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## Sobol' sensitivity analysis of the Holocene Peat Model: What drives carbon accumulation in peatlands?

Anne Quillet,<sup>1</sup> Michelle Garneau,<sup>2</sup> and Steve Frolking<sup>3</sup>

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[1] Understanding the development of northern peatlands and their carbon accumulation dynamics is crucial in order to confidently integrate northern peatlands into global carbon cycle models. To achieve this, northern peatland models are becoming increasingly complex and now include feedback processes between peat depth, decomposition, hydrology, and vegetation composition and productivity. Here we present results from a global sensitivity analysis performed to assess the behavior and parameter interaction of a peatland simulation model. A series of simulations of the Holocene Peat Model were performed with different parameter combinations in order to assess the role of parameter interactions on the simulated total carbon mass after 5000 years of peatland development. The impact of parameter uncertainty on the simulation results is highlighted, as is the importance of multiple parameter interactions. The model sensitivity indicates that peat physical properties play an important role in peat accumulation; these parameters are poorly constrained by observations and should be a focus of future research. Furthermore, the results show that autogenic processes are able to produce a wide range of peatland development behaviors independently of any external environmental changes.

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### 1. Introduction

[2] Decomposition of organic matter in peatlands is less than its production. This allowed the buildup of a northern peatland carbon stock estimated at 273–547 Pg during the Holocene [Gorham, 1991; Turunen *et al.*, 2002; Yu *et al.*, 2010], which places peatlands among the major components of the global carbon cycle. However, carbon storage in peatlands is linked to several processes, which are the foundation of the complexity of these ecosystems. Indeed, the productivity and decomposition of peatlands are a function of hydroclimatic and geomorphic conditions. The physical and hydraulic properties of peat create specific conditions for decomposition and influence the ecosystem water balance. Moreover, nutrient availability affects vegetation composition, which in turn affects productivity, decomposition, hydrology, and thus carbon storage. Therefore, peatlands are described as complex adaptive systems and present a large variety of properties that make the

detection of the leading processes difficult [Belyea, 2009; Belyea and Baird, 2006].

[3] Several modeling studies have attempted to represent the processes of accumulation in peatland development [Clymo, 1984, 1992]. Following Clymo, models that include the different feedbacks between production, decomposition, and water balance have been developed [Baird *et al.*, 2012; Frolking *et al.*, 2001; Hilbert *et al.*, 2000; Morris *et al.*, 2012; Yu *et al.*, 2001a, 2001b]. Inclusion of a description of species-specific characteristics and their influence on peatland development is more recent [Frolking *et al.*, 2010; Heijmans *et al.*, 2008; Heinemeyer *et al.*, 2010].

[4] However, in order to assess the validity of postulates underlying these models, their capacity to reproduce processes, as they are observed in the field, has to be evaluated. In cases where the modeler focuses on understanding the processes rather than aiming to reproduce the state of a system at a specific location, sensitivity analysis appears to be an interesting tool. Sensitivity analysis explores the variability of the model response when different parameter values are applied, quantifying the influence of the various parameters on the model results. Sensitivity analyses can be grouped into two types: local sensitivity analysis and global sensitivity analysis (GSA). Whereas local sensitivity analysis focuses on a limited number of parameter values and tests their influence on the model output, GSA has the advantage of accounting for interactions between parameters in the model. This is particularly valuable when nonlinear behaviors are expected. Saltelli *et al.* [2004, 2008] reviewed various sensitivity analysis methods and their application potential in great detail.

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[5] Although in many studies model evaluation is limited to local sensitivity analyses [e.g., *Frolking et al.*, 2010; *Hilbert et al.*, 2000; *St-Hilaire et al.*, 2010; *Wania et al.*, 2009], *Quillet et al.* [2013] gained additional insight into the sensitivity of the Holocene Peat Model (HPM) [*Frolking et al.*, 2010] by using a screening method in addition to local sensitivity analysis and comparing the results of the two methods. The authors ranked the model parameters according to their influence on the total carbon mass. Moreover, they pointed out that some parameters might be involved more or less strongly in interactions with other parameters. In the current paper, we propose to investigate the role of the interactions in more detail. We postulate that the analysis of the influence of parameter interactions on carbon accumulation simulated by the HPM will enable the exploration of the processes controlling carbon accumulation in the field and more specifically highlight the role of the different groups of plant functional types (PFTs) in the carbon accumulation process. For these purposes, we propose to perform a GSA and a calculation of sensitivity indices following *Sobol'* [1993] and to examine the influential interactions in more detail.

## 2. The HPM

[6] A description of the main processes within the HPM is provided by *Quillet et al.* [2013] and in the following sections, and a more detailed description is given by *Frolking et al.* [2010]. The model simulates the development of an ombrotrophic peatland in one dimension, i.e., at one point. It reproduces the development of a peatland at its center and delivers a year-by-year reconstruction of production, decomposition, hydraulic properties, and vegetation assemblages over several millennia. Outputs include annual peat thickness, peat composition, carbon accumulation, and water table depth. The HPM, in its original version, is parameterized to represent specific peatlands: located in northern latitudes, reflecting a fen-bog transition, and with negligible trees and soil mineral effects. The model is a semiempirical model based on laboratory and field data (e.g., decomposition rates of different species) as well as on numerical representations (e.g., hydraulic properties derived from known functions).

### 2.1. Vegetation Representation and Productivity

[7] The model is based on the assumption that water table depth and nutrient status influence vegetation composition at the surface [e.g., *Rydin and Jeglum*, 2006]. A particularity of the HPM is the inclusion of 12 PFTs differentiated through their ability to grow at different water table depths and under different conditions of nutrient availability, with the use of peat depth as a proxy for nutrient status (based on observations by *Tuittila et al.* [2007, 2013] and *Väiliranta et al.* [2007]). For example, certain PFTs have an optimal productivity when the water table is high and the peat height is low, i.e., when nutrient availability is high. Other PFTs have optimal productivity when the water table is low and the peat height is high enough to isolate the surface from groundwater-derived nutrients. Trees are not represented yet in the model. These characteristics are represented by PFT-specific parameters describing the impact on productivity for conditions on each side of the optimal mean annual water table depth and optimal peat depth (Table 1). Moreover, the different PFTs also have different

litter properties (aboveground versus belowground litter production and litter quality or decomposability).

### 2.2. Water Balance and Hydraulic Properties

[8] In the HPM, an annual water balance is estimated from the precipitation ( $P$ ) regime, potential evapotranspiration (ET) reduced as a function of water table depth, and estimated runoff based on both a site-specific component and peatland slope. Three parameters control the runoff:  $R_0$ , which controls the net amount of water exiting the system (similar to an outlet);  $c_8$ , which controls the amount of water loss due to the general slope of the peatland (this slope is calculated by the model as proportional to total peat height when peat height reaches a certain level); and  $T_0$ , which influences runoff through transmissivity (Table 1). The amount of water resulting from this water balance calculation is added (subtracted) each year, and the water table depth can be inferred when different peat properties are taken into account.

