w_{rel\,=\,tloss}$) and ($\Psi_{wrel\,=\,1}$, 1). Relative water content at turgor loss ($w_{rel\,=\,tloss}$) is relatively invariant among species (Proctor 2000) and was fixed at 80%. The water potential variables Ψ_{soil} and Ψ_{bry} were assumed to be correlated linearly, with $\Psi_{bry} = \Psi_{soil} + \Psi_g$, where the effect of gravity (Ψ_g) is a function of the mean height (h) of the bryophyte layer above the water table multiplied by the gravitational constant (–9.8 m s^{-2}). Height is calculated based on bryophyte mass (Bond-Lamberty et al. 2005).

Figure 4, in effect a Höfler diagram with water potential taken as the x axis, shows the segmented model (Equations 10 and 11 (see below)) of the interaction between bryophyte water potential and water content. Although particular species are shown as examples, Biome-BGC is not generally used in species-specific simulations. Rather it simulates broader vegetation types defined by several basic traits: i.e., evergreen/deciduous, needle-leaf/broadleaf, C_3/C_4 photosynthesis, woody/nonwoody and now vascular/nonvascular. Thus we are less concerned with reproducing species-specific data exactly (e.g., Figure 4) than with the general relationship between Ψ_{bry} and w_{rel}.

Water conduction is partly or mostly external in most bryophytes, with the external portion highly variable among species (Dilks and Proctor 1979, Proctor 2000); the availability of this water for evaporation significantly affects ecosystem evapotranspiration patterns (Kim and Verma 1996, Proctor 2000). In each daily time step, bryophyte external water (kg H_2O m^{-2}) is computed as:

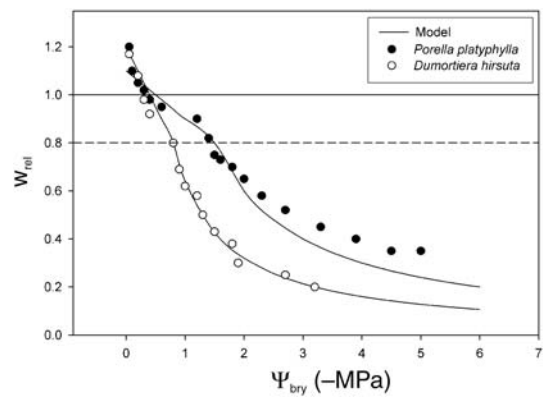

Figure 4. Bryophyte relative water content (w_{rel}) modeled using bryophyte water potential (Ψ_{bry}) as described in the text. Values for two example bryophytes, for both of which $w_{wrel=tloss}$ = 0.8, are redrawn from Proctor (2000; 1998). Solid horizontal line shows full-turgor point, and dashed line shows turgor-loss point.

$$w_{ext} = Mw_{rel}w_{wrel\,=\,1}f_{ext} \tag{11}$$

where M (kg C m^{-2}) is plant mass, $w_{wrel=1}$ (kg H_2O kg^{-1} C) is water content at full turgor, w_{rel} is calculated from Equation 10, and f_{ext} (dimensionless) is the fraction of water held externally. This water is added to any intercepted water in the bryophyte canopy and made available for evaporation via Biome-BGC's existing evapotranspiration routines. Water flow between the soil and bryophyte canopy is thus bidirectional, with the simulated bryophyte providing extra surface area for soil water evaporation.

Stand-level simulation and evaluation

In this study we (1) examined the effect of model changes on the ability of Biome-BGC to simulate poorly drained boreal forests, (2) briefly compared well and poorly drained forest simulations with field data from a variety of sources, and (3) performed a basic sensitivity analysis of model parameters introduced here. (In contrast, Bond-Lamberty et al. (2006) examined in detail the ability of Biome-BGC to replicate specific biomass and flux observations from well and poorly drained boreal chronosequences.) These goals were accomplished by performing simulations of well and poorly drained boreal forest stands, based on data from the BOREAS Northern Study Area in Manitoba, Canada (55°53′ N, 98°20′ W). These forests are dominated by black spruce (*Picea mariana* (Mill.) BSP), with bryophyte layers of feather mosses in well-drained areas and *Sphagnum* spp. in poorly drained areas. Soils generally derive from sedimentary materials deposited by glacial Lake Agassiz, with discontinuous permafrost present at 100–150 cm (Veldhuis 1995).

Simulation site parameters (Table 1) were identical to those of previous studies (Kimball et al. 1997, Amthor et al. 2001, Bond-Lamberty et al. 2005), except for the N fixation value, which was lowered to match values given by Landsberg and Gower (1997). Initial stand conditions were similar to those in a recently burned black spruce stand: no live plant tissue, no available mineral N, and moderate woody debris (4.7 kg C m^{-2}) and soil C pools (17.4 kg C m^{-2}). These values matched those used by Bond-Lamberty et al. (2006). The meteorological data sources were the regional and global coverage of meteorological parameters available from the NCEP/NCAR Reanalysis Project. We used 20 years of these data (1980–1999), which have been described elsewhere (Bond-Lamberty et al. 2005). Mean annual, January and July air temperatures were –3.7, –23.5 and 15.6 °C, respectively; mean annual precipitation was 488 mm, of which 318 mm fell as rain. These values are typical for mid-continental boreal regions. Two vegetation types were modeled, bryophyte and evergreen needleaf tree (Table 2). Bryophyte parameters were not generally site-specific; values for *Sphagnum* were used where possible, reflecting the ubiquity of this genus in boreal regions.

The lateral flow parameters, α_0, α_1 and α_2 (Equations 2 and 3), were not measured directly at the field sites. Mitsch and Grosselink (1993) report hydrological response (α_0) values of 0.04–0.18 for a variety of temperate North American watersheds, but values in poorly drained northern systems can be much higher, e.g, 0.16–0.67 (Kane et al. 2003 and references therein). We used values in the ranges reported by Zhang et al. (2002) for three northern wetlands (α_0 = 0.2–0.5, α_1 = 0.0–0.05, α_2 = 0.0002) such that simulated and observed soil water contents were roughly equal.

The effects of two model changes—decomposition and stomatal response to flooded soils—on ecosystem C cycling were examined by running 150-year simulations of black spruce growing in poorly drained conditions, with and without these changes; a second 150-year run compared well-drained and poorly drained forests. The effects of interannual climate variability were removed by the the ensembling method of Thornton et al. (2002), which factors out the relative timing of disturbance relative to climate variation by taking the mean of 20 simulations, with each simulation commencing at a different year in the meteorological data file. Simulation results thus represent the mean of an ensemble of model simulations, all performed with the multi-vegetation version of Biome-BGC (Bond-Lamberty et al. 2005).

A basic sensitivity analysis was conducted for the new parameters introduced into the model. These parameters were individually changed by ±10% and the resulting change in model output recorded. Following White et al. (2000), net primary production (NPP) was examined as the primary response variable. We assumed a uniform distribution of parameter values and did not examine interactive effects.

Table 1. Simulation site parameters, typical of a Canadian boreal black spruce forest. Water inflow and outflow values were calibrated; other values follow those given by Bond-Lamberty et al. (2005) and Kimball et al. (1997).

Parameter	Value	Unit
Elevation	260	m
Latitude	55.9	° N
Albedo	10.0	%
Effective soil depth	0.5	m
Sand:silt:clay ratio	26:29:45	%
N deposition	0.00036	kg N m^{-2} $year^{-1}$
N fixation	0.00010	kg N m^{-2} $year^{-1}$
Water inflow (α_0)		
Well drained	0.0	Fraction
Poorly drained	0.5	Fraction
Surface outflow (α_1)		
Well drained	1.0	Fraction
Poorly drained	0.01	Fraction
Subsurface outflow (α_2)		
Well drained	0.5	Fraction
Poorly drained	0.001	Fraction

Results and discussion

Implementation of poor soil drainage

Manipulation of the inflow parameter α_0 and the outflow parameters α_1 and α_2 in Equations 2 and 3 resulted in a wide range of mean soil water contents in a bare-soil simulation (Figure 5). The relative water contents shown in Figure 5 (35–95%) encompass ranges measured in poorly drained boreal forests (Cuenca et al. 1997, Stangel and Kelly 1999). Biome-BGC uses a simple sand:silt:clay:mineral soil model, and does not simulate organic soils explicitly. The substitution of mineral soil for organic soils is problematic, particularly for applications involving water conductivity and storage (Comer et al. 2000).