[9] Hydraulic properties of peat depend on both water table depth and peat bulk density and thus on vegetation properties (particularly on decomposition properties). Peat layers identified as “well decomposed” have lower hydraulic conductivity than fresh peat layers. Several parameters ( $W_{\text{opt}}$ ,  $W_{\text{sat}}$ , and  $W_{\text{min}}$ ) characterize the water-filled pore space and its link to the saturation effect (Table 1).

### 2.3. Peat Decomposition

[10] Peat decomposes continuously (i.e., year after year) and follows different decomposition rates depending on the PFT (the  $k$  values in Table 2 are initial decomposition rates; these rates decline linearly with a fraction of total mass lost as the peat decomposes [e.g., *Frolking et al.*, 2001]). As a result, the formed peat includes a portion of decomposed peat originating from the different PFT portions of a former vegetation cover. At the end of each simulated year, a new water table depth is calculated and so some peat can transition from unsaturated to saturated. The impact of this transition on decomposition is represented by a gradient of anoxia below the mean annual water table (described by the anoxia scale length  $c_2$ ; Table 1). Decomposition rates differ according to the position of the layer in the peat column. Peat bulk density is calculated for each annual cohort, and it increases nonlinearly by a maximum of  $\Delta\rho$  from a prescribed minimum value ( $\rho_{\text{min}}$ ) as the cohort decomposes and mass is lost. The increase in bulk density is a function of cohort mass lost and controlled by two parameters,  $c_3$  and  $c_4$  (Table 1).

### 2.4. Peat Accumulation

[11] Peat accumulates when productivity exceeds decomposition. Productivity depends on the PFTs (each of which has a specific relative productivity in order to represent vegetation composition according to realistic distribution values; see Table 2) and on the total maximum potential net primary productivity ( $\text{NPP}_{\text{pot}}$ ), which is a site-specific parameter (Table 1). Depending on water table depth and peat depth, different PFTs dominate the vegetation assemblages. Peat accumulation thus takes into account the litter properties of each PFT with respect to its representation in the assemblage.

**Table 1.** Characteristics of the 26 Selected Model Parameters and Their Associated Range and Distribution for the Sensitivity Analysis<sup>a</sup>

Parameter Description	Parameter Abbreviation	Units	Range		Probability Density Function
			Minimum Value	Maximum Value	
Annual precipitation	$P$	$\text{m yr}^{-1}$	0.30	1.20	normal
Factor for annual potential evapotranspiration	$ET_f$	dimensionless	0.10	1.00	normal
Water table depth threshold for maximal evapotranspiration	$z_1$	m	0.01	0.40	uniform
Annual runoff adjustment factor	$R_0$	$\text{m yr}^{-1}$	-0.01	0.10	uniform
Increase in runoff with peat height	$c_8$	$\text{m}^{-1}$	0.05	0.30	uniform
Minimum profile relative transmissivity	$T_0$	dimensionless	0.05	0.80	normal
Maximum potential NPP	$NPP_{\text{pot}}$	$\text{kg m}^{-2} \text{yr}^{-1}$	0.50	5.00	uniform
Scale length for the anaerobic effect on decomposition rate	$c_2$	m	0.10	2.00	uniform
Decomposition rate multiplier at annual mean water table depth	$W_{\text{sat}}$	dimensionless	0.15	0.45	uniform
Minimal decomposition rate multiplier	$f_{\text{min}}$	dimensionless	0.0001	0.01	uniform
Minimum litter/peat degree of saturation	$W_{\text{min}}$	dimensionless	0.01	0.05	uniform
Fraction of initial mass input remaining at which bulk density reaches half of its amplitude	$c_3$	dimensionless	0.10	0.30	uniform
Controls steepness of the bulk density curve	$c_4$	dimensionless	0.05	0.20	uniform
Minimum peat bulk density	$\rho_{\text{min}}$	$\text{g m}^{-3}$	20.00	70.00	normal
Maximum potential increase in peat bulk density	$\Delta_\rho$	$\text{kg m}^{-3}$	55.00	140.00	uniform
Peat depth for optimum productivity for PFTs 7 and 8	$h_{\text{PD}i}^{\text{opt}}$	m	50% <sup>b</sup>	150% <sup>b</sup>	normal
Productivity curve variance for the shallow side of the optimum	$\sigma_{\text{PD}i}^-$	m	50% <sup>b</sup>	150% <sup>b</sup>	normal
peat depth for PFTs 7, 8, and 10					
Productivity curve variance for the shallow side of the optimum water table depth for PFT 4	$\sigma_{\text{WT}4}^-$	m	75% <sup>b</sup>	125% <sup>b</sup>	normal
Relative net primary productivity for PFTs 5, 7, and 8	$NPP_{\text{rel}i}$	dimensionless	50% <sup>b</sup>	200% <sup>b</sup>	uniform
Decomposition rates for PFTs 3 and 8	$k_{0_i}$	$\text{yr}^{-1}$	75% <sup>b</sup>	125% <sup>b</sup>	normal

<sup>a</sup>After *Quillet et al.* [2013]. Example of notation for PFT parameters:  $h_{\text{PD}7}^{\text{opt}}$  is peat depth optimum productivity for PFT 7, lawn *Sphagnum*.

<sup>b</sup>Percentage is of the nominal values (Table 2).

## 2.5. Model Calibration and Initiation

[12] The inputs needed in the model are  $NPP_{\text{pot}}$ ,  $P$  regime, as well as minimum bulk density ( $\rho_{\text{min}}$ ) and magnitude of the bulk density ( $\Delta_\rho$ ) expected at the site.

[13] Initialization is set by constraining the model to accumulate peat until the total peat height reaches a certain level (here 0.15 m). During this period, the water balance is not dynamic and the water table depth is prescribed. The water table depth during initialization is shallow (i.e., 0.07 m).

## 3. Global Sensitivity Analysis

[14] A common method for assessing the influence of parameters is the analysis of the influence of the parameters

on one output of the simulation individually, i.e., a local sensitivity analysis. While one parameter value changes, all others remain constant. This method gives insight into the impact of changing parameter values on the value of the output. However, it does not take account of interactions between model parameters or the potential nonlinearity of the model results. This drawback is highlighted in several studies [e.g., *Campolongo et al.*, 2011; *Saltelli et al.*, 2008] as well as in the study of *Quillet et al.* [2013] also dealing with the HPM. Moreover, interactions between parameters are not taken into account in local sensitivity analysis. Global sensitivity analysis aims to fill this gap by considering the entire model space as well as higher-order interactions (i.e.,  $n$ -way interactions between parameters for  $n$  greater than 1). The chosen variance-based method has the advantage of being model independent; that is, nonlinearity or

**Table 2.** Nominal Values of PFTs<sup>a</sup>

PFT	PFT ID	$Z_{\text{WT}i}^{\text{opt}}$	$\sigma_{\text{WT}i}^-$	$\sigma_{\text{WT}i}^+$	$h_{\text{PD}i}^{\text{opt}}$	$\sigma_{\text{PD}i}^-$	$\sigma_{\text{PD}i}^+$	$NPP_{\text{rel}}$	$k_0$
		(m)	(m)	(m)	(m)	(m)	(m)		
Grass	1	0.40	0.40	0.40	0.01	1.00	1.00	0.75	0.20
Minerotrophic herb	2	0.10	0.30	0.30	0.30	1.00	1.00	0.75	0.30
Minerotrophic sedge	3	0.10	0.40	0.40	0.10	2.00	2.00	1.00	0.30
Minerotrophic shrub	4	0.20	0.20	1.00	1.00	2.00	2.00	0.50	0.20
Brown moss	5	0.01	0.20	0.05	0.10	1.50	1.50	0.50	0.10
Hollow <i>Sphagnum</i>	6	0.01	0.20	0.05	2.00	1.00	19.00	0.50	0.10
Lawn <i>Sphagnum</i>	7	0.10	0.30	0.40	2.00	1.00	19.00	0.50	0.07
Hummock <i>Sphagnum</i>	8	0.20	0.10	0.50	2.00	1.00	19.00	0.50	0.05
Feather moss	9	0.40	0.40	0.60	4.00	6.00	19.00	0.25	0.10
Ombrotrophic herb	10	0.20	0.20	0.20	4.00	2.00	19.00	0.25	0.25
Ombrotrophic sedge	11	0.20	0.30	0.30	4.00	2.00	19.00	0.50	0.15
Ombrotrophic shrub	12	0.30	0.30	1.00	4.00	2.00	19.00	0.50	0.15

<sup>a</sup>After *Frolking et al.* [2010].

nonmonotonicity in the model does not have an impact on the results of the sensitivity calculation, because the results are based on the relationship between the parameters and the output only [Saltelli *et al.*, 2004]. The method consists of comparing distinct runs of the largest possible set of simulations. Each simulation is run with a unique parameter combination. A very high number of runs are needed to cover the model space and the possible interactions among all parameters present in the model. Analyzing high-order interactions between parameters is very computationally expensive. The number of runs is calculated as follows:

$$C = \left(2 + \sum_{i=1}^n \binom{k}{i}\right) \times 2^{j+4}, \quad (1)$$

where  $C$  is the number of runs,  $n$  is the maximum order of the sensitivity indices (e.g., 2 for two-way interactions) to be computed,  $k$  is the number of parameters, and  $j$  is called base sample, which can assume values of 0, 1, 2, 3, etc., depending on the computing resources available.

### 3.1. Screening Method

[15] In order to fulfill a GSA with the HPM, 127 parameters had to be considered. As the GSA is far too expensive to be performed on so many parameters (i.e., more than 5 million runs would be required), a screening method allowing the sorting of parameters according to their influence on the simulation results had to be applied first. The method chosen is the Morris elementary effects screening method [Morris, 1991] that consists of randomly choosing a series of parameter combinations that best represent the model space. The calculation of the influence of each parameter on the output enables the filtering of noninfluential parameters. The Morris elementary effects for total carbon mass are presented in the work of Quillet *et al.* [2013]. After screening, the number of relevant parameters was reduced to a group of 26 parameters (as described in Table 1).

### 3.2.. Sobol' Indices

[16] At this stage, it is possible to complete the experiment by an estimation of the influence of these parameters, as well as that of interactions between them, on the variance of the output. To assess the role of each parameter or interaction between parameters, sensitivity measures are needed. The chosen measures are based on Sobol' [1993] and therefore known as Sobol' indices. These indices aim at representing the bias in the variance of the output (here total carbon mass) that can be attributed to a parameter or a combination of parameters (in the case of interactions). The measure of the influence  $S_i$  of the parameter  $P_i$  on the variance  $V$  of the output  $Y$  is called a first-order effect and defined as follows:

$$S_i = \frac{V(E(Y|P_i))}{V_y}. \quad (2)$$

[17] This measure represents the main effect contribution of the parameter  $P_i$  to the variance of the output. Thus, if the model is additive, then the sum of the  $S_i$  of all parameters equals 1.

[18] An interaction is defined as the combined effect of two parameters that exceeds the sum of their individual effects. This effect is called a second-order effect of two parameters,  $P_1$  and  $P_2$ , and can be computed as

$$S_{P_1P_2} = \frac{V(E(Y|P_1, P_2))}{V_y} - \frac{V(E(Y|P_1))}{V_y} - \frac{V(E(Y|P_2))}{V_y} \quad (3)$$

[19] Even though the number of parameters has been restricted to 26 through the screening method, the number of computations necessary to assess the second-order interactions of all model space parameters with confidence is still high (~45,000 runs with a  $j$  value of 4 in equation (1)). We thus limited our analysis to the second-order interactions.

### 3.3. Experimental Setting

[20] For this study, the experiment followed the setting presented for the screening experiment performed by Quillet *et al.* [2013]. The calculation of the Sobol' indices is based on the results of the simulation runs. Nevertheless, the manner in which parameter values are sampled matters. Quasi-random sampling is chosen because it more adequately represents the model space than does the traditional Monte Carlo sampling [Beven, 2009; Saltelli *et al.*, 2008]. The quasi-random sample contains parameter values following a specific range and probability distribution that are assigned to each parameter individually. When the distribution of the parameter is unknown, a uniform distribution was assumed (Table 1). The quasi-random sampling as well as the calculation of the Sobol' indices were performed with the software package SimLab 3.2.6 [Joint Research Centre of the European Commission, 2011].

[21] In addition, the experiment was designed so that each simulation had the same initialization period. During initialization, the parameters are represented by nominal values from the Mer Bleue Bog located in Ontario, Canada (Tables 1 and 2) [Roulet *et al.*, 2007]. In the current setting, the initialization lasts 8 years. Parameter values change when the simulation becomes dynamic, i.e., as soon as the accumulating peat reaches 15 cm of thickness.

[22] Regarding the output, we focus here on the total quantity of carbon sequestered (kg C) after 5000 simulation years. This value can be compared to data sets, and carbon sequestration processes are now very important topics in peatland science. As it is the net result of several processes, this output is a useful metric to evaluate the overall model.

## 4. Results

[23] With the help of a screening method, Quillet *et al.* [2013] identified the 26 parameters having a significant influence on total carbon mass in the HPM. In addition, they showed that slightly different parameter values could lead the model simulations on different peatland development trajectories. Indeed, different fen-bog transition pathways could be identified, while simulations showed comparable output responses.

[24] Of the 26 influential parameters identified by Quillet *et al.* [2013],  $NPP_{pot}$  and the decomposition rate multiplier  $W_{sat}$  had a strong influence on total carbon mass. The authors could also identify three groups of parameters that are potential sources of uncertainty in peat accumulation: a group of parameters related to the peatland water balance, a group of PFT-specific parameters, and a group of parameters controlling the shape of the bulk density curve. These are identified as parameters involved in interactions with other parameters and associated with nonlinearity. The GSA

performed here is based on these 26 parameters. A description of parameters and their value ranges can be found in Table 1.