The α parameters introduced here are not easy to measure in the field (Mitsch and Gosselink 1993), but provide a conceptually simple method of allowing lateral inflow and retention of water in the simulated soil. Similar mechanisms have been employed by models such as Wetland-DNDC (Zhang et al. 2002). In theory, models such as RHESSys (http://geography.sdsu.edu/Research/Projects/RHESSYS) could be used to quantify α_0, α_1 and α_2; however, Biome-BGC's current hydrology is so simple that fine-tuning these parameters is probably not useful—broad drainage categories, similar in concept to broad plant functional types, are more useful. An alternative approach was taken by Pietsch et al. (2003), who extended Biome-BGC to account for seasonal flooding and groundwater infiltration, but at the cost of greatly expanding the input parameter set. The tradeoff between accurate complexity and coarse simplicity is a fundamental feature of modeling; the BGC family of models has traditionally chosen fewer parameters and simpler process representations when possible (Running and Hunt 1993).

Effect of model changes on vascular plant modeling

In a simulated poorly drained evergreen forest, two additions to the model (stomatal closure in flooded soils and anoxically

Table 2. Simulation ecophysiological parameters, with references, by vegetation type (bryophyte, BRY, and evergreen needle-leaf, ENL). Abbreviations: GS, growing season; C, carbon; N, nitrogen; SLA, specific leaf area; $g_s/g_c/g_{bl}$, stomatal/cuticular/boundary layer conductance, respectively; Ψ_L, leaf water potential; and VPD, vapor pressure deficit. A dash (–) indicates that the parameter is inapplicable to that vegetation type; a blank reference means that the value given is the default value distributed with BIOME-BGC; see White et al. (2000) for more details on these values.

Parameter	BRY Value	Ref[1]	ENL Value	Ref[1]	Unit
Phenology and turnover					
Transfer growth period	20		30		% GS
Litterfall period	20		30		% GS
Leaf turnover	0.2		0.12	9, 10	$year^{-1}$
Live wood turnover	–		0.7		
Whole plant mortality	0.01		0.01	9	$year^{-1}$
Allocation and N requirements					
Fine root C:leaf C	–		1.6	9, 10	
Stem C:leaf C	–		2.3	9, 10	
Live wood C:total wood C	–		0.1		
Coarse root C:stem C	–		0.3	9	
Growth C:storage C	0.5		0.5		
Leaf C:leaf N	40.0	13	59.6	11	
Leaf litter C:leaf litter N	87.0	13	90.0	11	
Fine root C:fine root N	–		60.0	11	
Leaf litter labile:cellulose:lignin	19:44:37	8	39:44:17	%	
Fine root labile:cellulose:lignin	–		30:45:25	%	
Dead wood cellulose:lignin	–		76:24	%	
Canopy parameters					
Water interception	0.01		0.01		LAI^{-1} day^{-1}
Light extinction	–0.5	1	–0.5		
SLA (projected area basis)	20.0	6	8.3	12	m^2 kg^{-1} C
Shaded/sunlit SLA	2.0		2.0		
All sided:projected leaf area	2.0		3.1		
Maximum vegetation height	0.1	5, 6	15.8	12	m
Mass at maximum height	1.0	6, 7	12.0	12	kg C m^{-2}
Leaf N in Rubisco	14.0		6.0		%
Maximum g_s	0.0		2.0	4, 11	mm s^{-1}
Maximum g_c	0.03	1, 4	0.01	4, 11	mm s^{-1}
Maximum g_{bl}	50.0	2, 4	80.0	4, 11	mm s^{-1}
Ψ_L start of g_s reduction	–		–0.5	4	MPa
Ψ_L complete g_s reduction	–		–1.7	4	MPa
VPD start of g_s reduction	–		1.0	4	kPa
VPD complete g_s reduction	–		4.1	4	kPa
Flooded g_s reduction (E_{min})	–		50	14	%
Days to reach g_s reduction (D)	–		10	14	days
Bryophyte-specific parameters					
w_c at full turgor ($w_{wrel = 1}$)	5.0	3, 5	–		H_2O:C
External water	0.5	3	–		fraction
Ψ_L at full turgor ($\Psi_{wrel = 1}$)	–1.0	3	–		MPa
Ψ_L at turgor loss (Ψ_{tloss})	–2.0	3	–		MPa
Excess H_2O g_c reduction (E_{gcmin})	67.0	1	–		%
w_{rel} at g_c reduction ($w_{wrel = gcmin}$)	2.3	1	–		