#### 4.1. Main Processes Affecting Carbon Mass

##### 4.1.1. Maximum Potential Productivity

[25] First-order effects highlight the direct influence of a parameter on the total carbon mass. Figure 1a shows that  $NPP_{pot}$  has a high influence on the total carbon mass. This direct link between the quantity of carbon and the potential productivity is straightforward because enhancing productivity potential allows the system to accumulate more carbon.

[26] The sum of the second-order effects of each parameter gives an indication of the influence of the interactions involved for each parameter (Figure 1b). The  $NPP_{pot}$  also has the first rank here. The influence of interactions of this parameter with other parameters is very high. The variability of total peat mass is thus linked to the potential NPP available. The total effects of each parameter (Figure 1c) give an estimate of the overall influence of the parameter on total peat mass. More details on the nature of interactions are presented in Figure 2. For example, Figure 2f shows the second-order effects of  $NPP_{pot}$ . Only six parameters interact significantly with  $NPP_{pot}$ , with all other nonpositive values not shown because they are not significant. A strong interaction between  $NPP_{pot}$  and the minimum profile relative transmissivity ( $T_0$ ) influences total carbon mass. Indeed,  $NPP_{pot}$  has an impact on the overall thickness of the peatland in the HPM and  $T_0$  influences the total runoff. The combination of both parameters influences the water table depth of the peatland, which in turn controls productivity (Figure 3). As a result, total carbon mass is sensitive to these parameters, which should thus be better constrained to improve the simulation.

##### 4.1.2. Physical Peat Properties

[27] The  $c_2$  parameter, minimum and maximum increases in peat bulk density ( $\rho_{min}$  and  $\Delta\rho$ , respectively), and parameters controlling the shape of the bulk density curve ( $c_3$  and  $c_4$ ) (Table 1) show both direct (Figure 1a) and indirect (Figure 1b) impacts on the total carbon mass. These parameters influence peat hydraulic properties, water balance and decomposition, and thus the bulk density profile. Apart from  $\rho_{min}$  and  $\Delta\rho$ , these parameters are difficult to constrain with field data. They can therefore be considered as parameters inducing uncertainty in the simulations.

[28] Similarly to  $c_2$ ,  $W_{sat}$  is a parameter for the anoxia impact on decomposition of the peat located below the mean annual water table. Although this parameter has a low direct effect on carbon mass (Figure 1a), it is involved in a series of interactions (Figure 2i). Besides its interaction with bulk density-associated parameters ( $\Delta\rho$  and  $c_4$ ),  $W_{sat}$  also interacts with the  $NPP_{pot}$  and several parameters related to the description of the PFT productivity.

##### 4.1.3. Water Balance

[29] Several parameters influencing the water balance calculation have an impact on total carbon mass. These parameters are annual  $P$ , the factor for annual potential ET ( $ET_f$ ), the annual runoff adjustment factor ( $R_0$ ), the increase in runoff with peat height ( $c_8$ ),  $T_0$ , and the water table depth threshold for maximal ET ( $z_1$ ). Of these,  $c_8$  and  $T_0$  show a strong influence on the output, while  $c_8$  impacts mostly

through its first-order effect and  $T_0$  through its second-order effect, where it interacts with  $NPP_{pot}$ , as described earlier. While  $P$  can be relatively well constrained if paleoreconstructions of  $P$  are available for the site studied, it is challenging to estimate other parameter values and thus difficult to reduce the uncertainty in the simulation.

[30] To conclude this section, two major shortcomings hinder the improvement of the representation of system processes: bulk density and water balance. In the model, the representation of the transition from low to high bulk density is not very realistic and water balance is poorly represented at a yearly time scale.

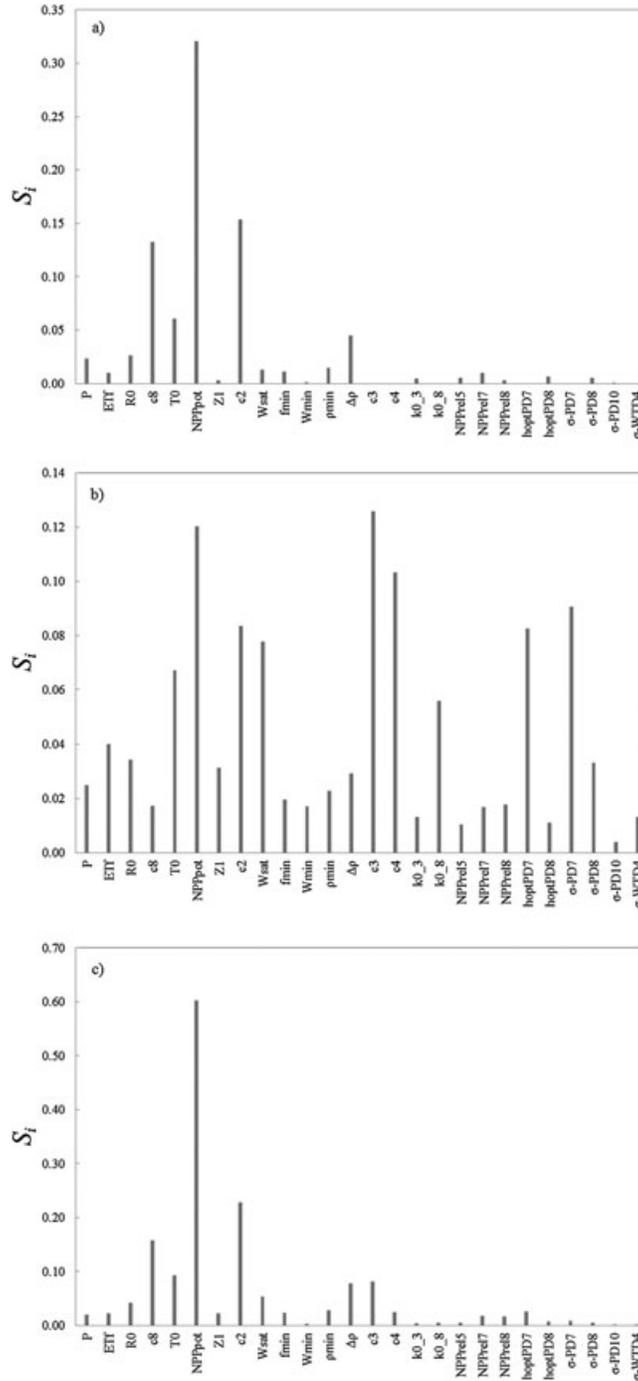
#### 4.2. Relationships Between PFTs and Accumulated Carbon Mass