[1] References: 1. Williams and Flanagan (1998). 2. Kim and Verma (1996). 3. Proctor (2000). 4. Nobel (1999). 5. Titus et al. (1983). 6. Wang et al. (2003). 7. Harden et al. (1997). 8. Calculated from Scheffer et al. (2001) and Maass and Craigie (1964). 9. Bond-Lamberty et al. (2004). 10. Gower et al. (1997). 11. Ewers et al. (2005). 12. Bond-Lamberty et al. (2005). 13. Aerts et al. (2001). 14. Islam et al. (2003).

limited decomposition) had large effects on ecosystem carbon cycling metrics such as net primary production, NPP and net ecosystem production, NEP (Figure 6). Simulations without these changes produced unrealistic results (e.g., boreal tree NPP of ~500 g C m^{-2} $year^{-1}$ in Figure 6; cf. Gower et al. (2001)). The limitation of decomposition by anoxia had a much stronger effect than that of stomatal closure in flooded soils, greatly reducing both NPP and NEP. This was expected

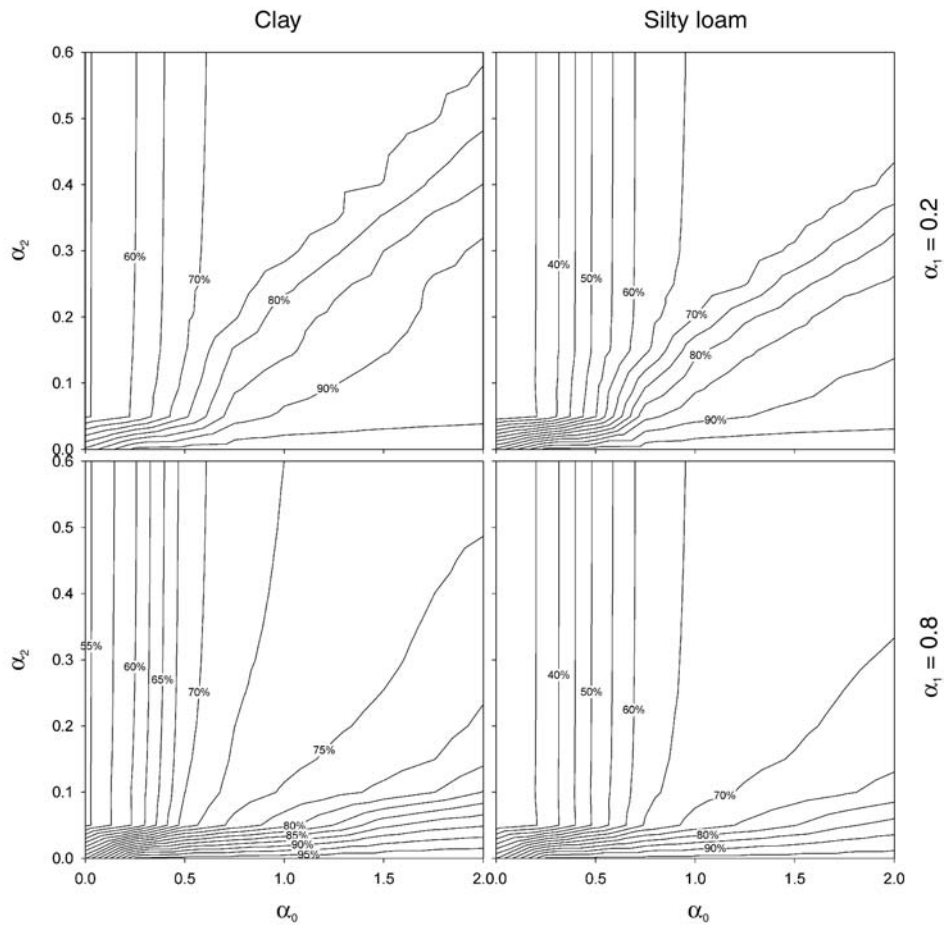

Figure 5. Soil water as a function of inflow (α_0) and subsurface outflow (α_2) rates for two soil types (clay and silty loam with sand:salt:clay ratios of 26:29:45 and 20:70:10, respectively) and two rates of surface outflow (α_1). Contours show means of relative soil volumetric water content (θ_v/ε, where θ_v is volumetric water content, and ε is total pore volume), based on a 40-year bare soil simulation in Biome-BGC. Effective soil depth was set to 1 m. Values of α_1 are given to the right of each row.