##### 4.2.1. Influence of Various PFTs on Carbon Mass

[31] Several PFT parameters showed low first-order effects and substantial second-order effects (Figures 1a and 1b). These included parameters describing the decomposition capacity of minerotrophic sedges ( $k_{0_3}$ ) and hummock *Sphagnum* ( $k_{0_8}$ ), parameters describing the productivity potential of brown mosses ( $NPP_{rel5}$ ), lawn *Sphagnum* ( $NPP_{rel7}$ ), and hummock *Sphagnum* ( $NPP_{rel8}$ ), as well as others describing the optimal peat depth and NPP sensitivity on the shallow side of this optimum for lawn *Sphagnum* ( $h_{PD7}^{opt}$  and  $\sigma_{PD7}^-$ , respectively), hummock *Sphagnum* ( $h_{PD8}^{opt}$  and  $\sigma_{PD8}^-$ , respectively), and ombrotrophic herb productivity ( $\sigma_{PD10}$ ). An additional parameter describes the NPP sensitivity of minerotrophic shrubs to water table depth on the shallow side of the optimum:  $\sigma_{WTD4}$ . However, this is the only parameter showing the influence of the water table depth as a proxy for productivity. Parameterization of productivity through water table depth constraints thus seems to have limited impact on the simulation results. Overall, it is noteworthy that among the 12 PFTs competing in the model, the characteristics of only 5 PFTs appear to have an impact on total carbon mass. From this observation, we can conclude that the other PFTs have limited impact on the response of the model. However, several characteristics of PFT 7 (lawn *Sphagnum*) and PFT 8 (hummock *Sphagnum*) appear to have a particular impact on the output, showing high second-order interactions (Figure 1b). This result raises the question of the function of these PFTs in the model.

##### 4.2.2. The Role of Lawn *Sphagnum* (PFT 7)

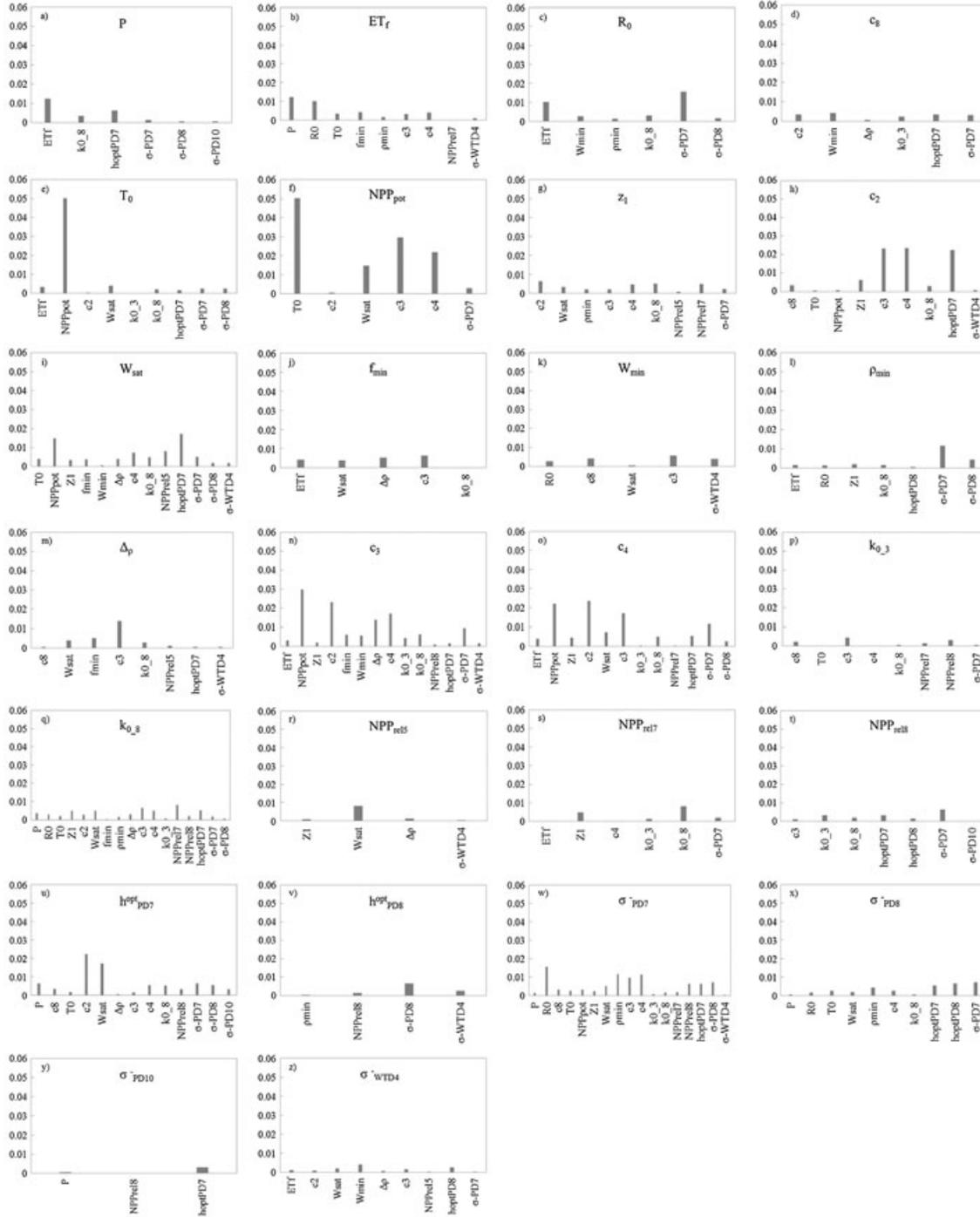
[32] Two lawn *Sphagnum* parameters describing peat depth conditions for optimum productivity ( $h_{PD7}^{opt}$  and  $\sigma_{PD7}^-$ ) were selected after the screening [Quillet et al., 2013]. They both show negligible first-order effects (Figure 1a) but important sums of second-order effects ( $>0.08$ ; Figure 1b). Figures 2v and 2w show that  $h_{PD7}^{opt}$  and  $\sigma_{PD7}^-$  interact, respectively, with different parameters:  $h_{PD7}^{opt}$  interacts strongly with  $c_2$  and  $W_{sat}$ , two parameters controlling the decomposition of saturated peat underlying the water table depth (Figure 2v), whereas  $\sigma_{PD7}^-$  interacts with  $R_0$ ,  $\rho_{min}$ , as well as  $c_3$  and  $c_4$  (Figure 2w). Their respective influences on total carbon mass thus take different pathways. We hypothesize that interactions between these parameters and  $P$  or  $R_0$  also represent the combinations of environmental conditions in the model that are most favorable to impact total carbon mass. Overall, maximum carbon mass occurs when  $P$  ranges from  $\sim 0.6$  to  $\sim 1.1$  m yr<sup>-1</sup> and  $R_0$  is low because it limits water outflow and thus favors anaerobic conditions with low decomposition. Lower  $P$  leads to deeper water tables



**Figure 1.** Sobol' indices ( $S_i$ ) calculated for the total carbon mass after 5000 simulation years: (a) first-order effect of each parameter, (b) sum of the second-order effects for each parameter, and (c) total effect of each parameter. The magnitude of the first-order effect represents the direct influence of that parameter on the variance in the model output assessed, i.e., total carbon mass; note that the first-order effect is very small for some parameters. The magnitude of the second-order effect represents the variance of the output related to a parameter's interactions with other parameters. The total effect includes first-order and second-order effects as well as all higher-order interactions (i.e., three or more parameters) and represents the variance in the output that would remain if only this parameter were to stay undetermined.

and an increase in decomposition. Very high  $P$ , on the contrary, favors high productivity at first but leads to a rapid increase in peat height and a reduction of the water table. With a deep water table, decomposition is high and productivity is

limited. When  $P$  and  $R_0$  are in their optimal ranges, lawn *Sphagnum* can maximize the carbon mass accumulated if they establish at relatively low peat depths. This can be achieved with large values of  $\sigma_{PD7}$ ,  $h_{PD7}^{opt}$ , or a combination



**Figure 2.** Sobol' indices: second-order effects for each of the 26 parameters. Each parameter is designated by its abbreviation; details on each parameter are in Table 1. Only positive values are shown; zero or negative values are not significant, and the corresponding parameters were omitted.