because black spruce (modeled here) is relatively flood tolerant, and boreal systems are generally nitrogen-limited; because of reduced decomposition, N immobilization operates in a feedback manner in the model (Bond-Lamberty et al. 2006). Some decomposition proceeds in flooded soils, but Biome-BGC does not explicitly model anaerobic processes (e.g., CH_4 production in anaerobic soils). The use of a nonzero value under anaerobic conditions for the $E_{\Psi,\theta}$ scalar in Equation 5 allows temperature-sensitive decomposition to proceed under anoxic conditions, without explicitly modeling the underlying anaerobic processes.

Stand-level simulation and comparison with observations

In a two-vegetation simulation, NEP recovered much more quickly from disturbance in the poorly drained forest simulation (data not shown) because decomposition was suppressed and tree NPP was much lower as a result of anaerobic soil conditions, which accords with results from many studies (O'Neill 2000). Simulated and observed values for NPP, NEP, biomass, and leaf area were generally close to observed values, although simulated tree NPP was higher than the observed value in the well-drained stand (Table 3). This discrepancy likely reflects the uncertainties surrounding some of the parameter estimates used, as discussed by Bond-Lamberty et

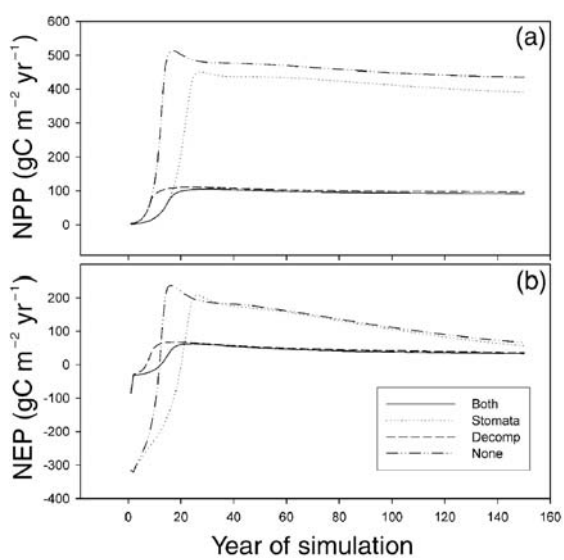

Figure 6. Individual and combined effects of two model changes on (a) net primary production (NPP) and (b) net ecosystem production (NEP) for the poorly drained forest simulation. Simulation had a single vegetation type, an evergreen needle-leaf vascular plant. Lines show response in original model ("none"), with effect of anoxia on soil decomposition ("decomp"), with stomatal closure in flooded soils ("stomata") and with both changes ("both").

al. (2005). In particular, Biome-BGC is known to be sensitive to leaf turnover and CO_2 conductance values (White et al. 2000). Few studies have documented these parameters in bryophytes, and we used values based primarily on vascular plants (Nobel 1999).

One point in time (e.g., Table 3) is insufficient to test how the model represents an ecosystem. Bond-Lamberty et al. (2006) compared this model's results to boreal forest pools and fluxes in much more detail and found that the new bryophyte model performed adequately but probably underestimated leaf area, although this is difficult to evaluate because of the paucity of observed data (Bond-Lamberty et al. 2006). The model's integrated photosynthetic response for bryophytes (Figure 7) fits observed results from many species well (Titus et al. 1983, Silvola and Aaltonen 1984, Silvola 1990, Tuba et al. 1996, Williams and Flanagan 1998). The next challenge is implementing and parameterizing a better soil water model for Biome-BGC.