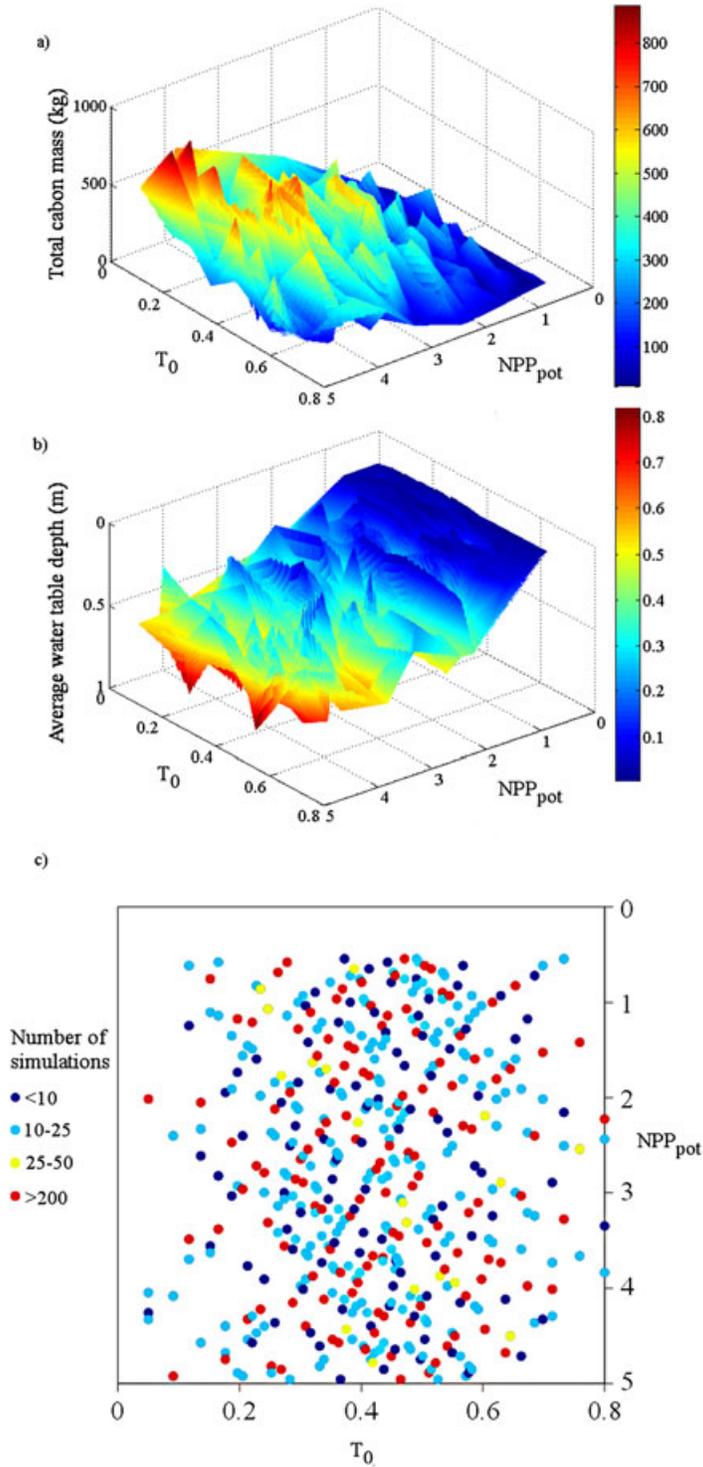
of both. Indeed, lawn *Sphagnum* decomposes relatively slowly (Table 2) and thus accumulates rapidly. Again, this rapid accumulation is followed by a deepening of the water table to a level at which lawn *Sphagnum* spp. are better competitors. This allows the buildup of maximized carbon masses at the end of the simulation.

[33] The  $\sigma_{PD7}^{opt}$  and  $h_{PD7}^{opt}$  parameters also interact with other PFTs' characteristics, and we hypothesize that interactions

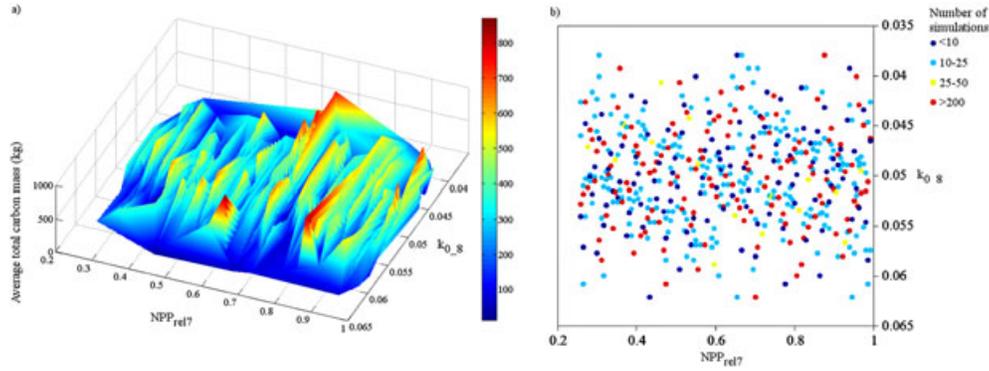
between different parameters related to PFT characteristics describe the conditions for which combinations of PFT characteristics are the most influential, i.e., optimal conditions leading to variance in total carbon mass.

#### 4.2.3. Feedbacks Between Lawn and Hummock *Sphagnum*

[34] The parameter  $k_{0.8}$  shows a sum of second-order effects lying around 0.06 (Figure 1b) and is the most influential compared with the other parameters (relative NPP,  $NPP_{rel8}$ ,  $h_{PD8}^{opt}$ ,



**Figure 3.** (a) Average response of total carbon mass (kg) to different values of  $NPP_{pot}$  and  $T_0$ . (b) Average response of water table depth (positive down) to different values of  $NPP_{pot}$  and  $T_0$ . (c) Number of simulations for each combination of parameter values. Note that Figures 3a and 3b show the average response of the model for these specific combinations of parameter values and that for a specific combination of parameters (here  $T_0$  and  $NPP_{pot}$ ) all other parameters may take different values within their range so that large amplitudes in the model response can be observed (see Figure 5b). As a limited number of combinations of parameter values were tested (relative to the  $10^{26}$  possible combinations), the potential variation of the model response for some combinations of  $T_0$  and  $NPP_{pot}$  might be poorly represented (especially if the number of simulations in Figure 3c is low). Therefore, the ridge/valley character of the plot results from sampling the full parameter space, while the general trends are more representative of overall model behavior.