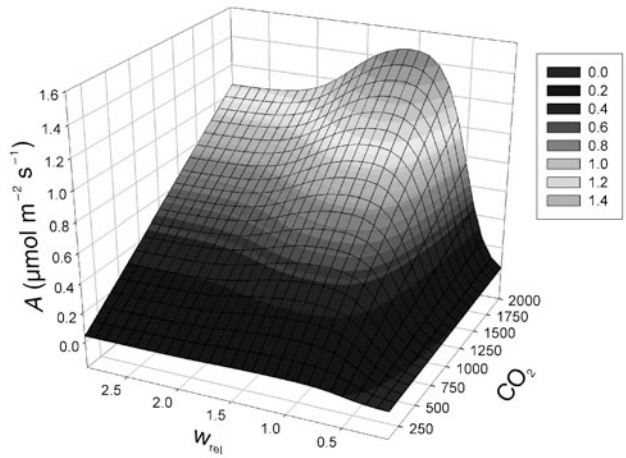

Figure 7. Effects of relative water content (w_{rel}) and ambient CO_2 concentration on bryophyte assimilation (A). Data are for sun leaf temperature of 14.8 °C, and a photon flux of 316 µmol m^{-2} s^{-1} per unit leaf area. Low bryophyte cuticular conductance (Table 2) results in a strong A response even at high CO_2 concentrations.

Sensitivity analysis

Varying most of the new parameters introduced here by ±10% affected NPP by 0–6%, with two notable exceptions (Table 4). The limiting effect of oxygen on soil processes was the most influential variable (see also Figure 6), and increasing $\theta_{min\ E}$ (i.e., reducing the O_2 restriction) resulted in large increases in NPP; the converse was also true, although with a weaker response. This matches expected peatland behavior, with nutrients increasingly immobilized in poorly drained conditions (Robinson 2002). In addition, the extent of stomatal closure in flooded soil (E_{min}) was highly influential, affecting bryophyte NPP more than vascular NPP, despite stomatal closure occurring only in vascular vegetation types. Net primary production in Biome-BGC is known to be sensitive to leaf and fine root C:N, maximum g_s, specific leaf area, and percent of leaf nitrogen in Rubisco (White et al. 2000); both $\theta_{min\ E}$ and E_{min} should be recognized as similarly influential in poorly drained systems. Conversely, many of the parameters had little or no influence on model output (Table 4), in particular most of the bryophyte parameters. More testing is needed to ascertain whether these non-significant effects are particular to the simulations performed here, or whether the model could be simplified by eliminating some input parameters.

Strengths and limitations of Biome-BGC

The changes to Biome-BGC implemented here improved Biome-BGC simulations of biogeochemical cycles in poorly drained boreal forests. The ability to simulate (1) overland water inflow from a surrounding watershed and reduced surface

Table 3. Comparison of simulated and observed values at well and poorly drained boreal forest sites near NSA-OBS (151 years old). Biomass, leaf area index (LAI), net primary production (NPP), and net ecosystem production (NEP) are compared for evergreen needle-leaf (ENL) and bryophyte (BRY) vegetation types. Observed values given are mean ± plot-to-plot standard deviation; simulated values are mean ± effect of interannual meteorological variability (Thornton et al. 2002).

Parameter	Well drained		Poorly drained		Units	Ref[1]
	Simulated	Observed	Simulated	Observed		
Biomass						
ENL	7.6 ± 0.0	6.7 ± 1.2	2.2 ± 0.0	2.3 ± 0.9	kg C m^{-2}	1
BRY	0.3 ± 0.0	0.5 ± 0.1	0.3 ± 0.0	0.4 ± 0.0	kg C m^{-2}	1, 2
LAI						
ENL	2.6 ± 0.1	3.5 ± 0.6	0.5 ± 0.0	0.7 ± 0.3	m^2 m^{-2}	3
BRY	5.7 ± 0.2	na	4.3 ± 0.1	na	m^2 m^{-2}	
NPP						
ENL	226 ± 32	119 ± 29	38 ± 2	63 ± 14	g C m^{-2} $year^{-1}$	4
BRY	55 ± 12	12 ± 6	42 ± 2	24 ± 12	g C m^{-2} $year^{-1}$	2, 4
NEP	44 ± 36	–19 ± 106	5 ± 5	11 ± 112	g C m^{-2} $year^{-1}$	4

[1] References: 1. Wang et al. (2003); 2. Gower et al. (1997); 3. Bond-Lamberty et al. (2002); 4. Bond-Lamberty et al. (2004).