**Figure 4.** (a) Average response of total carbon mass (kg) for different  $k_{0_8}$  values and different values of  $NPP_{rel7}$ . (b) Number of simulations for each combination of parameter values. See the note in the legend to Figure 3.

and  $\sigma_{PD8}$ ). It interacts with a series of parameters (Figure 2q) related to all model processes, suggesting that it is involved in several feedbacks. For example,  $k_{0_8}$  interacts with  $NPP_{rel7}$  (Figure 4). As the decomposition factor of hummock *Sphagnum* is low, the average total carbon mass reaches high levels. However, total carbon mass can also reach high levels when the decomposition factor of hummock *Sphagnum* is high. This is due to a feedback effect: an increased decomposition of hummock *Sphagnum* causes an increase in peat bulk density while the water table rises. This, in turn, shrinks the thickness of the acrotelm and enables a decrease in decomposition and an increase in net accumulation. After 5000 simulation years, more carbon remains in the peatland. Overall,  $NPP_{rel7}$  values above 0.5 are necessary to optimize total carbon mass. Below this level, hummock *Sphagnum* benefits from the low productivity of lawn *Sphagnum* and occupies a larger portion of the plant assemblage. In this case, high decomposition of hummock *Sphagnum* no longer favors carbon accumulation and the total carbon mass shows relatively low values at the end of the simulation.

[35] The  $c_2$  parameter shows a relatively important interaction with  $h_{PD7}^{opt}$  (Figure 2u). The impact of this combination of parameters on the average total carbon mass is presented in Figure 5. It is obvious that for short  $c_2$  (a stronger limit on decomposition below the water table), decomposition is lower and simulation results show high carbon mass values. However, Figure 5 also shows that it is possible to reach a high carbon mass when the anoxia scale is long under certain values of  $h_{PD7}^{opt}$ . Indeed, this is possible if the  $NPP_{pot}$  is high and compensates for decomposition and because highly decomposed peat prevents a decline of the water table as bulk density increases. However, this case only occurs for specific values of  $h_{PD7}^{opt}$ . Having a relatively low productivity compared to minerotrophic species but also being relatively resistant to decomposition (Table 1), lawn *Sphagnum* is not an efficient carbon accumulator when settling at low peat thicknesses but favors carbon accumulation by means of its low decomposition rate when a certain amount of peat has already accumulated. A late onset of lawn *Sphagnum* productivity does not lead to high carbon accumulation, given that the simulation time is limited to 5000 years.

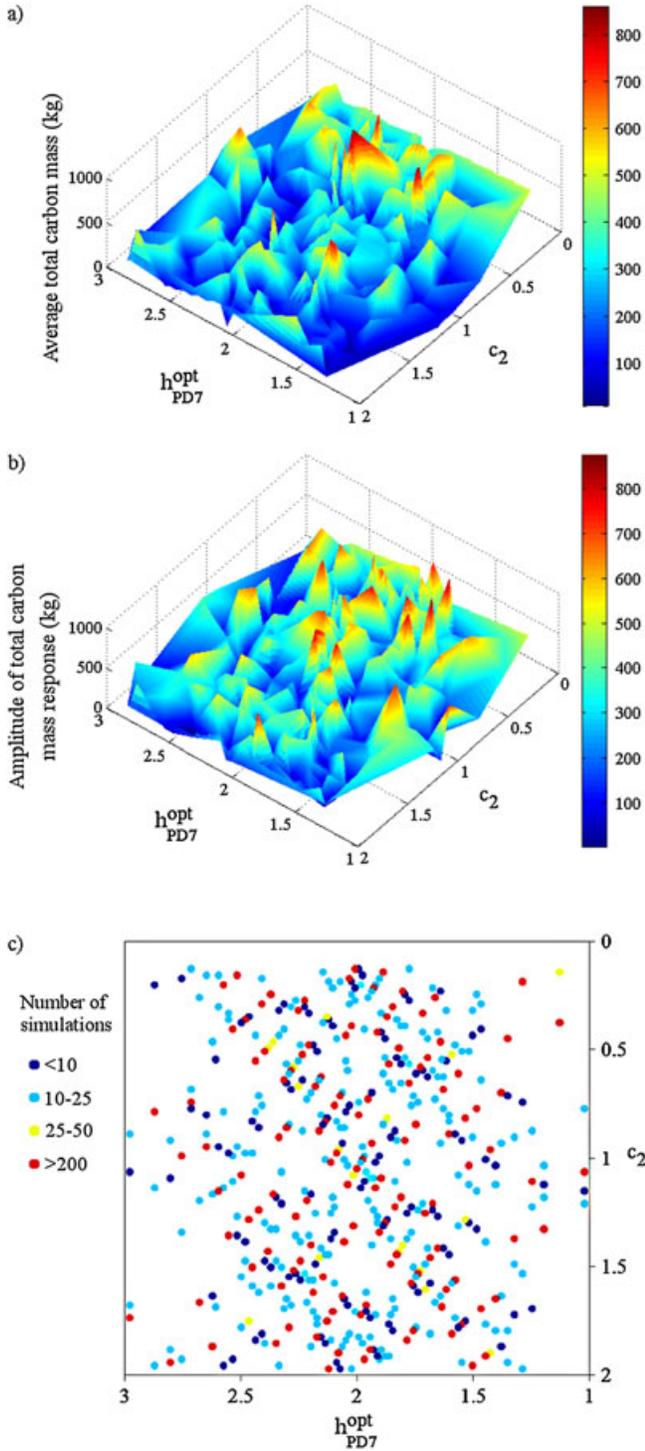
[36] The parameters having the most powerful influence on the variance of total carbon mass have been identified as  $NPP_{pot}$ ,  $c_2$ , and the parameters related to peatland

hydrology ( $T_0$  and  $c_8$ ). Overall, the influence of PFT parameters is not important compared to the influence of other parameters, such as  $NPP_{pot}$  or  $c_2$ . However, their sensitivity to the different lawn and hummock *Sphagnum* parameters suggests the importance of these PFTs to peat accumulation.

## 5. Discussion

[37] The  $NPP_{pot}$  causes a large variability in the results, with direct influence on carbon accumulation in peatlands. Moreover, it interacts with  $T_0$  and influences runoff so that uncertainty in  $NPP_{pot}$  leads to a variability of different processes and feedbacks. However, for the HPM to be effective in case studies, it is necessary to have a better constraint on these parameters, because the response can vary widely. The response of total carbon mass can vary for a single  $NPP_{pot}$  value, although total NPP depends on changes in water table depth and nutrient availability (by means of vegetation changes with peat depth). We thus argue that NPP is probably influenced by temperature or other climatic variables, such as photosynthetically active radiation (PAR) or growing season length, because these factors are not included in the  $NPP_{pot}$  parameter. *Loisel et al.* [2012] performed a meta-analysis to investigate the response of *Sphagnum* to a series of climatic variables and showed that *Sphagnum* growth is sensitive to PAR integrated over the growing season. Moreover, *Ise et al.* [2008] found that the feedback between water table and peat depth leads to an increased sensitivity of peat decomposition to temperature. Therefore, isolating the effect of temperature on productivity might improve the representation of this feedback in the model.

[38] Other parameters influence the water balance calculation, such as annual  $P$ ,  $ET_F$ ,  $R_0$ ,  $c_8$ ,  $T_0$ , and  $z_1$ . While  $P$  data may be obtained or derived from reconstruction, data on both ET and runoff/run-on characteristics are rarely available. Usually, the outflows of a peatland are not known unless specific instrumental field measurements are made. As hydrological changes and lateral expansion also affect water balance [*Belyea and Clymo*, 2001; *Belyea and Malmer*, 2004; *Glaser et al.*, 2004], additional information is needed to properly reconstruct early peatland development. A better representation of the amount of water available in the peatland, based on the physical properties of peat, would help limit



**Figure 5.** (a) Average response of total carbon mass (kg) for different values of  $h_{PD7}^{opt}$  and  $c_2$ . (b) Response amplitude of total carbon mass for different values of  $h_{PD7}^{opt}$  and  $c_2$ . (c) Number of simulations for each combination of parameter values. See the note in the legend to Figure 3.

uncertainty. Another avenue circumventing the improvement of the physical peat property representation would be the use of a proxy, such as testate amoebae, allowing water table depth reconstructions [Booth, 2008; Charman et al., 2007] and thus limiting the uncertainty associated with the water balance

calculation. Such proxies could also be used to test model water table depth simulations.

[39] Sobol' indices highlight the influence of several parameters related to bulk density ( $c_3$  and  $c_4$  controlling the shape of the curve as well as  $\rho_{min}$  and  $\Delta\rho$  describing the minimum increase and maximum increase in bulk density, respectively). These parameters are involved in multiple interactions with  $NPP_{pot}$ , water balance, or PFT parameters. In the HPM, bulk density is represented as a distinct function, because little is known quantitatively about the relationship between hydraulic properties, decomposition, water table depth, and bulk density. Nevertheless, the results show that bulk density plays an important role when studying total carbon mass in the model. We thus advise care in choosing the different parameter values and when possible trying to fit the curve to the bulk density records from several cores sampled at the study site. Processes underlying hydraulic properties or decomposition are identified as weakly known and should be integrated in upcoming research. Overall, as noted by Belyea and Baird [2006] and Morris et al. [2012], this study points out that there is a lack of data and understanding of the anoxia gradient, peat bulk density, as well as hydraulic properties in the peat column and how they are linked with decomposition and water balance.

[40] This study shows that a great variability of results can be obtained when various parameter combinations are used. It appears possible to simulate different peatlands characterized by either a small or a large amount of carbon and following different development pathways. This is an important result because this experiment did not take any environmental changes into account. Values of  $NPP_{pot}$ , annual  $P$ ,  $ET_5$ , and runoff ( $R_0$  and  $c_8$ ) were constant during the simulations. Although behavior could change if environmental changes were included, internal (i.e., autogenic) processes by themselves are sufficiently influential to induce a large variety of peatland development patterns and, as stated by several authors [e.g., Almquist-Jacobson and Foster, 1995; Anderson et al., 2003; Belyea and Baird, 2006], can affect peatland development and carbon accumulation.

[41] The results of the sensitivity analysis highlighted the dominance of certain PFTs (particularly, lawn and hummock *Sphagnum*) over the others with respect to long-term carbon accumulation. *Sphagnum* is identified as an important builder able to outcompete other species [Van Breemen, 1995], and specifically the *Sphagnum* *Sphagnum* and *Sphagnum* *Acutifolia* sections (lawn and hummock *Sphagnum* in the HPM) influence peat formation [Malmer and Wallén, 2004; Rydin and Jeglum, 2006]. We hypothesize that this bias between PFTs emphasizes the complexity and adaptability of carbon accumulation processes in peatlands. This delicate balance is thus more affected by transitional species tolerant of a wide range of conditions than by species that have only a narrow niche. Robroek et al. [2007] studied the competition between *Sphagnum* species in a greenhouse by intermingling six *Sphagnum* species collected in Ireland and growing them under different water level treatments. Their results showed that species growing higher above the water table (e.g., *Sphagnum magellanicum*, *Sphagnum rubellum*, and *Sphagnum fuscum*) outcompete others having a preferred habitat close to the water table (e.g., *Sphagnum cuspidatum*). This indicates that not all *Sphagnum* species have the same competitive abilities and resilience and is

consistent with the sensitivity finding that lawn and hummock species play an important role in the system by outcompeting other groups of species.

[42] Although the representation of competition between PFTs in the HPM does not capture the true complexity of the role of PFTs in peat accumulation, the simulation results show that lawn and hummock *Sphagnum* interact in a complex way in the model. Combinations of their parameters can create optimal conditions for carbon accumulation or, on the contrary, limit carbon accumulation. Furthermore, nutrient limitation properties of these PFTs, simplistically represented by the peat height gradient for optimum productivity, seem to have a stronger impact on total carbon mass than their water table optima. The PFT nutrient tolerance interacts with other parameters and through other processes (e.g., anoxia gradient or runoff) on the water table depth, but this is not the case for the water table optima. *Robroek et al.* [2007] pointed out that interspecific competition occurs independently of water table depth, supporting the result of limited influence of parameters describing water table optima for the different PFTs. Moreover, the sensitivity of carbon mass to nutrient limitations of *Sphagnum* might also be representative of competition between *Sphagnum* and vascular plants. *Malmer et al.* [2003] conducted fertilization experiments on different *Sphagnum* and vascular species in southern Sweden and found that an increasing proportion of *Sphagnum* species in the vegetation biomass tended to increase peat accumulation rates. Moreover, the effects of nutrient transport on peatland patterning also suggest that the distribution of nutrients influences vegetation cover and thus peat accumulation rates [Eppinga et al., 2009]. Thus, the different vegetation PFT characteristics, although described in the HPM in one dimension, are useful for the representation of complex feedbacks in peatland development processes.

## 6. Conclusions

[43] Carbon accumulation in peatlands is the result of complex interactions between productivity, decomposition, and hydrology. Therefore, accurate modeling of these processes requires representing many aspects of the system. We performed a GSA on the HPM in order to assess its representation of the feedback processes influencing carbon accumulation. Moreover, attention was paid to the specific influence of the different PFTs, which is a distinctive feature of this model.

[44] The results highlight several processes that should be better characterized (e.g., maximum potential productivity) or subjected to further research (e.g., vertical gradients in anoxia, bulk density, and peat hydraulic properties) in order to constrain uncertainty in the model. Furthermore, without any external environmental variability through time, the autogenic processes in the HPM are able to produce a variety of peatland development patterns. Lawn and hummock *Sphagnum* species come out as “effective ecosystem engineers,” following the terminology of *Van Breemen* [1995], that compete with other plants (nonvascular and vascular) to potentially shift the carbon accumulation pattern of the system.

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