Table 4. Sensitivity analysis for selected parameters. Parameters of the poorly drained forest simulation were changed (Δ, %) by the specified amount from the baseline values given in Table 2 or the text. Resulting change (all % relative to baseline output) in net ecosystem production (NEP), soil decomposition (R_H), and net primary production (NPP) at 150 years are given for bryophyte (BRY) and evergreen needle-leaf (ENL). Relevant equation numbers from the text are also given.

Parameter	Equation	Δ	ΔNPP		ΔR_H	ΔNEP
			BRY	ENL		
Surface inflow (α_0)	2	+10	–2	–1	–1	–2
		–10	2	2	2	2
Surface outflow (α_1)	3	+10	0	0	1	0
		–10	–1	–1	–1	–1
Subsurface outflow (α_2)	3	+10	0	0	0	0
		–10	0	0	0	0
Maximum decomposition ($\theta_{max\ E}$)	5	+10	5	3	4	2
		–10	–3	–2	–3	–2
Minimum decomposition ($\Psi_{min\ E}$)	5	+10	0	0	0	0
		–10	0	0	0	0
Minimum decomposition ($\theta_{min\ E}$)	5	+10	103	358	356	226
		–10	–13	–20	–21	–17
Flooded soil stomatal closure (E_{min})	6	+10	–25	8	–4	12
		–10	43	–8	10	–15
Days to reach E_{min} (D)	6	+10	0	0	0	0
		–10	0	0	0	0
Flooded soil g_c level (E_{gcmin})	9	+10	3	1	1	–1
		–10	–3	0	–1	1
Relative water content of E_{gcmin} ($w_{wrel = gcmin}$)	9	+10	5	2	1	–2
		–10	–8	–1	–2	3
Turgor-loss point (Ψ_{tloss})	10	+10	0	0	0	0
		–10	–1	0	0	0
Relative water content of Ψ_{tloss} ($w_{wrel = tloss}$)	10	+10	1	0	1	0
		–10	–1	0	–1	0
Leaf water potential at full turgor ($\Psi_{rwc = 1}$)	10	+10	2	0	1	0
		–10	–2	0	–1	0
Fraction external water ($f_{external}$)	11	+10	4	3	4	2
		–10	–3	–3	–3	–2

and subsurface drainage; (2) damping effects of anoxic soil on decomposition processes; (3) closure of leaf stomata in flooded soils; and (4) growth of bryophytes represents a significant advance for this model. We are aware that the use of dimensionless scalars to constrain model processes is conceptually problematic because they have no fundamental basis in biological or physical theory; nonetheless, most ecophysiological process models use such techniques.

Biome-BGC remains unable to simulate true wetlands, including forested peatlands that are flooded for long periods. Effective simulation of such systems requires modeling of anaerobic pathways, organic soil layers and peat deposits, vertical soil water flow, soil oxygenation, and redox potential (Trettin et al. 2001). These processes are not currently part of Biome-BGC, which employs simple soil, soil water, and soil heat transfer models (Running and Hunt 1993). Wetland-specific models remain better suited for such simulations (Frolking et al. 2001, Yu et al. 2001, Zhuang et al. 2001). The usefulness of Biome-BGC for ecosystem modeling derives from its broad applicability, its explicit biochemical treatment of photosynthesis, and known parameter sensitivities.

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Appendix

Table A1. A list of the new algorithms given in the text by equation number, along with the Biome-BGC function of the algorithm and the file in which it was implemented and additional notes. The table will be of most use when working with the model source code; this code, with a user's guide and extensive internal documentation, is available from the Numerical Terradynamic Simulation Group at the School of Forestry, University of Montana, USA, http://www.ntsg.umt.edu.

Equation	Function and file	Notes
2	`inflow()` in `outflow.c`	New function, called `outflow()`.
3	`outflow()` in `outflow.c`	Water balance check in `check_balance.c` modified to account for inflow and outflow
5	`decomp()` in `decomp.c`	Relative soil volumetric water content (θ) calculated in `soilpsi.c`.
6, 7	`canopy_et()` in `canopy_et.c`	Days since flooding (T_f) calculated in `soilpsi.c`.
8	`bry_a_reduction()`	New functions, all in `bryophytes.c`. Data structures for bryophytes defined in
9	`bry_gc_reduction()`	`bgc_struct.h`.
11	`bry_water_content()`	
12	`bry_ectohydric()`	